

High levels of hidden phylogenetic structure within Central and West African *Trachylepis* skinks

KAITLIN E. ALLEN^{1,5}, WALTER P. TAPONDJOU N.^{2,5}, ELI GREENBAUM³,
LUKE J. WELTON^{4,5} & AARON M. BAUER¹

¹Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, USA

²Laboratory of Zoology, University of Yaoundé I, P.O. Box 812, Yaoundé, Cameroon

³Department of Biological Sciences, University of Texas at El Paso, 500 W. University Ave., El Paso, TX 79968, USA

⁴Department of Biology, Brigham Young University, Provo, Utah, 84602, USA

⁵Current address: Department of Ecology and Evolutionary Biology, University of Kansas, 1450 Jayhawk Boulevard, Lawrence, Kansas 66045, USA

Corresponding author: KAITLIN E. ALLEN, e-mail: kallen9@ku.edu

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Abstract. The genus *Trachylepis* is widespread throughout most of continental Africa and its surrounding islands. However, the majority of phylogenetic studies on this genus have focused on species occurring in eastern and southern Africa. Herein, we examine relationships among ten *Trachylepis* taxa that occur in Central and West Africa: *T. affinis*, *T. albilabris*, *T. aureogularis*, *T. gonwouoi*, *T. maculilabris*, *T. mekuana*, *T. perrotetii*, *T. polytropis polytropis*, *T. polytropis paucisquamis*, and *T. quinquetaeniata*. Five genes (two mitochondrial and three nuclear) were sequenced for 153 individuals, revealing much higher levels of diversity than previously realized, and justifying the need for future taxonomic investigations. Because of high levels of morphological conservatism in *Trachylepis*, the taxonomy of each of these species is complex, and previously synonymized names may be available for several lineages. Molecular dating techniques suggest that while the two major clades of *Trachylepis* represented in this study diverged approximately 23 million years ago, the majority of diversification took place in the last 17 million years. Further work is needed to fill in sampling gaps and increase genetic coverage for some clades before the full genetic diversity of this group can be realized.

Key words. Squamata, Scincidae, phylogeography, taxonomy, species complex, Cameroon Volcanic Line, Albertine Rift, Kwahu Plateau, Pleistocene refugia, Miocene aridification.

Introduction

The scincid genus *Trachylepis* FITZINGER, 1843 is widespread throughout most of continental Africa and its surrounding islands and comprises over 80 species (UETZ et al. 2019). *Trachylepis* diversity in Central and West Africa, with the exception of a few “hotspots,” including the Cameroon Volcanic Line in Central Africa (LEBRETON 1999, MAUSFELD-LAFDHIYA et al. 2004), has been considered lower than elsewhere on the continent. However, the majority of phylogenetic research on these skinks has been conducted on East and South African or insular lineages (e.g., LIMA et al. 2003, GÜNTHER et al. 2005, ROCHA et al. 2010, PORTIK et al. 2010, 2011, SINDACO et al. 2012, VENCES et al. 2014), but limited studies on *Trachylepis* in Central Africa have hinted at higher levels of diversity than are currently recognized (e.g. MAUSFELD-LAFDHIYA et al. 2004, JESUS et al. 2005, CHIRIO & LEBRETON 2007, CERÍACO et al. 2016, MARQUES et al. 2019, WEINELL et al. 2019).

Thirteen species of *Trachylepis* can be found across mainland Central and West Africa. We focus on ten taxa for which genetic sampling is available: *T. affinis* (GRAY 1838), *T. albilabris* (HALLOWELL, 1857), *T. gonwouoi* ALLEN et al., 2017, *T. maculilabris* (GRAY, 1845), *T. mekuana* (CHIRIO & INEICH, 2000), *T. perrotetii* (DUMÉRIL & BIBRON, 1839), *T. polytropis* (BOULENGER, 1903), *T. quinquetaeniata* (LICHTENSTEIN, 1823), the subspecies *T. polytropis paucisquamis* (HOOGMOED, 1978), and the putative species *T. aureogularis* (MÜLLER, 1885). Many of these species have widespread sub-Saharan ranges with the exception of *T. mekuana*, which is endemic to the Bamboutos Massif in the Cameroon Volcanic Line (CHIRIO & LEBRETON 2007, CERÍACO et al. 2016).

Most *Trachylepis* were referred to the genus *Euprepes* (or *Euprepis*) WAGLER, 1830 during the 19th century, and to *Mabuya* (or *Mabuia*) FITZINGER, 1826 throughout the 20th century. MAUSFELD et al. (2002), in the context of the dismantling of circumtropical *Mabuya*, resurrected *Eupre-*

pis as the name applicable to the primarily African lineage. However, BAUER (2003) demonstrated that *Trachylepis* was the oldest available name for this clade. Because of high levels of morphological conservatism in this genus, many of these species have complex taxonomic histories. *Trachylepis affinis* was described by GRAY in 1838 from a single museum specimen of unknown origin. The nominal taxa *Euprepes blandingii* HALLOWELL, 1844, *Euprepis raddoni* GRAY, 1845, *Euprepis frenatus* HALLOWELL, 1857, *Euprepes aeneofuscus* PETERS, 1864, *Euprepes gracilis* BO-CAGE, 1872, and *Euprepes pantaenii* FISCHER, 1885 were all synonymized with *T. affinis* in the comprehensive taxonomic revision of HOOGMOED (1974), which simultaneously raised *Euprepis albilabris* to species status. *Trachylepis maculilabris* was described from “W. Africa,” and has at various times been considered to include the subspecies *Mabuia m. albotaeniata* BOETTGER, 1913, *Mabuya m. comorensis* PETERS, 1854, *Mabuya m. boulengeri* STERNFELD, 1911, *Mabuya m. casuarinae* BROADLEY, 1974, and *Mabuya m. infralineata* BOETTGER, 1913. Today all of these taxa are considered valid species (UETZ et al. 2019), whereas the one subspecies and six varieties of *T. maculilabris* from eastern Africa described by STERNFELD (1912) are now considered to be synonyms of the nominotypical form (CERÍACO et al. 2016). *Trachylepis polytropis* comprises two subspecies, the nominotypical form and *T. p. paucisquamis*, the latter taxon is sometimes considered as specifically distinct, e.g. by TRAPE et al. 2012, who also considered *T. aureogularis* as a distinct species, although many authors consider it as a synonym of *T. albilabris* (e.g., UETZ et al. 2019).

Previous research has suggested that the widespread species *Trachylepis maculilabris*, *T. affinis* and *T. perrotetii* represent species complexes (MAUSFELD-LAFDHIYA et al. 2004, CHIRIO & LEBRETON 2007, CERÍACO et al. 2016), but genetic analyses of these taxa are lacking, and *T. polytropis*, *T. p. paucisquamis*, *T. aureogularis* and *T. mekuana* have never been assessed in an explicit phylogenetic context. This study aims to conduct the most comprehensive phylogenetic analysis of Central and West African *Trachylepis* to date, and to provide a comprehensive time calibrated assessment of historical biogeography for this group.

Materials and methods

Taxon sampling

A total of 153 samples from the species *Trachylepis affinis*, *T. albilabris*, *T. aureogularis*, *T. gonwouoi*, *T. maculilabris*, *T. mekuana*, *T. perrotetii*, *T. polytropis*, *T. p. paucisquamis*, and *T. quinquetaeniata* were examined from throughout Central and West Africa. Two species from the genus *Eutropis*, the sister group to the rest of the circumtropical Mabuyinae radiation (KARIN et al. 2016), were used as outgroups. Specimens from Cameroon, Nigeria, Niger, the Gulf of Guinea islands, Ghana, Gabon, Guinea, Mali, Uganda, the Central African Republic, Democratic Republic of the Congo, Burundi, Tanzania, and Mozambique were collected by the authors or borrowed from the fol-

lowing institutions: American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Monte L. Bean Life Science Museum (BYU), Museum of Comparative Zoology, Harvard University (MCZ), Museum of Natural History of Geneva (MNHG), Museum of Vertebrate Zoology, Berkeley (MVZ), North Carolina Museum of Natural Sciences (NCSM), United States National Museum of Natural History (USNM), University of Texas at El Paso Biodiversity Collections (UTEP), and the University of Washington Burke Museum (UWBM). A list of all specimens used in this study and associated GenBank numbers can be found in Supplementary Table S1.

Laboratory protocols

Five genes, two mitochondrial: 16S rRNA (16S) and NADH Dehydrogenase Subunit 2 (ND2); and three nuclear: Recombination Activating Gene 1 (RAG1), Exophilin 5 (EXPH5) and Kinesin Family Member 24 (KIF24), were sequenced for each specimen. Genomic DNA was isolated from liver tissue stored in 95% ethanol with salt extractions (ALJANABI & MARTINEZ 1997). The target genes were amplified using double-stranded polymerase chain reaction (PCR). A list of gene specific primers can be found in Table 1. All PCR reactions used an Eppendorf Mastercycler gradient thermocycler for 34 cycles with an annealing temperature of 50°C, followed by visualization of PCR product on a 1.5% agarose gel stained with ethidium bromide. PCRs were cleaned using a homemade magnetic bead solution (ROHLAND & REICH 2012). Cycle sequencing was performed using Big Dye v3.1, followed by an additional cleaning with the magnetic bead solution. Samples were sequenced using an ABI 3730 automated sequencer at Villanova University.

The 5' and 3' strands were sequenced separately, then combined in Geneious™ version 5.6 (KEARSE et al. 2012), with ambiguous base pairs edited by eye. Sequences were aligned using MAFFT v.7 (KATOH et al. 2002) with default parameters (gap opening penalty = 1.53, offset value = 0.123). Uncorrected genetic distance matrices were generated in MEGA 7 (KUMAR et al. 2016)

Gene tree analyses

We concatenated mitochondrial and nuclear data and implemented PartitionFinder (LANFPEAR et al. 2014) to determine the appropriate substitution model for each gene using the greedy algorithm and the Bayesian Information Criterion (BIC) for model selection. Phylogenetic analyses were performed in a Maximum Likelihood framework using RAXML v.8.1.1 (STAMATAKIS 2014) with the GTR-GAMMA model. Support was assessed using bootstrap analysis (FELSENSTEIN 1985) with 1000 pseudoreplications. We constructed a Bayesian phylogeny of our partitioned dataset with Mr. Bayes v. 3.2 (RONQUIST et al. 2012). The Markov chain was run for 20 million generations for two

Table 1. Primers used to amplify the genes in this study.

Gene	Primer	Sequence	Citation
ND2	METF1	5'-AAGCTTTCGGGCCCATACC -3'	MACEY et al. 1997
ND2	CO1R1	5'-AGRGTGCCAATGTCTTTGTGRTT-3'	ARÉVALO et al. 1994
16S	16sA-L	5' CGCCTGTTTATCAAAAACAT-3'	SIMON et al. 1994
16S	16sB-H	5'- CCGGTCTGAACTCAGATCACGT-3'	SIMON et al. 1994
RAG1	RAG1SF1	5'-TTCAAAGTGAGATCGCTTGAAA-3'	PORTIK et al. 2010
RAG1	RAG1SR1200	5'- CCCTTCTTCTTTCTCAGCAAAA-3'	PORTIK et al. 2010
EXPH5	EXPH5F1	5'-AATAAACTKGCAGCTATGTACAAAACAAGTC-3'	PORTIK et al. 2010
EXPH5	B1811R	5'-CRCACGTCTAGAACCAAAGGTCC-3'	KARIN et al. 2016
KIF24	KIF24F1	5'-SAAACGTRTCTCCMAAACGCATCC-3'	PORTIK et al. 2010
KIF24	KIF24R1	5'-WGGCTGCTGRAAYTGCTGGTG-3'	PORTIK et al. 2010

separate runs. Convergence of the posterior likelihood values was assessed using Tracer v 1.6 (RAMBAUT et al. 2014). The first 25% of trees were discarded as burn in, and the phylogeny was visualized using FigTree 1.4.2 (RAMBAUT & DRUMMOND 2012). Maps were created in QGIS (QGIS Development Team 2014) with Natural Earth: vector and raster map data at naturalearthdata.com.

Species tree analysis

We performed a species tree analysis and estimated divergence times between *Trachylepis* species using the program *BEAST implemented through BEAST v. 1.8.2 (DRUMMOND & RAMBAUT 2007). Several taxa, including *T. mekuana*, *T. polytropis* and *T. p. paucisquamis*, were excluded from the species tree because of missing data for some genes (Supplementary Table S1). Heterozygous sites were phased using the program seqPHASE (FLOT 2010) and PHASE 2.1.1 (STEPHENS et al. 2001, STEPHENS & DONNELLY 2003). Each gene was partitioned separately for a total of five partitions. The following substitution models were applied to each partition based on BIC support: 16S (GTR +G), ND2 (TN₉₃+G), RAG1, EXPH5 and KIF24 (HKY+G). For the species tree prior we specified a Yule model and for the population size we used a piecewise linear model with a constant root prior. We used uncorrelated lognormal relaxed clocks on each of the gene partitions and, as no fossils are available for *Trachylepis* or even the wider Mabuyinae group, divergence times were estimated using both 16S and ND2 substitution rates. Variation in rates was specified by a normally distributed prior on the lognormal clock mean. 16S was given a mean rate of 0.0080 with a standard deviation of 0.0020, and ND2 was given a mean rate of 0.00895 with a standard deviation of 0.0025. These rates are based on BARLEY et al. (2015) and represent the span of estimated mitochondrial clock rates across many different lizard species. All other genes were assigned clock mean priors from 0 to 0.2 and standard deviations with exponential distributions with a mean of 0.05 (BARLEY et al. 2015). Substitution parameters were assigned a uniform prior from 0 to 100 (initial = 1) and the gamma

shape parameters were assigned a uniform prior from 0 to 10 (initial = 0.5). The Markov chain was run for 300 million generations with sampling every 30,000 generations. Convergence of the posterior likelihood values was assessed using Tracer v 1.6 (DRUMMOND et al. 2012), with the first 30 million trees discarded as burn in. The species tree was visualized in FigTree 1.4.2, and variation in the species tree was visualized using a cloudogram created in DensiTree v2.2.2 (BOUCKAERT & HELED 2014).

Results

Phylogenetic analyses

Our concatenated dataset consisted of 4376 base pairs: 16S (540 bp), ND2 and tRNA flanking region (1376 bp), RAG1 (1095 bp), EXPH5 (786 bp), and KIF24 (579 bp). Our dataset contained 26.9% missing data. PartitionFinder identified the following models of substitution for each gene for the MrBayes analysis: 16S (SYM+I+G), ND2 coding region (HKY+I+G) ND2 tRNAs (SYM+I+G), RAG1 (HKY+G), EXPH5 (HKY+G), and KIF24 (K80+G). The model K80+G was not available in MrBayes and HKY+G was used instead. Topologies between the maximum likelihood and Bayesian phylogenies did not differ at any highly supported (>95% pp and 70 bs) node. Uncorrected genetic pairwise distances were 4.3–13.7 for 16S, 12.8–24.5 for ND2, 1.3–7.3 for EXPH5, 0.4–5.5 for KIF24, and 0.5–2.3 for RAG1 (Supplementary Tables S2 and S3). These values are similar to those found for mitochondrial and nuclear loci in other skink genera (e.g. POULAKAKIS et al. 2005, BARLEY et al. 2013, RABOSKY et al. 2009).

Trachylepis p. paucisquamis, which had previously been thought to be closely related to, or even a subspecies of, *T. polytropis*, was found to be part of a species complex that includes *T. aureogularis* and *T. albilabris*, whereas *T. polytropis* was found to be more closely related to *T. maculilabris* (Fig. 1). *Trachylepis affinis* was recovered as a monophyletic group containing two divergent lineages, one from Central-West Africa and one south of the Kwahu Plateau in Ghana (Fig. 2). *Trachylepis aureogularis* was found to be distinct from, but sister to, *T. albilabris*. *Trachylepis*

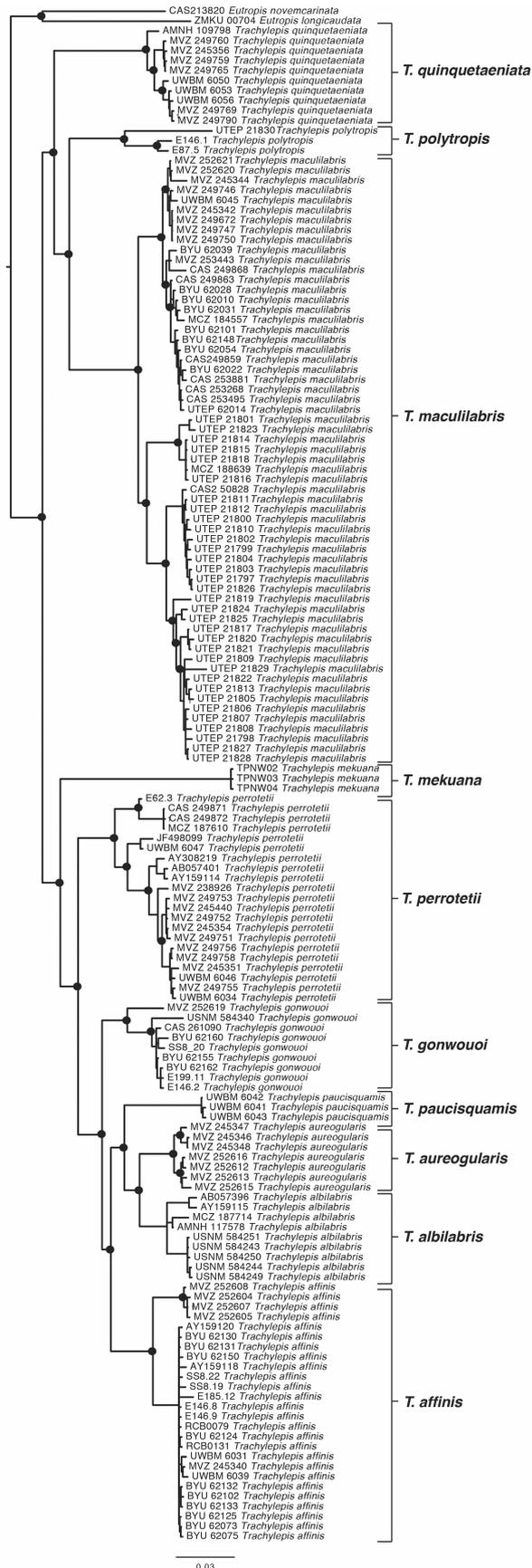


Figure 1. Bayesian phylogeny of all *Trachylepis* species sampled during this study; well-supported nodes (PP ≥ 0.95) are denoted by a black circle.

perrotetii was found to comprise three lineages: one from Guinea and northwestern Ghana, one widespread across Ghana, Niger and northern Cameroon, and one from the Cameroon Volcanic Line in northwest Cameroon and western Nigeria (Fig. 2).

Trachylepis maculilabris was recovered as a species complex, more diverse than previously recognized (see MAUSFELD-LAFDHIYA et al. 2004), and comprising four previously unidentified and divergent lineages. Of these lineages, one clade is distributed across Cameroon and Ghana, two are widespread throughout the Congo Basin, and one is isolated in the Albertine Rift in eastern Democratic Republic of Congo (Fig. 2). *Trachylepis mekuana*, which has never before been placed in a phylogenetic context, was recovered as sister to the clade comprising *T. perrotetii*, *T. gonwouoi*, *T. p. paucisquamis*, *T. albilabris*, and *T. affinis*.

Species tree

The *BEAST species tree analysis recovered similar relationships to the maximum likelihood and Bayesian analyses, with the exception that it recovered *Trachylepis gonwouoi* as sister to *T. affinis* instead of the clade containing *T. albilabris*, *T. aureogularis*, *T. p. paucisquamis* and *T. affinis* (Fig. 3). Uncertainty in the *BEAST tree can be visualized with a DensiTree plot (Fig. 4). This plot shows high levels of uncertainty in the placement of *T. gonwouoi* and

T. quinquetaeniata, and in the relationships between the relatively young *T. maculilabris* lineages.

Dating analyses recovered the two major clades of *Trachylepis* in Central-West Africa diverging from one another during the late Oligocene, around 23.8 million years ago. Subsequent diversification in the *T. gonwouoi*, *T. albilabris*, *T. aureogularis*, *T. p. paucisquamis* and *T. affinis* clade occurred during the mid- to late Miocene, and in the *T. maculilabris* clade during the Pliocene and Pleistocene (Fig. 3).

Discussion

Genetic diversity

Several taxa of *Trachylepis* in Central and West Africa were included in this study that had never before been placed in a phylogenetic context. These species include *T. aureogularis*, *T. mekuana*, *T. polytropis*, and its subspecies *T. p. paucisquamis*. *Trachylepis mekuana* is a Cameroon endemic found only on the Bamboutos Massif. This species was found to be highly divergent and sister to the clade containing *T. perrotetii*, *T. gonwouoi*, *T. p. paucisquamis*, *T. albilabris*, and *T. affinis*.

Based on morphology, TRAPE et al. (2012) suggested that *T. aureogularis* should be raised from synonymy with *T. albilabris*. Our results suggest that the two species are closely related but genetically distinct, providing further evidence in support of this interpretation. Likewise, TRAPE

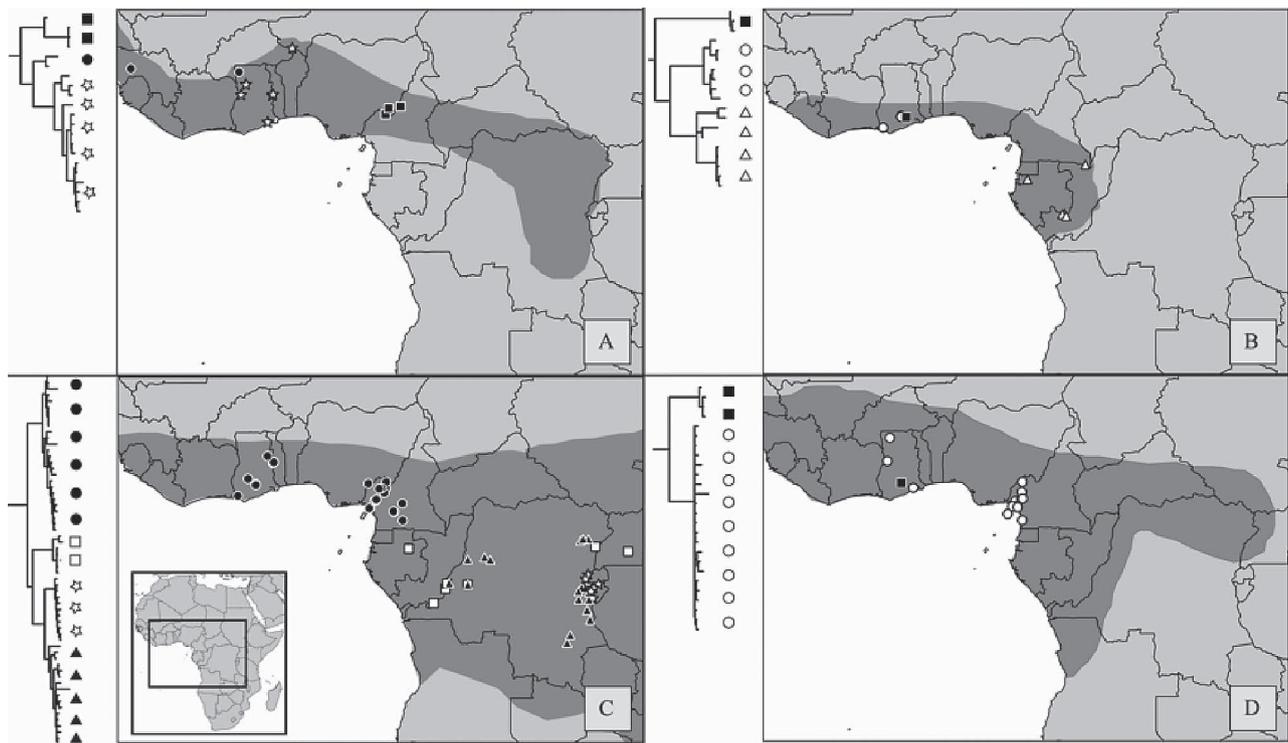


Figure 2. Sampling localities and major clades in A) *Trachylepis perrotetii*, B) the *T. albilabris* complex: *T. albilabris* (triangles), *T. aureogularis* (circles) and *T. p. paucisquamis* (squares) C) *T. maculilabris* and D) *T. affinis*. The distributional ranges, shown in dark grey, are approximate and courtesy of the Global Assessment of Reptile Distribution Group.

et al. (2012) suggested that *T. p. paucisquamis* is morphologically distinct from *T. polytropis* and should be raised from its subspecies status. Our analyses support this assessment and found *T. p. paucisquamis* to be the sister species to a clade including *T. albilabris* and *T. aureogularis*, and *T. polytropis* is sister to *T. maculilabris*. While describing the subspecies *T. p. paucisquamis*, HOOGMOED (1974, 1978) noted that it differed from *T. polytropis* in having a solid, versus broken, lateral band, supranasals in contact, and in the mid-body and sub-lamellar scale counts. Geographically, these species are found in two distinct ranges: *T. p. paucisquamis* and *T. aureogularis* in West Africa, throughout the Ivory Coast, Liberia and Ghana; and *T. polytropis* and *T. albilabris* in Central Africa, in Cameroon, Bioko Island, Democratic Republic of Congo, Gabon, and the Central African Republic (TRAPE et al. 2012, UETZ et al. 2019; Fig. 2).

Many of the species evaluated in this study contained several highly divergent lineages or comprised species

complexes. An integrated taxonomic approach combining a more thorough sampling of genetic data, as well as morphology, is recommended before species diversity within these complexes can be fully assessed (PADIAL et al. 2010). However, high levels of unrecognized diversity would not be surprising given the morphologically conserved nature of *Trachylepis* and the paucity of research focusing on the Central African representatives of this group in the past (MAUSFELD-LAFDHIYA et al. 2004).

Names may be available for several of these divergent lineages. For instance, STERNFELD (1912) described one subspecies and six varieties of *Trachylepis maculilabris*, most from the Albertine Rift of eastern Democratic Republic of the Congo and Uganda. The varietal forms *bergeri*, *graueri*, *kwidjwiensis*, *rohrbecki*, *schubotzi*, and *wauensis*, being infrasubspecific, are unavailable according to the International Code of Zoological Nomenclature (BAUER et al. 2003, CERÍACO et al. 2016), but the subspecies, *T. m. major*, considered a synonym of *T. maculilabris*, may

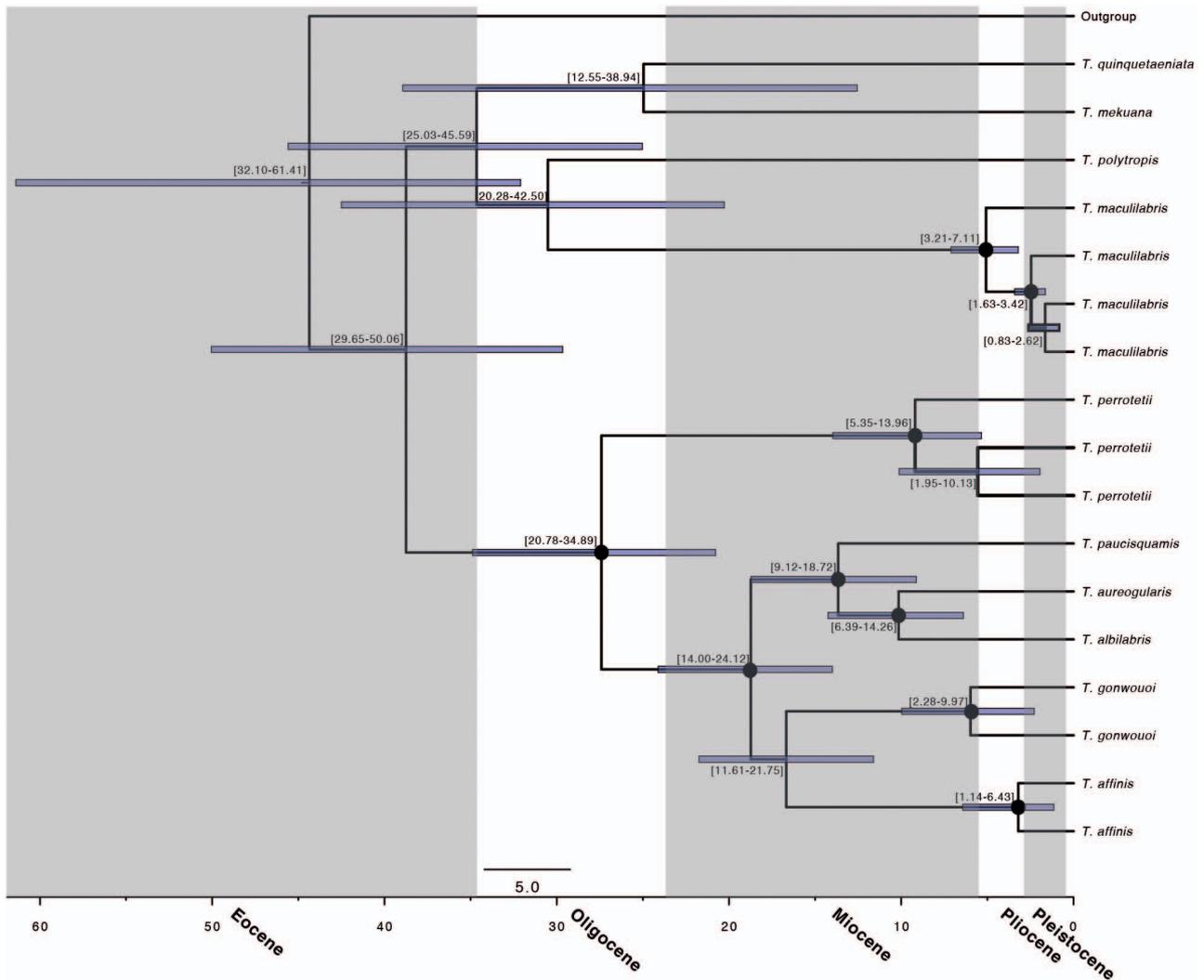


Figure 3. Dated *BEAST species tree including all major lineages of *Trachylepis* in this study. Divergence date ranges are shown in blue, and median divergence dates are listed by each node. Well-supported nodes (PP ≥ 0.95) are denoted by a black circle.

require reinvestigation. A divergent lineage of *Trachylepis affinis* south of the Kwahu Plateau in Ghana may correspond to one of several synonymized names from western Africa including: *Euprepis raddoni*, *Euprepis aeneofuscus*, *Euprepis gracilis*, *Euprepis stangeri* MÜLLER, 1882, and *Euprepis pantaenii*. Additional divergent lineages that require further sampling as well as taxonomic assessment include the *Trachylepis polytropis* individual (UTEP 21830) from the Salonga River in Democratic Republic of the Congo, the *T. gonwouoi* individual from Ghana (MVZ 25261) and the *T. perrotetii* clade from Cameroon (Figs 1 and 2).

Biogeography

Although sampling areas were strongly biased (i.e., Ghana often being the only sampled country in West Africa, no sampling in Nigeria and sampling only for *Trachylepis maculilabris* and *T. polytropis* in Democratic Republic of the Congo, Fig. 2), several common biogeographic patterns can be seen across the *Trachylepis* species in this study. The

most common of which was in Ghana, where high levels of genetic divergence existed either across the Volta River (now Lake Volta), or south of the Kwahu Plateau in southwestern Ghana (Fig. 2). This area was likely a rainforest refugium throughout the glacial cycles of the Pleistocene (MALEY 1996), but the diversification seen between *T. albilabris* and *T. aureogularis* is older, dating to the late Miocene (Fig. 3). It is possible that the same processes that created rainforest refugia during the colder, drier glacial periods of the Pleistocene were also in effect during the cooling and aridification of sub-Saharan Africa during the Miocene (MALEY 1996, HAFFER 1997).

High levels of endemism can be found within the Cameroon Volcanic Line. Two montane endemics, *Trachylepis nganghae* and *T. mekuana* were described from this area (CHIRIO & LEBRETON 2007). This study identifies another divergent lineage in the *T. perrotetii* complex occurring in an isolated region of the Cameroon Volcanic Line (Fig. 2). The *T. perrotetii* clade originated in the mid-Miocene, a period of dramatic cooling and major vegetation shifts throughout sub-Saharan Africa (JACOBS 2004, KISSLING et

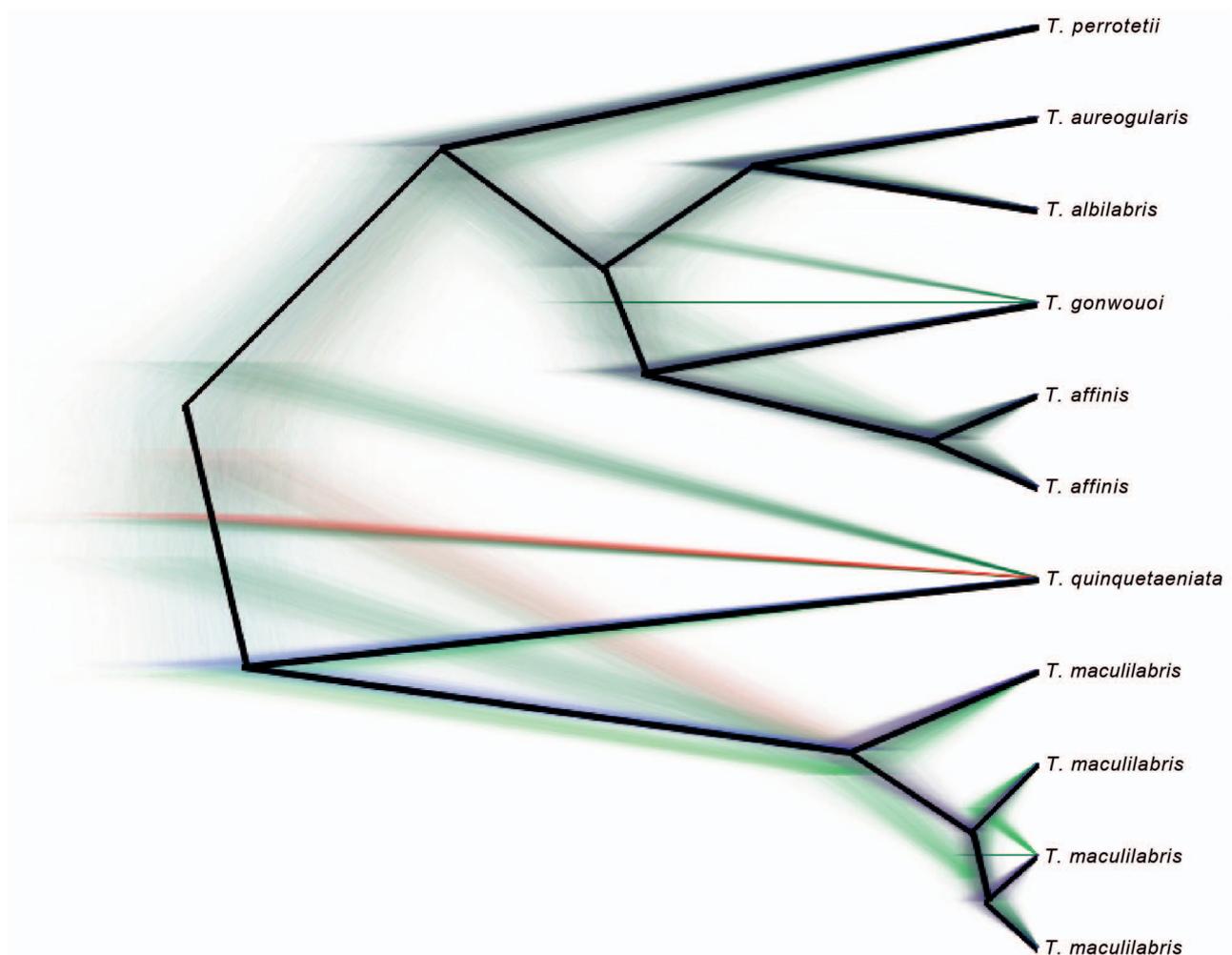


Figure 4. Cloudogram of uncertainty in the *Trachylepis* species tree. Individual trees ($n = 5770$) are shown in green and the consensus tree is shown in black.

al. 2012, MENEGON et al. 2014), and may have diverged as a result of the uplift of the Cameroon Volcanic Line (CONARCCHIA & DARS 1983, UBANGO et al. 1998, BATE TIBANG et al. 2017).

Trachylepis maculilabris was the only species for which extensive sampling was available across the Democratic Republic of the Congo. Three clades were found in this country, two widespread throughout lowland areas and one in the Albertine Rift in the east. All of these divergences are relatively young and date back to the Pliocene and Pleistocene. It is possible that separate historic rainforest refugia in Cameroon and the Congo played a role in the diversification of these lineages (MALEY 1996). Further analysis is necessary to determine if these divergences represent distinct species or genetically structured populations. The Albertine Rift highlands house an extremely high number of endemic species (GREENBAUM 2017), especially birds (STUART et al. 1990), amphibians (GREENBAUM & KUSAMBA 2012) and reptiles (HUGHES et al. 2018), and it is likely that some of the genetic diversity recovered here is representative of unrecognized taxonomic diversity.

High levels of uncertainty were seen in the species tree for the placement of *Trachylepis gonwouoi* relative to *T. affinis*, *T. albilabris* and *T. aureogularis*, and in the relationships between the *T. maculilabris* populations from Democratic Republic of Congo (Fig. 4). In both cases, clades are either largely overlapping in geographic distribution or are parapatric (i.e., the Albertine Rift *T. maculilabris*). It is possible that historic introgression is responsible for the uncertainty in the relatively young clades (*T. affinis*, *T. gonwouoi*, *T. albilabris* clade: 12 MYA; *T. maculilabris* clade: 1.8 MYA). It is also possible, particularly with *T. gonwouoi* and *T. quinquetaeniata*, that there was simply not enough information in our matrix to accurately place these taxa, and further geographic and taxonomic sampling is necessary.

Divergence dates

The two major clades of *Trachylepis* in Central Africa diverged from each other approximately 23.8 million years ago, around the end of the Oligocene. However, most of the diversification within these clades occurred during the last 17 million years, from the mid-Miocene to the present. The period from the Miocene through the Pleistocene was characterized by dramatic climatic changes, including cycles of aridification and humidification across Africa (MALEY 1996, MALEY & BRENAC 1998) that correspond to diversification patterns in many other organisms (e.g., trees: HARDY et al. 2013; rodents: NICOLAS et al. 2011, 2012; primates: CLIFFORD et al. 2004, TOSI 2008, HAUS et al. 2013). Several of the divergences between clades are distributed in areas that have been previously hypothesized as Pleistocene rainforest refugia (MALEY 1996). These lineages include the three clades of *T. maculilabris* in Democratic Republic of the Congo, and *T. affinis* and *T. gonwouoi* south of the Kwa-hu Plateau, suggesting that these areas of climatic stability may have played a role in rainforest species dynamics

over a relatively long timeframe in Central Africa (HAFFER 1997). These results are also congruent with recent herpetological studies that suggest allopatric speciation associated with rainforest refugia in the Upper and Lower Guinean forest blocks (PORTIK et al. 2017, KPAN et al. 2018), across Central Africa (JONGSMA et al. 2018) and even in the north-west African Sahara–Sahel region (GONÇALVES et al. 2018).

This study highlights the high degree of unrecognized genetic diversity in Central African *Trachylepis*, but more work is necessary to fully understand the origins and extent of this diversity and additional taxonomic implications. Our data support TRAPE et al. (2012) in elevating *T. aureogularis* from synonymy and *T. paucisquamis* from subspecies status, and we recognize both taxa as valid species. Further taxonomic work is needed to determine if the additional genetically divergent lineages recovered here are morphologically diagnosable, and if any warrant the assignment of names currently residing in synonymy. As several of these lineages represent range-restricted endemics, conservation measures may need to be taken to assess the viability of populations and to protect them from the widespread deforestation in Central African rainforests.

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References

- ALJANABI, S. M. & I. MARTINEZ (1997): Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. – *Nucleic Acids Research*, **25**: 4692–4693.
- ALLEN, K. E., W. P. TAPONDJOU N., L. J. WELTON & 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**: 255–269.
- ARÉVALO, E., S. K. DAVIS & J. W. SITES JR (1994): Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosomate races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. – *Systematic Biology*, **43**: 387–418.
- BARLEY, A. J., J. WHITE, A. C. DIESMOS & R. M. BROWN (2013): The challenge of species delimitation at the extremes: Diversification without morphological change in Philippine sun skinks. – *Evolution*, **67**: 3556–3572.
- BARLEY, A. J., A. DATTA-ROY, K. P. KARANTH & R. M. BROWN (2015): Sun skink diversification across the Indian–Southeast Asian biogeographical interface. – *Journal of Biogeography*, **42**: 292–304.
- BATE TIBANG, E. E. B., C. E. SUH, J. COTTLE, K. I. ATEH, A. F. TIABOU, L. A. NCHE, V. B. CHE & A. VISHITI (2017): Petrology and geochronology of felsic volcanics in the Sabga area (Bamenda Highlands): Implications for age variation along the Cameroon Volcanic Line. – *Journal of Geosciences*, **62**: 231–246.
- BAUER, A. M. (2003): On the identity of *Lacerta punctata* Linnaeus 1758, the type species of the genus *Euprepis* Wagler 1830, and the generic assignment of Afro-Malagasy skinks. – *African Journal of Herpetology*, **52**: 1–7.
- BAUER, A. M., G. SHEA & R. GÜNTHER (2003): An annotated catalogue of the types of scincid lizards (Reptilia, Squamata, Scincidae) in the collection of the Museums für Naturkunde der Humboldt-Universität zu Berlin (ZMB). – *Zoosystematics and Evolution*, **79**: 253–321.
- BOCAGE, J. (1872): Diagnoses de quelques espèces nouvelles de Reptiles d'Afrique occidentale. – *Jornal de Ciências, Matemáticas, Physicas e Naturaes*. Lisboa, **4**: 72–82.
- BOETTGER, O. (1913): Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas. – pp. 269–375 in: VOELTZKOW, A. (ed.): *Reise in Ostafrika in den Jahren 1903–1905. Wissenschaftliche Ergebnisse. Vol. 3. Systematische Arbeiten.* – Schweizerbart'sche Verlagsbuchhandlung, Nägele und Spöcker, Stuttgart.
- BOUCKAERT, R. & J. HELED (2014): DensiTree 2: Seeing trees through the forest. – *bioRxiv*: 012401.
- BOULENGER, G.A. (1903): Descriptions of new lizards in the collection of the British Museum. – *Annals and Magazine of Natural History*, **7**: 429–435.
- BROADLEY, D. G. (1974): A review of the *Mabuya maculilabris* group in South-Eastern Africa (Sauria: Scincidae). – *Arnoldia (Rhodesia)*, **6**: 1–10.
- CERÍACO, L. M., M. P. MARQUES & 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 maculilabris* (Gray, 1845) species complex. – *Zootaxa*, **4109**: 284–314.
- CHIRIO, L. & I. INEICH (2000): Description d'un nouveau scincidé endémique des montagnes du Cameroun. – *Bulletin de la Société Zoologique de France*, **125**: 185–196.
- CHIRIO, L. & M. LEBRETON (2007): *Atlas des Reptiles du Cameroun* (Vol. 67). – IRD Editions, Paris, France.
- CLIFFORD, S. L., N. M. ANTHONY, M. BAWE-JOHNSON, K. A. ABERNETHY, C. E. TUTIN, L. J. WHITE, M. BERMEJO, M. GOLDSMITH, K. MCFARLAND, K. J. JEFFERY, M. W. BRUFORD & E. J. WICKINGS (2004): Mitochondrial DNA phylogeography of western lowland gorillas (*Gorilla gorilla gorilla*). – *Molecular Ecology*, **13**: 1551–1565.
- CONARCCHIA, M. & R. DARS (1983): Un trait structural majeur du continent Africain. Linéaments Central-Africains du Cameroun au Golf d'Aden. – *Bulletin de la Société Géologique de France*, **25**: 101–109.
- DRUMMOND A.J. & A. RAMBAUT (2007): BEAST: Bayesian evolutionary analysis by sampling trees. – *BMC Evolutionary Biology*, **7**: 214.
- DRUMMOND, A. J., M. A. SUCHARD, D. XIE & A. RAMBAUT (2012): Bayesian phylogenetics with BEAUti and the BEAST 1.7. – *Molecular Biology and Evolution*, **29**: 1969–1973.
- DUMÉRIL, A.M.C. & G. BIBRON (1839): *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Tome cinquième. – Librairie Encyclopédique de Roret, Paris.
- FELSENSTEIN, J. (1985): Confidence limits on phylogenies: An approach using the bootstrap. – *Evolution*, **39**: 783–791.
- FISCHER, J. G. (1885): *Ichthyologische und herpetologische Bemerkungen.* – *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten*, **2**: 47–121.
- FLOT, J.-F. (2010): SeqPHASE: A web tool for interconverting PHASE input/output files and FASTA sequence alignments. – *Molecular Ecology Resources*, **10**: 162–166.
- GONÇALVES, D. V., P. PEREIRA, G. VELO-ANTÓN, D. J. HARRIS, S. CARRANZA & J. C. BRITO (2018): Assessing the role of aridity-induced vicariance and ecological divergence in species diversification in North-West Africa using *Agama* lizards. – *Biological Journal of the Linnean Society*, **124**: 363–380.
- GRAY, J. E. (1838): Catalogue of the slender-tongued saurians, with descriptions of many new genera and species. – *Annals and Magazine of Natural History, Series 1*, **2**: 287–293.
- GRAY, J. E. (1845): Catalogue of the Specimens of Lizards in the Collection of the British Museum. – Trustees of the British Museum, London.
- GREENBAUM, E. (2017): *Emerald Labyrinth: A Scientist's Adventures in the Jungles of the Congo.* – ForeEdge, Lebanon, NH.
- GREENBAUM, E. & C. KUSAMBA (2012): Conservation implications following the rediscovery of four frog species from the Itombwe Natural Reserve, eastern Democratic Republic of the Congo. – *Herpetological Review*, **43**: 253–259.
- GÜNTHER, R., A. WHITING & A. M. BAUER (2005): Description of a new species of African skink of the genus *Trachylepis*. – *Herpetozoa*, **18**: 11–24.
- HAFER, J. R. (1997): Alternative models of vertebrate speciation in Amazonia: An overview. – *Biodiversity & Conservation*, **6**: 451–476.
- HALLOWELL, E. (1844): Description of new species of African reptiles. – *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1844**: 169–172.
- HALLOWELL, E. (1857): Notice of some new and rare species of Scincidae in the collection of the Academy of Natural Sciences of Philadelphia. – *Transactions of the American Philosophical Society*, **11**: 71–82.

- HARDY, O. J., C. BORN, K. BUDDE, K. DAÏNOU, G. DAUBY, J. DUMINIL, B. K. EWÉDJÉ, C. GOMEZ, M. HEUERTZ, G. K. KOFFI, A. J. LOWE, C. MICHENEAU, D. NDIADÉ-BOUROBOU, R. PIÑEIRO & V. PONCET (2013): Comparative phylogeography of African rain forest trees: A review of genetic signatures of vegetation history in the Guineo-Congolian region. – *Comptes Rendus Geoscience*, **345**: 284–296.
- HAUS, T., E. AKOM, B. AGWANDA, M. HOFREITER, C. ROOS & D. ZINNER (2013): Mitochondrial diversity and distribution of African green monkeys (*Chlorocebus* Gray, 1870). – *American Journal of Primatology*, **75**: 350–360.
- HOOGMOED, M. S. (1974): Ghanese lizards of the genus *Mabuya* (Scincidae, Sauria, Reptilia). – *Zoologische Verhandelingen*, **138**: 1–62.
- HOOGMOED, M. S. (1978): A new name for *Mabuya polytropis occidentalis* HOOGMOED 1974. – *Zoologische Mededelingen*, **53**: 106.
- HUGHES, D. F., K. A. TOLLEY, M. BEHANGANA, W. LUKWAGO, M. MENEGON, J. M. DEHLING, J. STIPALA, C. R. TILBURY, A. M. KHAN, C. KUSAMBA & E. GREENBAUM (2018): Cryptic diversity in *Rhampholeon boulengeri* (Sauria: Chamaeleonidae), a pygmy chameleon from the Albertine Rift biodiversity hotspot. – *Molecular Phylogenetics and Evolution*, **122**: 125–141.
- JACOBS, B. F. (2004): Paleobotanical studies from Tropical Africa: Relevance to the evolution of forest, woodland and savannah biomes. – *Philosophical Transactions of the Royal Society B*, **359**: 1573–1583.
- JESUS, J., D. J. HARRIS & A. BREHM (2005): Phylogeography of *Mabuya maculilabris* (Reptilia) from São Tomé island (Gulf of Guinea) inferred from mtDNA sequences. – *Molecular Phylogenetics and Evolution*, **37**: 503–510.
- JONGSMA, G. F., M. F. BAREJ, C. D. BARRATT, M. BURGER, W. CONRADIE, R. ERNST, E. GREENBAUM, M. HIRSCHFELD, A. D. LEACHÉ, J. PENNER, D. M. PORTIK, A.-G. ZASSI-BOULOU, M.-O. RÖDEL & D. C. BLACKBURN (2018): Diversity and biogeography of frogs in the genus *Amnirana* (Anura: Ranidae) across sub-Saharan Africa. – *Molecular Phylogenetics and Evolution*, **120**: 274–285.
- KARIN, B. R., M. METALLINO, J. L. WEINELL, T. R. JACKMAN & 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.
- KATO, K., K. MISAWA, K. I. KUMA & T. MIYATA (2002): MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. – *Nucleic Acids Research*, **30**: 3059–3066.
- KEARSE, M., R. MOIR, A. WILSON, S. STONES-HAVAS, M. CHEUNG, S. STURROCK, S. BUXTON & A. DRUMMOND (2012). Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. – *Bioinformatics*, **28**: 1647–1649.
- KISSLING, W. D., W. L. EISERHARDT, W. J. BAKER, F. BORCHSENINUS, T. L. COUVREUR, H. BALSLEV & J. C. SVENNING (2012): Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. – *Proceedings of the National Academy of Sciences (USA)*, **109**: 7379–7384.
- KPAN, T. F., N. G. KOUAMÉ, M. F. BAREJ, P. J. ADEBA, M. EMMRICH, C. OFORI-BOATENG & M.-O. RÖDEL (2018): A new Puddle Frog, genus *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae), from the eastern part of the Upper Guinea biodiversity hotspot, West Africa. – *Zootaxa*, **4388**: 221–237.
- KUMAR, S., G. STECHER & K. TAMURA (2016): MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. – *Molecular Biology and Evolution*, **33**: 1870–1874.
- LANFEAR, R., B. CALCOTT, D. KAINER, C. MAYER & A. STAMATAKIS (2014): Selecting optimal partitioning schemes for phylogenomic datasets. – *BMC Evolutionary Biology*, **14**: 82.
- LEBRETON, M. (1999): A Working Checklist of the Herpetofauna of Cameroon: With Localities for Species Occurring in Southern Cameroon and a List of Herpetofauna for the Dja Faunal Reserve. – Netherlands Committee for IUCN, Amsterdam, The Netherlands.
- LICHTENSTEIN, H. (1823): Verzeichniss der Doubletten des zoologischen Museums der Königl Universität zu Berlin nebst Beschreibung vieler bisher unbekannter Arten von Säugethieren, Vögeln, Amphibien und Fischen. – Königl Universität, Berlin, Germany.
- LIMA, A., D. J. HARRIS, S. ROCHA, A. MIRALLES, F. GLAW & M. VENCES (2013): Phylogenetic relationships of *Trachylepis* skink species from Madagascar and the Seychelles (Squamata: Scincidae). – *Molecular Phylogenetics and Evolution*, **67**: 615–620.
- MALEY, J. (1996): The African rain forest—main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. – *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences*, **104**: 31–73.
- MALEY, J. & P. BRENAC (1998): Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years BP. – *Review of Palaeobotany and Palynology*, **99**: 157–187.
- MARQUES, M. P., L. M. CERÍACO, S. BANDEIRA, O. S. PAUWELS & A. M. BAUER (2019): Description of a new long-tailed skink (Scincidae: *Trachylepis*) from Angola and the Democratic Republic of the Congo. – *Zootaxa*, **4568**: 51–68.
- MAUSFELD, P., A. SCHMITZ, W. BÖHME, B. MISOF, D. VRCIBRADIC & C. ROCHA (2002). Phylogenetic affinities of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean archipelago of Fernando de Noronha (Brazil): Necessity of partitioning the genus *Mabuya* Fitzinger, 1826 (Scincidae: Lygosominae). – *Zoologischer Anzeiger*, **241**: 281–293.
- MAUSFELD-LAFDHIYA, P., A. SCHMITZ, I. INEICH & 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.
- MENEGON, M., S. P. LOADER, S. J. MARSDEN, W. R. BRANCH, T. R. B. DAVENPORT & S. URSENBACHER (2014): The genus *Atheris* (Serpentes: Viperidae) in East Africa: Phylogeny and the role of rifting and climate in shaping the current pattern of species diversity. – *Molecular Phylogenetics and Evolution*, **79**: 12–22.
- MÜLLER, F. (1882): Erster Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. – *Verhandlungen der Naturforschenden Gesellschaft in Basel*, **7**: 120–165.
- MÜLLER, F. (1885): Vierter Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. – *Verhandlungen der Naturforschenden Gesellschaft in Basel*, **7**: 668–717.
- NICOLAS, V., A. D. MISSOUB, C. DENYS, J. KERBIS PETERHANS, P. KATUALA, A. COULOUX & M. COLYN (2011): The roles of rivers and Pleistocene refugia in shaping genetic diversity in *Pratomys misonnei* in tropical Africa. – *Journal of Biogeography*, **38**: 191–207.

- NICOLAS, V., V. HERBRETEAU, A. COULOUX, K. KEOVICHIT, B. DOUANGBOUPHA & J. P. HUGOT (2012). A remarkable case of micro-endemism in *Laonastes aenigmamus* (Diatomyidae, Rodentia) revealed by nuclear and mitochondrial DNA sequence data. *PLoS ONE*, **7**: e48145.
- PADIAL, J. M., A. MIRALLES, I. DE LA RIVA & M. VENCES (2010): The integrative future of taxonomy. – *Frontiers in Zoology*, **7**: 1–14.
- PETERS, W. (1854): Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechen mitgeteilt werden. – Bericht über die zur Bekanntmachung geeigneten Verhandlungen der königlich-preussischen Akademie der Wissenschaften zu Berlin, **1854**: 614–628.
- PETERS, W. (1864): Über die Eidechsenfamilie der Scincoiden, insbesondere über die Schneider'schen, Wiegmann'schen und neue Arten des zoologischen Museums zu Berlin. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin. **1864**: 44–58.
- PORTIK, D. M., A. M. BAUER & T. R. JACKMAN (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.
- PORTIK, D. M., A. M. BAUER & T. R. JACKMAN (2011): Bridging the gap: Western rock skinks (*Trachylepis sulcata*) have a short history in South Africa. – *Molecular Ecology*, **20**: 1744–1758.
- PORTIK, D. M., A. D. LEACHÉ, D. RIVERA, M. F. BAREJ, M. BURGER, M. HIRSCHFELD, M.-O. RÖDEL, D. C. BLACKBURN & M. K. FUJITA (2017): Evaluating mechanisms of diversification in a Guineo-Congolian tropical forest frog using demographic model selection. – *Molecular Ecology*, **26**: 5245–5263.
- POULAKAKIS, N., P. LYMBERAKIS, C. S. TSGENOPOULOS, A. MANGOULAS & M. MYLONAS (2005): Phylogenetic relationships and evolutionary history of snake-eyed skink *Ablepharus kitaibelii* (Sauria: Scincidae). – *Molecular Phylogenetics and Evolution*, **34**: 245–256.
- QGIS Development Team (2014): QGIS Geographic Information System. Open Source Geospatial Foundation Project. – Available from <http://qgis.osgeo.org>
- RABOSKY, D. L., A. L. TALABA, S. C. DONNELLAN & I. J. LOVETTE (2009): Molecular evidence for hybridization between two Australian desert skinks, *Ctenotus leonhardii* and *Ctenotus quattuordecimlineatus* (Scincidae: Squamata). – *Molecular Phylogenetics and Evolution*, **53**: 368–377.
- RAMBAUT, A., M. A. SUCHARD, D. XIE & A. J. DRUMMOND (2014): Tracer v1.6 – Available from <http://beast.bio.ed.ac.uk/Tracer>.
- RAMBAUT, A. & A. DRUMMOND (2012): FigTree: Tree figure drawing tool, v1. 4.2. – Institute of Evolutionary Biology, University of Edinburgh, Edinburgh.
- ROCHA, S., M. A. CARRETERO & D. J. HARRIS (2010): Genetic diversity and phylogenetic relationships of *Mabuya* spp. (Squamata: Scincidae) from western Indian Ocean islands. – *Amphibia-Reptilia*, **31**: 375–385.
- ROHLAND, N. & D. REICH (2012): Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. – *Genome Research*, **22**: 939–946.
- RONQUIST, F., M. TESLENKO, P. VAN DER MARK, D. L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M. A. SUCHARD & J. P. HUELSENBECK (2012): MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. – *Systematic Biology*, **61**: 539–542.
- SINDACO, R., M. METALLINO, F. PUPIN, M. FASOLA & S. CARRANZA (2012): Forgotten in the ocean: Systematics, biogeography and evolution of the *Trachylepis* skinks of the Socotra Archipelago. – *Zoologica Scripta*, **41**: 346–362.
- STAMATAKIS, A. (2014): RAXML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. – *Bioinformatics*, **30**: 1312–1313.
- STEPHENS, M., N. SMITH & P. DONNELLY (2001): A new statistical method for haplotype reconstruction from population data. – *American Journal of Human Genetics*, **68**: 978–989.
- STEPHENS, M. & P. DONNELLY (2003): A comparison of Bayesian methods for haplotype reconstruction from population genotype data. – *American Journal of Human Genetics*, **73**: 1162–1169.
- STERNFELD, R. (1911): Zur Reptilienfauna Deutsch-Ostafrikas. – Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, **1**: 245–251.
- STERNFELD, R. (1912): “1913.” Reptilia. – pp. 197–279 + figs. 1–4 + pl. VI–IX in: SCHUBOTZ, H. (ed.): Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika-Expedition 1907–1908 unter Führung Adolf Friedrichs, Herzogs zu Mecklenburg. Band IV, Zoologie II. – Klinkhardt & Biermann, Leipzig, Germany.
- STUART, S. N., R. J. ADAMS & M. JENKINS (1990): Biodiversity in sub-Saharan Africa and its Islands: Conservation, Management, and Sustainable Use (Vol. 6). – IUCN, Gland, Switzerland.
- TOSI, A. J. (2008): Forest monkeys and Pleistocene refugia: A phylogeographic window onto the disjunct distribution of the *Chlorocebus lhoesti* species group. – *Zoological Journal of the Linnean Society*, **154**: 408–418.
- TRAPE, J.-F., S. TRAPE & L. CHIRIO (2012): Lézards, Crocodiles et Tortues d'Afrique Occidentale et du Sahara. – IRD Editions, Marseille, France.
- UETZ, P., P. FREED & J. HOŠEK (eds): The Reptile Database. – Available from <http://www.reptile-database.org>, accessed April 4, 2019.
- UBANGO, R. U., I. G. PACCA & J. B. NYOBE (1998): Palaeomagnetism of the continental sector of the Cameroon Volcanic Line, West Africa. – *Geophysical Journal International*, **135**: 362–374.
- VENCES, M., A. LIMA, A. MIRALLES & F. GLAW (2014): DNA barcoding assessment of genetic variation in two widespread skinks from Madagascar, *Trachylepis elegans* and *T. gravenhorstii* (Squamata: Scincidae). – *Zootaxa*, **3755**: 477–484.
- WEINELL, J. L., W. R. BRANCH, T. J. COLSTON, T. R. JACKMAN, A. KUHN, W. CONRADIE & 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.

Supplementary data

- Supplementary Table S1. Samples used with associated museum numbers, locality data and GenBank accession numbers.
- Supplementary Table S2. Pairwise uncorrected genetic distance matrix for mitochondrial genes 16S and ND2.
- Supplementary Table S3. A) Pairwise uncorrected genetic distance matrix for nuclear genes EXHP5 and KIF24. B) Pairwise uncorrected genetic distance matrix for nuclear gene RAG1.
- Addendum: Readers are directed to a complementary publication dealing with species level relationships of *Trachylepis* (WEINELL et al. 2019) that appeared when this paper was in press.