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


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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. gomwouoi, 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. gomwouoi Allen et al. 2017, T. maculilabris (Gray, 1845), T. mekuana (Chirio & Ineich, 2000), T. perrotetii (Duméril & Bibron, 1839), T. polytropis (Bolegner, 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 Bamkout Massif in the Cameroon Volcanic Line (Chirio & LeBreton 2007, Ceríaco et al. 2016).

Most Trachylepis were referred to the genus Euprepes (or Euprepi) 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 Eurep-
Trachylepis 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, Euprepes raddoni Gray, 1845, Euprepes frenatus Hallowell, 1857, Euprepes aeneofuscus Peters, 1864, Euprepes gracilis Boie, 1872, and Euprepes pantaeni Fischer, 1885 were all synonymized with T. affinis in the comprehensive taxonomic revision of Hoogmoed (1974), which simultaneously raised Euprepis albilarbis to species status. Trachylepis maculilabris was described from "Western Africa," and has at various times been considered to include the subspecies Mabuia m. albolaeniata Boettger, 1913, Mabuya m. co-动机is Peters, 1854, Mabuya m. boulengeri Sternfeld, 1911, Mabuya m. casuarinae Broadley, 1974, and Mabuya m. infrilineata 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. albilarbis (e.g., Uetz et al. 2019).

Previous research has suggested that the widespread species Trachylepis maculilabris, T. affinis and T. perrotetti represent species complexes (Mausfeld-Lafdiya 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. albilarbis, T. aureogularis, T. gonwouei, T. maculilabris, T. mekuana, T. perrotetti, T. polytropis, T. p. paucisquamis, and T. quinquetacta 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 (Karín 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 following 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 (NCM), 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.

Gene tree analyses
We concatenated mitochondrial and nuclear data and implemented PartitionFinder (Lanfear 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
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Table 1. Primers used to amplify the genes in this study.

<table>
<thead>
<tr>
<th>Gene</th>
<th>Primer</th>
<th>Sequence</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>ND2</td>
<td>METF1</td>
<td>5’-AAGCTTCGGCGCCATACC-3’</td>
<td>MACKEY et al. 1997</td>
</tr>
<tr>
<td>ND2</td>
<td>CO1R1</td>
<td>5’-AGRTGCGCAATGCTTGTGRTT-3’</td>
<td>AREVALO et al. 1994</td>
</tr>
<tr>
<td>16S</td>
<td>16SA-L</td>
<td>5’-CGCTGTTTATCAAACAT-3’</td>
<td>SIMON et al. 1994</td>
</tr>
<tr>
<td>16S</td>
<td>16SB-H</td>
<td>5’-CCGGTCTGAACTAGTACGCTG-3’</td>
<td>SIMON et al. 1994</td>
</tr>
<tr>
<td>RAG1</td>
<td>RAG1SF1</td>
<td>5’-TTCAAAAGTGACTGGCTTGAAN-3’</td>
<td>PORTIK et al. 2010</td>
</tr>
<tr>
<td>RAG1</td>
<td>RAG1SR1200</td>
<td>5’-CCCTCTTTCTTCTCAGGAAAAAA-3’</td>
<td>PORTIK et al. 2010</td>
</tr>
<tr>
<td>EXPH5</td>
<td>EXPH5F1</td>
<td>5’-ATAAAACTKCGACGTATGACAAACAAAGTC-3’</td>
<td>PORTIK et al. 2010</td>
</tr>
<tr>
<td>EXPH5</td>
<td>B1811R</td>
<td>5’-CRCACGTCTAGACCAAGGGTC-3’</td>
<td>KARIN et al. 2016</td>
</tr>
<tr>
<td>KIF24</td>
<td>KIF24F1</td>
<td>5’-SAAAAGTRTCTCCMAAAGCGATGC-3’</td>
<td>PORTIK et al. 2010</td>
</tr>
<tr>
<td>KIF24</td>
<td>KIF24R1</td>
<td>5’-WGGCTGCTGRAAYTGCTGGTG-3’</td>
<td>PORTIK et al. 2010</td>
</tr>
</tbody>
</table>

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 (RAMBAUT & DRUMMOND 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 & DONELLY 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 to model the clock rate variation 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 cladeogram 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 S1 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.
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*Trachylepis 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-Lafdiya 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...
et al. (2012) suggested that *T. paucisquamis* is morphologically distinct from *T. polytropis* and should be raised from its subspecies status. Our analyses support this assessment and found *T. 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. 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-Lafdiya 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*, *kwidiwiensis*, *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

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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 (UETP 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
al. 2012, Menegon et al. 2014), and may have diverged as a result of the uplift of the Cameroon Volcanic Line (Conrckhia & Dars 1983, Ubango & al. 1998, Bate Ti-bang 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. albilibaris* 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. albilibaris* 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 the last 17 million years, from the mid-Miocene to the present. Divergence dates

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. paucisquama* 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


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Rambaut, A. & A. Drummond (2012): FigTree: Tree figure drawing tool, v1.4.2. – Institute of Evolutionary Biology, University of Edinburgh, Edinburgh.


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 EXH5 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.