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Systematics and phylogeography of the widely distributed African skink *Trachylepis varia* species complex

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ABSTRACT

A systematic study of the *Trachylepis varia* complex was conducted using mitochondrial and nuclear DNA markers for individuals sampled across the species range. The taxonomic history of *T. varia* has been complicated and its broad geographic distribution and considerable phenotypic variation has made taxonomic revision difficult, leading earlier taxonomists to suggest that *T. varia* is a species complex. We used maximum likelihood and Bayesian inference to estimate gene trees and a multilocus time-tree, respectively, and we used these trees to identify the major clades (putative species) within *T. varia*. Additionally, we used morphological and color pattern data to distinguish and revise the taxonomy of the southern African clades. The major clades recovered in the multilocus time-tree were recovered in each of gene trees, although the relationships among these major clades differed across gene trees. Genetic data support the existence of at least eight species within the *T. varia* complex, each of which originated during the mid to late Miocene or early Pliocene. We focus our systematic discussion on the southern African members of the *T. varia* complex, revive *Trachylepis damarana* (Peters, 1870) and *T. laevigata* (Peters, 1869), and designate lectotypes for *T. damarana* and *T. varia*.

1. Introduction

1.1. Background

Trachylepis (Lygosominae) is a large group (> 80 species) of skinks occurring in Sub-Saharan Africa and Madagascar that likely includes multiple species complexes (Mausfeld et al., 2000; Karin et al., 2016; Metallinou et al., 2016; Uetz and Hallermann, 2016). The phylogenetic position of *Trachylepis* within the *Mabuya* group (Lygosominae) was recently inferred from a multilocus DNA dataset (Karin et al., 2016), but species-level relationships are not well understood within *Trachylepis*. Furthermore, relatively few studies have used genetic data to resolve relationships within *Trachylepis* species complexes (Mausfeld-Lafdhiya et al., 2004; Jesus et al., 2005; Ceriaco et al., 2016; Lima et al., 2013; Sindaco et al., 2012; Portik et al., 2011; Portik and Bauer, 2012). Nevertheless, morphological data suggest that several wide-ranging species, including *Trachylepis affinis*, *T. maculilabris*, and *T. varia*, are each composed of multiple species (Broadley, 1966; Jacobsen, 1989). Phylogeographic studies using genetic and phenotypic data are needed to clarify species relationships within taxa that are suspected of being species complexes and to aid future studies examining species relationships within *Trachylepis*.

The Variable Skink (*Trachylepis varia*) is broadly distributed across Sub-Saharan Africa, has been considered a species complex (Jacobsen, 1989), and has six junior synonyms (Peters, 1869, 1870, 1871; Bocage, 1867, 1872; Loveridge, 1953). Loveridge (1920, 1933) noted that *T. varia* populations frequently differ in color pattern and morphology, but this species' large range (Fig. 1) prevented earlier taxonomists from conducting a comprehensive phylogeographic study. Peters (1867) described *T. varia* (as *Euprepes varius*) and three additional *Trachylepis* that were later synonymized with *T. varia* by Loveridge (1957), including *Euprepes laevigatus* Peters, 1869 (type locality: “ebbenfalls in Gerlachshoop” [northern Limpopo Province, South Africa]; holotype: ZMB 6224); *Euprepes damaranus* Peters, 1870 (type locality: “Damaraland” [Namibia]; syntypes: ZMB 6153 and NRM 2149); and *Euprepes isselii* Peters, 1871 (type locality: “Keren, im Bogoslande” [Eritrea]; syntypes: ZMB 7272 (9 specimens) and MSNG 27778 (23 specimens)). Additionally, Boulenger (1887) synonymized *Euprepes Olivierii* var. *albopunctatus* Bocage, 1867 (type localities: Benguella and Catumbella, Angola; type specimens destroyed by fire) and *Euprepes angolensis* Bocage, 1872 (type localities: Biballa and Dondo, Angola; syntypes: five individuals, including two individuals collected by Anchieta from Biballa and three individuals collected by Bayão from Dondo, destroyed by fire) with *T. varia*, an arrangement with which Bocage (1895) later concurred. Broadley (1966) synonymized *Mabuya varia nyikae* Loveridge, 1953 (type locality: “Nyika Plateau above Nchenachena, at

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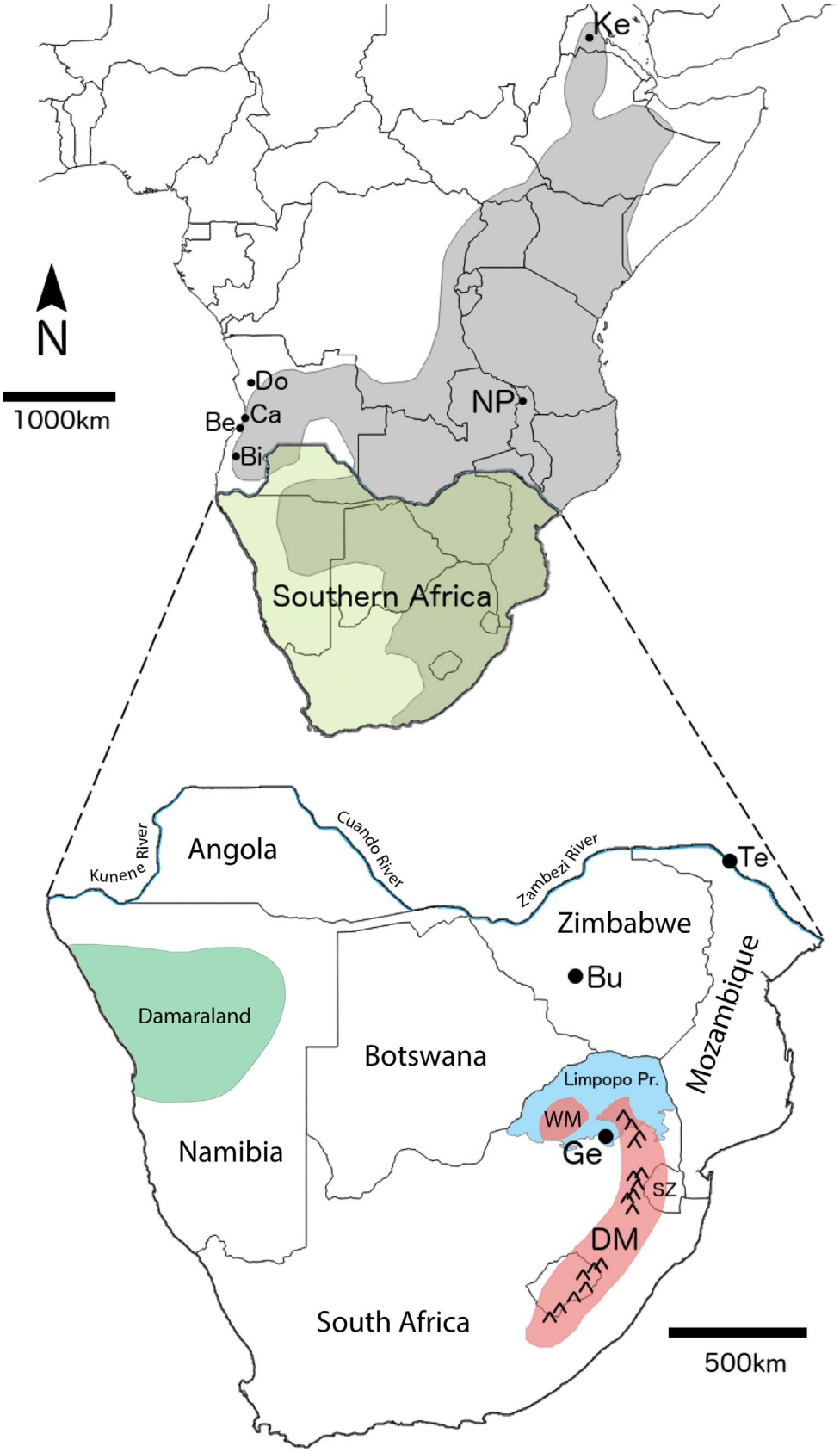

Fig. 1. Map of the study area. Gray shading indicates the distribution of the *Trachylepis varia* complex, based on occurrences reported by Bates et al. (2014), Broadley (1966), Jacobsen (1989), Largen and Spawls (2010), Parker (1942), Pietersen et al. (2013), Pietersen (2014), Spawls et al. (2004), and Scortecci (1928, 1930, 1931). Abbreviations: *Angola*: Benguella (Be); Biballa (Bi), Catumbella (Ca), Dondo (Do); *Eritrea*: Keren (Ke); *Malawi*: Nyika Plateau (NP); *Mozambique*: Tete (Te); *South Africa*: Drakensberg Mountains (DM), Gerlachshoop (Ge), Waterberg Massif (WM); *Swaziland* (SZ); *Zimbabwe*: Bulawayo (Bu). Southern Africa traditionally does not include Angola, but we chose to include southeastern Angola in this study to capture additional occurrence records for Maxent analyses. Damaraland is approximated for when Peters (1870) described *Euprepes damaranus* (= *Trachylepis damarana*).

7000 feet, northwest of Lake Nyasa, Nyasaland" [Malawi]; holotype: MCZ R-50860) with *T. varia*.

Jacobsen (1989) recognized an additional species that he considered to be closely related to *Trachylepis varia* and morphologically intermediate between *T. varia* and *Trachylepis lacertiformis*. Although Jacobsen (1989) collected specimens of this new species (which he referred to as "*Mabuya* sp. aff. *M. lacertiformis*" or "*Mabuya* sp. nov.") from northeastern South Africa and provided a species account in his

unpublished PhD dissertation, he did not designate a name or type specimen. In a review of the species of *Trachylepis* (then *Mabuya*) occurring in southern Africa, Broadley (2000) examined type specimens of *E. varius*, *E. damaranus*, and *M. v. nyikae*, plus additional *T. varia* specimens from across southern Africa, and concluded that subdivision of *T. varia* is not justified. However, some reports of intraspecific reproductive bimodality have been disproven (or at least called into question) following the discovery of cryptic species or independently evolving lineages that differ in their reproductive modes (e.g., Lobo and Espinoza (1999, 2004) and Cornetti et al. (2015); but, see Fairbairn et al. (1998) and Smith et al. (2001) for exceptions) and the possibility that *T. varia* includes multiple species must be reinvestigated.

The taxonomic history of *Trachylepis varia* has been complicated, in part, because of the presence of other, superficially similar-looking *Trachylepis* species in Southern Africa, which earlier authors confused with *T. varia*. In particular, members of the *Trachylepis variegata* group (= *Mabuya lacertiformis* complex Broadley, 1975)), which includes *Trachylepis variegata* (Peters, 1870), *Trachylepis punctulata* (Bocage, 1872), *Trachylepis chimbana* (Boulenger, 1887), and *Trachylepis lacertiformis* (Peters, 1854), were frequently mistaken for *T. varia* by earlier authors (Broadley, 1975, 2000). The names *Mabuia varia* var. *longiloba* Methuen and Hewitt, 1914 (a synonym of *Trachylepis variegata*) and *Mabuya damarana rhodesiana* Broadley, 1960 (a synonym of *Trachylepis lacertiformis*) are especially misleading because their specific epithets (i.e. *varia* and *damarana*, respectively) suggest a close association with *Trachylepis varia*. See Broadley (1975, 2000) for a more detailed account of the nomenclatural history and synonymy of the *T. variegata* group (including a detailed list of references in which earlier authors misapplied names associated with *Trachylepis varia* to members of the *T. variegata* group). Despite being superficially similar-looking, members of the *Trachylepis varia* complex can be distinguished from species in the *Trachylepis variegata* group (and all other *Trachylepis*) by having all of the following characters: (1) nostrils positioned more laterally than dorsally on the snout and are even with or posterior to the rostrolabial suture, (2) subdigital lamellae keeled, (3) subocular scale narrowed inferiorly, (4) distinct white or cream-colored lateral stripe extending from the subocular scale across the ear opening to the groin, (5) single row of dorsal scales on the proximal phalanx of the fourth toe, (6) 30–36 scale rows around midbody, (7) tricarinate dorsal scales (Broadley, 1975, 2000).

Within *Trachylepis varia*, the geographic patterns of phenotypic variation and whether phenotypically distinct populations correspond to undescribed species has been unclear. Loveridge (1933) and Branch et al. (2005) reported that some *T. varia* populations in northern Mozambique have black flecking on the throat, whereas populations elsewhere lack this feature. Additionally, these authors reported that *T. varia* in Kenya and in Uganda sometimes have five (rather than three) keels on each dorsal scale. Loveridge (1920) also noted that *T. varia* from the Uluguru Mountains, Tanzania, have an unusually dark venter. In northern Zambia, *T. varia* have more midbody scale rows and more supraciliary scales than in other populations (Broadley, 1991), whereas *T. varia* from Kenya and Somalia have fewer midbody scale rows than usual (Loveridge, 1936b; Parker, 1942). Loveridge (1929, 1936a) reported that *T. varia* from arid regions of Kenya and South Africa sometimes have long auricular scales. Additionally, Loveridge (1933) observed that the subocular scale is separated from the lip on one or both sides in *T. varia* from Tandala and Unyanganyi, Tanzania. A pale vertebral stripe is variably present across most of the range of *T. varia* (Broadley, 2000), whereas pale lateral and dorsolateral stripes are variably present in Kenyan and Tanzanian populations but present elsewhere (Loveridge, 1933). However, some of the specimens that Loveridge (1929, 1933) called *T. varia* are probably misidentified members of other *Trachylepis* species and Loveridge (1920, 1929, 1933) frequently synonymized (or considered synonymizing) taxa that are now widely accepted species (e.g., *Trachylepis hildebrandtii*, *Trachylepis brauni,* and *Trachylepis bayonii*) into *T. varia* (Branch, 1998; Uetz and Hallermann, 2016). An integrative systematic study of *T. varia* across its range is needed to clarify phylogenetic relationships and geographic patterns of phenotypic variation and to identify major clades (putative species) within *T. varia*.

1.2. Research goals

We sequenced two mitochondrial and three nuclear DNA loci to infer phylogenetic relationships and to identify the major clades (putative species) occurring across the range of the *Trachylepis varia* complex. Additionally, we analyzed phenotypic data for the southern African (Fig. 1) populations to (1) examine whether southern African populations that are genetically deeply divergent are also phenotypically distinct, (2) map the distributions of putative southern African species, and (3) to update the taxonomy of the *T. varia* complex in southern Africa. We test the hypothesis that *T. varia* is composed of multiple species, which we considered to be supported if deep genetic divergences coupled with diagnostic morphological differences exist between individuals or populations. Following the General Lineage Species Concept (de Queiroz, 2007), we considered morphological divergence and reciprocal monophyly between genetically distinct populations to be additional evidence for the existence of multiple species.

2. Methods

2.1. Collection acronyms

Acronyms associated with tissues or specimens in this study include: AMB and MCZ A (Aaron M. Bauer field numbers); AMNH (American Museum of Natural History, New York); BMNH (The Natural History Museum, London [formerly British Museum of Natural History]); CAS (California Academy of Sciences); DFH (Daniel F. Hughes field numbers); DGB (Don G. Broadley field numbers); DQ (Genbank IDs); EBG or ELI (Eli Greenbaum field numbers); J or P (field numbers [reported in Jacobsen (1989)]); JM (Johan Marais field numbers); JVV (Jens V. Vindum field numbers); Mab (un-cataloged *Mabuya*-group tissues); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge); MSNG (Museo Civico di Storia Naturale “Giacomo Doria” Genova); NMZB (Natural History Museum, Bulawayo); NRM (Naturhistoriska Riksmuseet, Stockholm); PEM R (Port Elizabeth Museum); PW (Philipp Wagner field numbers); TJC (Timothy J. Colston field numbers); TM (Ditsong National Museum of Natural History [formerly Transvaal Museum]); WC or WCANG (Werner Conradie field numbers); WCDNA or WCQQ (Werner Conradie DNA samples); WRB (Bill Branch field numbers); ZFMK (Zoologisches Forschunginsmuseum Alexander Koenig, Bonn); ZMB (Museum für Naturkunde, Berlin). Most samples in private collections are currently awaiting accessioning in CAS, MCZ, the National Museum of Namibia (AMB, JVV, MCZ A), PEM (WC, WCANG, WCDNA, WCQQ, WRB) or the National Museum of Ethiopia (TJC).

2.2. Tissue sampling, DNA extraction, and sequencing

We sampled tissues from 199 individuals from the *T. varia* complex, including from newly collected individuals from Angola, Namibia, South Africa, Zambia, and Zimbabwe and from previously collected *T. varia* tissues from across its range. We included one *T. megalura*, one *T. hoeschi*, and one *Chioninia delalandii* as outgroup taxa, because preliminary phylogenetic data support (> 0.95 posterior probability) *T. megalura* as sister to the *T. varia* complex and *T. hoeshi*, *T. varia*, and *T. megalura* as members of a sub-clade within *Trachylepis*, and because an earlier phylogenetic study recovered *Chioninia* as sister to *Trachylepis* (Karin et al., 2016). We extracted genomic DNA from tissues using a salt DNA extraction protocol (Aljanabi and Martinez, 1997), performed polymerase chain reactions (PCR) in an Eppendorf Mastercycler nexus gradient thermocycler for two mitochondrial and three nuclear loci, cleaned PCR product with a magnetic-bead solution (Rohland and

Reich, 2012), conducted cycle sequencing using Big-Dye v3.1 chemistry, performed an additional magnetic-bead cleanup, and analyzed cycle sequencing product on an ABI3730xl. PCR reactions began with a 2 min denaturation step at 95 °C followed by 34 cycles of: DNA denaturation at 95 °C for 35 s, primer annealing at 50 °C (for 16S, ND2, KIF24, and RAG1) or at 52 °C (for BRCA2) for 35 s, and extension at 72 °C for 1 min 35 s. Primers for PCR are shown in Table S1.

We sequenced nuclear loci for a subset of individuals representing the major mitochondrial DNA lineages. Mitochondrial genes included ribosomal 16S (16s) and NADH dehydrogenase subunit 2 (ND2) and nuclear genes included recombination activation protein 1 (RAG1), kinesin family member 24 (KIF24), and breast cancer 2 early onset (BRCA2). These genes were chosen because they are rapidly evolving and have previously been used to resolve difficult nodes across a large range of time scales (Portik et al., 2012; Karin et al., 2016). We used MUSCLE (Edgar, 2004) implemented in Geneious v6.1.8 (Biomatters Ltd.) to generate ND2, KIF24, RAG1, and BRCA2 alignments and we used LocARNA v1.8.11 (Smith et al., 2010), which uses a structural model of RNA, to align 16S sequences.

2.3. Phylogenetic inference

We used BEAST v1.8.2 (Drummond and Rambaut, 2007) to infer a multilocus time tree under a coalescent tree process and we used RAxML v8.0 (Stamatakis, 2014) with GTR + Gamma substitution models (1000 bootstraps) to infer maximum likelihood gene trees. For each gene partition of the concatenated BEAST analysis, we assigned a relaxed lognormal clock and the best-fit substitution model estimated with Bayesian Information Criterion (BIC) in PartitionFinder (Lanfear et al., 2012). Zheng and Wiens (2016) inferred a time-tree for Squamata using 52 genes, 4162 species, and 13 fossils (see Mulcahy et al. (2012) for a discussion of the fossils) and estimated the divergence time between *Trachylepis varia* and *T. hoeschi* to be 27.1 Ma. Using this estimate, we applied a normal distribution prior (mean 27.1 Ma, ± 1.5 SD) for the divergence time between *T. varia* and *T. hoeschi* (an outgroup taxa in this study) to infer a time-tree for the *T. varia* complex. During the BEAST analysis, we sampled from the posterior distribution every 10,000 generations for 100 million generations and omitted the first 10 million generations as burnin. We used Tracer v1.5 (Rambaut et al., 2014a) to confirm that BEAST reached posterior convergence, TreeAnnotator v1.8.1 (Rambaut et al., 2014b) to generate a Maximum Clade Credibility tree with median divergence times, and FigTree v1.4.0 (Rambaut, 2012) to visualize trees. We considered posterior probabilities (PP) greater than 0.95 and bootstrap support (BS) greater than 70% to be strong support for a clade.

2.4. Phenotypic data

We examined color pattern, meristic, and mensural characters for individuals spanning the species range and we tested the hypothesis that phenotype significantly differs among the major genetic clades occurring in southern Africa (Fig. 1). We conducted *t*-tests and contingency tests to determine whether the major genetic lineages occurring in southern Africa are phenotypically distinct (see Section 2.7). Color pattern characters included the background color of dorsal (DC) and ventral (VC) surfaces of the body; the presence or absence of a pale vertebral (PVS) stripe; the presence or absence of dark longitudinal stripes beginning within a few scale rows after the nuchal scales (SBN); the presence or absence of white spots or flecks on the dorsum (WSD); the presence or absence of black transverse bars or blotches between the pale lateral and dorsolateral stripes (TBL) or between the pale dorsolateral stripes (TBD); the presence or absence of a broad, longitudinal, dark brown or black stripe between the pale lateral and pale dorsolateral stripes (BLS); and the presence or absence of black spots or flecks on the chin or belly (BSV) (see Figs. S7–13 for images of alternative character states for color pattern characters). Meristic characters included the number of scale rows around midbody (MSR); the number of ventral scale rows (VS) between (not including) the first pair of chin shields and the anal scales; the number of the supraciliary scales (SC) between the loreals and the pretemporals (head scalation terminology following Broadley (2000): Fig. 1); the number of anterior supralabial scales (SL) between the rostral and the last subocular (Broadley, 2000); the number of auricular scales projecting posteriorly from the anterior margin of the ear opening (AR); whether auricular scales project posterodorsally or posteroventrally (ARD); the number of subdigital lamellae beneath the fourth toe (LT4); whether supranasal scales are touching or separated (SNC) (Broadley, 2000); and whether parietal scales are touching or separated (PC) (Broadley, 2000). Mensural characters included snout-vent length (SVL), fourth toe length (TIVL), fifth toe length (TVL), head length (HL; measured from the tip of the snout to the anterior margin of the ear opening), head width (HW; measured between the opening of the ears), head height (HH; measured at the anterior margin of the ear opening), axilla-groin length (AGL) measured from just posterior to the insertion of the forelimb to just anterior of the insertion of the hindlimb, the length of the anterior margin of the second loreal (L2AML), and the length of the ventral margin of the second loreal scale (L2VML) (see Figs. S14–18 for depictions of meristic and mensural characters). Each mensural character was measured with dial calipers to the nearest 0.02 mm, except for L2AML and L2VML, which were measured in Fiji v2.0.0 to the nearest 0.02 mm using photographs of a lateral view of the head. We standardized mensural characters by dividing each measurement by the individual's SVL prior to conducting *t*-tests.

2.5. Principle components analysis of head shape

We conducted geometric morphometric analyses on two-dimensional landmark data to determine if *Trachylepis varia* clades are phenotypically distinct and to generate principle components for downstream discriminant function analysis. We used Fiji v2.0.0 (Schindelin et al., 2012) to collect landmark data from photographs of dorsal and lateral views of the head (see Fig. S6 for depiction of each landmark). To avoid introducing a strong effect of parallax when photographing specimens, we only took photos when the entire surface of interest (i.e., lateral or dorsal region of the head) appeared to be in focus. To determine if head shape differs among the major lineages of *Trachylepis varia*, we used the R package geomorph (Adams and Otarola-Castillo, 2013) to perform generalized procrustes analyses on landmark data, which produced shape variables (scaled to unit-centroid sizes) that were analyzed using principal components analyses (PCA) separately for the lateral and dorsal landmark datasets. Additionally, for the set of individuals that we obtained both lateral and dorsal landmark data, we used the estimated principle components from the separate lateral and dorsal PCAs as input for a combined lateral + dorsal PCA. Following each PCA, we produced biplots of the first and second principal components to visualize head shape morphospace and clades were considered to have significantly different head shapes if their head shape morphospaces do not overlap.

2.6. Discriminant function analysis

We performed a discriminant function analysis on the first two principle components of head shape for lateral and dorsal views of the head to assign unsequenced individuals to one of the two most commonly sampled southern African clades (see phylogenetic results in Sections 3.2–3.3). We used the R package MASS (Venables and Ripley, 2002) to perform discriminant function analysis to assign 140 unsequenced individuals (i.e., individuals that were not DNA sequenced) from southern Africa to either clade A or clade F (Fig. 2). As training samples, we used head shape data for 46 sequenced individuals that were specified a priori as belonging to clade A or clade F based on our phylogenetic results. For each unsequenced individual, we estimated:

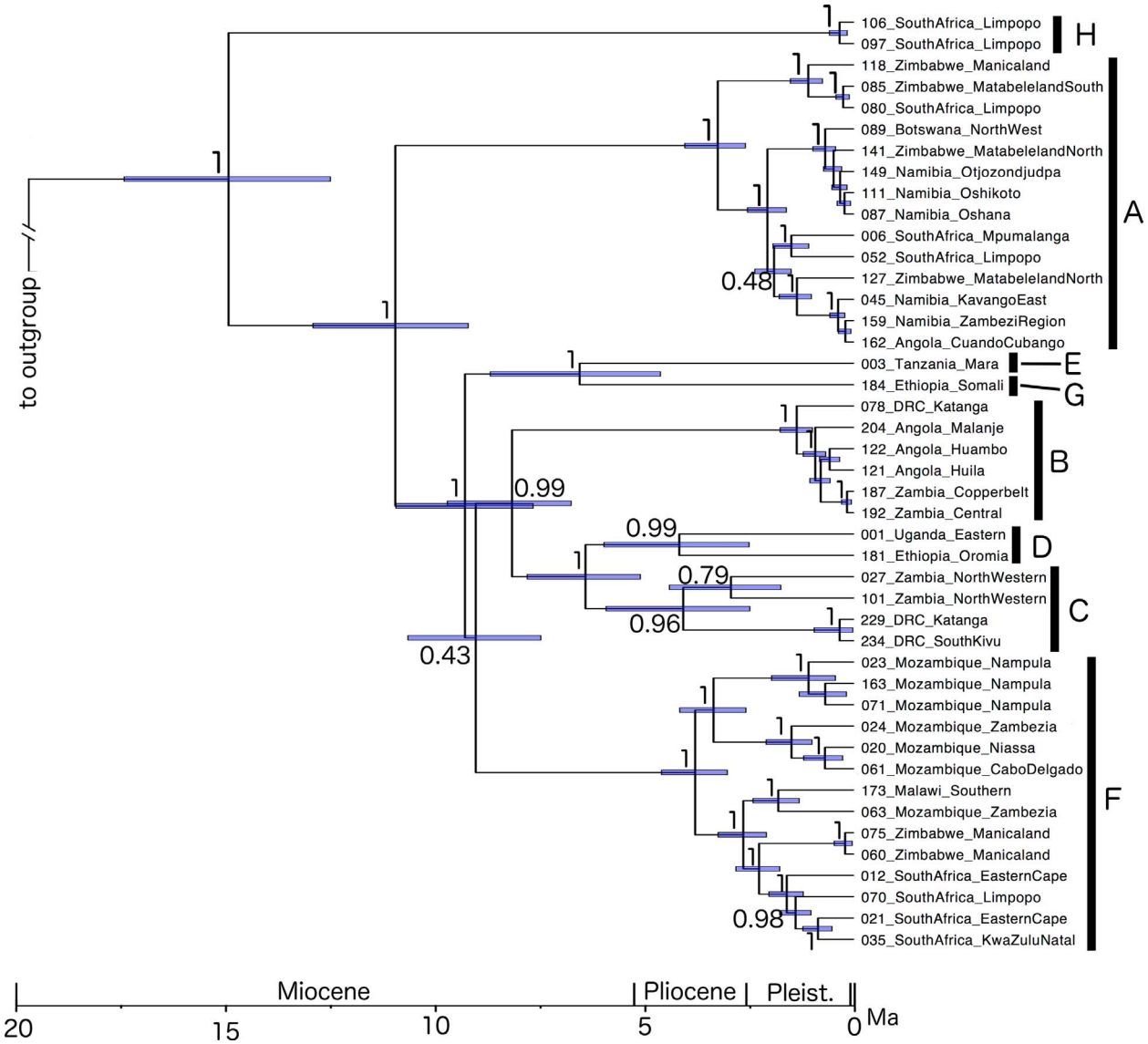

Fig. 2. Multilocus time-tree of the *Trachylepis varia* complex. Major clades (A–H) are indicated to the right of black vertical after tip names. Values at internal nodes are posterior probabilities. Shallow, unlabeled nodes have low (PP < 0.95) support. ID numbers shown at tips correspond to those shown in Table S3.

(1) the probability that the individual belongs to clade A, and (2) the probability that the individual belongs to clade F. Membership posterior probabilities > 0.95 were considered as strong support for the assignment of an individual to a particular clade.

2.7. Correlative analysis of phenotypic data

We performed *t*-tests in R (R Core Team, 2016) for each continuous meristic or mensural character and contingency tests for each categorical meristic or color pattern character to determine if phenotype significantly differs among the major *Trachylepis varia* clades occurring in southern Africa. Specifically, we used the *t* test function of the stats package in R to perform Welch t-tests on eight mensural characters (TIVL, TVL, HL, HW, HH, AGL, LA2ML, and LV2ML; each divided by SVL) and on two meristic characters (VS and LT4) to test the null hypothesis that these characters do not significantly differ between clades. Additionally, we used a custom R script to perform contingency tests of four meristic characters (PC, MSR, SC, and SL) and two color pattern characters (PVS and WSD) to test the null hypothesis that these characters are not contingent on clade. For both t-tests and contingency tests, we considered p-values < .05 as the threshold to reject null hypotheses and as additional evidence that major clades are distinct species.

2.8. Niche modeling

We used Maxent v3.3.3k (Phillips et al., 2006) to estimate geographic distributions for the major *Trachylepis varia* lineages occurring in southern Africa. Training samples for niche modeling included individuals from southern Africa that were either DNA sequenced (PP > 0.95 posterior probability or BS > 70 for clade containing the individual) or assigned to a particular clade with high support (PP > 0.95) according to discriminant function analysis of head shape. We only performed niche modeling for the southern African clades having ≥10 training localities, because the predictive performance of niche models is correlated with the number of training localities and Maxent can perform moderately well with as few as 10–30 training samples (Wisz et al., 2008). Bioclimatic data included 19 commonly used Bioclim variables (Hijmans et al., 2005), plus precipitation (mean) and temperature (mean, minimum, and maximum) data for each month of the year (Hijmans et al., 2005). Terrain data included nine layers describing elevation (median and standard deviation), aspect, and slope

(Danielson and Gesch, 2011), and vegetation data included mean forest canopy height (Simard et al., 2011). We ran Maxent with default parameter settings and auto-features, and supplied bioclimatic, terrain, and ecological data at 2.5 arcminutes resolution. Niche model results were used as the basis for distribution maps of the major southern African *T. varia* clades.

3. Results

3.1. DNA sequences

DNA sequence alignments included ND2 (1360 bp; 156 individuals), 16S (535 bp; 159 individuals), KIF24 (578 bp, 71 individuals), RAG1 (106 bp, 1143 individuals), and BRCA2 (1223 bp, 65 individuals). The concatenated alignment included all five genes and 45 individuals (33.45% missing data). Among ingroup taxa, the number of parsimony informative sites was greatest in the ND2 alignment (446), followed by 16S (84), KIF24 and BRCA2 (45), and RAG1 (44). Genbank numbers for sequences used in this study are shown in Table S2.

3.2. Multilocus Bayesian time-tree

The topology of the concatenated-gene time-tree suggests that the earliest divergence within the *Trachylepis varia* complex occurred during the Burdigalian or Langhian of the Miocene ($X = 14.9$ Ma, 17.4–12.5 Ma) and that at least eight lineages diverged during the Miocene or early Pliocene (Fig. 2). Clade A includes individuals from Namibia, southeastern Angola, Botswana, Zimbabwe, northeastern South Africa, and western Mozambique; clade B includes individuals from central and northern Angola, Zambia, and southern Democratic Republic of the Congo (DRC); clade C is only known from northwestern Zambia and from southern and eastern DRC; clade D individuals are from Ethiopia and Uganda; clade E includes individuals from northern Tanzania; clade F is broadly distributed and includes individuals from South Africa, eastern Zimbabwe, Malawi, and Mozambique; clade G is only known from a single individual (TJC 1409) from Ethiopia; and we sampled clade H in northeastern South Africa (Fig. 3). The relationships inferred among the eight major *T. varia* clades are generally highly supported (i.e., PP $>$ 0.95), except for the placement of clade F, which is recovered as the sister group to the group containing clades B, C, and D (Fig. 2). Clades C and D are strongly supported as being sister groups and together form the sister clade to clade B. The sister relationship of clade F to B (C, D) is not supported but E and G are strongly supported as each other's closest relatives, as is the group comprising clades B–G. Clades A and H receive strong support as sequential outgroups to all other sampled members of the *T. varia* complex.

3.3. RAxML gene trees

RAxML gene trees generally support ($>$ 70 BS) the monophyly of the *Trachylepis varia* complex as a whole, and, similar to the multilocus time-tree, gene trees show deep genetic divergences among up to eight clades (Figs. S1–S5). Unlike the multilocus tree, the RAG1 gene tree recovers clade F as paraphyletic, but with low support (Fig. S4). Additionally, gene trees frequently differ from the multilocus tree with respect to the relationships among the major *T. varia* clades. In particular, the ND2 tree (Fig. S2) strongly supports the relationship ((B, G), (F, (C, D))) rather than ((E, G), (F, B, (C, D))), as supported by the multilocus tree. Considering that clade E individuals were not sequenced for ND2, the multilocus tree and the ND2 gene tree essentially differ in the placement of clade B. In the BRCA2 tree, clade C is placed sister to a moderately well supported clade containing B + D + F, rather than sister to clade D as in the multilocus tree. The RAG1 and KIF24 trees only differ from the multilocus tree at weakly supported nodes.

3.4. Phenotypic data

T-tests and geometric morphometric analyses of meristic and mensural data and contingency tests of qualitative meristic and color-pattern characters support morphological distinctiveness of *Trachylepis varia* clades A and F. Due to low sample sizes for clades B, C, D, E, G, or H, we were unable to test whether these clades are morphologically distinct from each other or from clades A and F. Summary statistics (range, mean, relative frequency, and number of samples) are shown for mensural (Table 1), meristic (Table 2), and color pattern (Table 3) data. We found that *T. varia* complex clades A and F significantly differ in multiple phenotypic characters. Welsh two-tailed t-tests support significant differences in mean TIVL, TVL, HW, AGL, L2AML, L2VML, VS, and LT4 between clades A and F ($p < .05$), although overlap exists in the ranges observed for all characters examined (Tables 1–3). Additionally, contingency tests suggest that the fraction of individuals with WSD present is significantly greater in clade A than in clade F ($p < .05$) and the fraction of individuals with PVS present is significantly greater in clade F than in clade A ($p < .05$). In contrast, HH, HL, MSR, PC, SC, and SL do not significantly differ between clade A and clade F ($p > .05$).

3.5. Principle components analysis of head shape

Principle components analyses of head shape support clades A and F as phenotypically distinct when both lateral and dorsal landmarks are analyzed together (Fig. 5). Biplots of the first two principle components show that there is broad overlap in the head shape morphospaces of clades A and F when the lateral landmark dataset is analyzed alone (Fig. 5a) and that there is little overlap in the head shape morphospaces of clades A and F when the dorsal landmark dataset is analyzed alone (Fig. 5b). In contrast, the combined lateral + dorsal head shape PCA resulted in non-overlapping morphospaces for clades A and F (Fig. 5c), indicating that both the lateral and dorsal landmark datasets contained unique information that was useful for distinguishing clade A and clade F individuals. PCA results support our hypothesis that clades A and F have diverged phenotypically, which is expected considering that we also observed deep genetic divergence between these two clades.

3.6. Discriminant function analysis

Discriminant function analysis assigned most of the unsequenced *Trachylepis varia* complex individuals from southern Africa to either clade A or clade F with strong support (membership probability $>$ 0.95). Of the 140 unsequenced individuals included in the discriminant function analysis, 41 individuals were strongly supported as belonging to clade A and 42 individuals were strongly supported as belonging to clade F. The remaining 57 individuals received low or moderate support (clade membership probability $<$ 0.95) for their assignment to clade A or clade F. Discriminant function analysis supports clade A as occurring in Namibia, Botswana, Zimbabwe, northeastern South Africa, and central Mozambique, and supports clade F as occurring in eastern South Africa, eastern Zimbabwe, and Mozambique, which is consistent with the distributions suggested from genetic data.

An exception to geographic congruence between genetic and phenotypic data occurs in Zimbabwe, in the vicinity of Bulawayo. The discriminant function analysis of phenotypic data assigned three individuals from Bulawayo (individuals TM 66450, TM 66453, and TM 66459; DNA not sequenced from these individuals) to clade F, whereas phylogenetic analyses of DNA sequences place three different individuals from ~60 km northwest of Bulawayo (individuals MCZ R 190451 (= Tv137), MCZ R 190457 (= Tv137), and MCZ R 190462 (= Tv138); Figs. S1–S5) as members of clade A. To examine whether these Bulawayo individuals are morphologically more similar to clade F, despite being genetically assigned to clade A, we reran the discriminant function analysis of morphometric data with these three sequenced

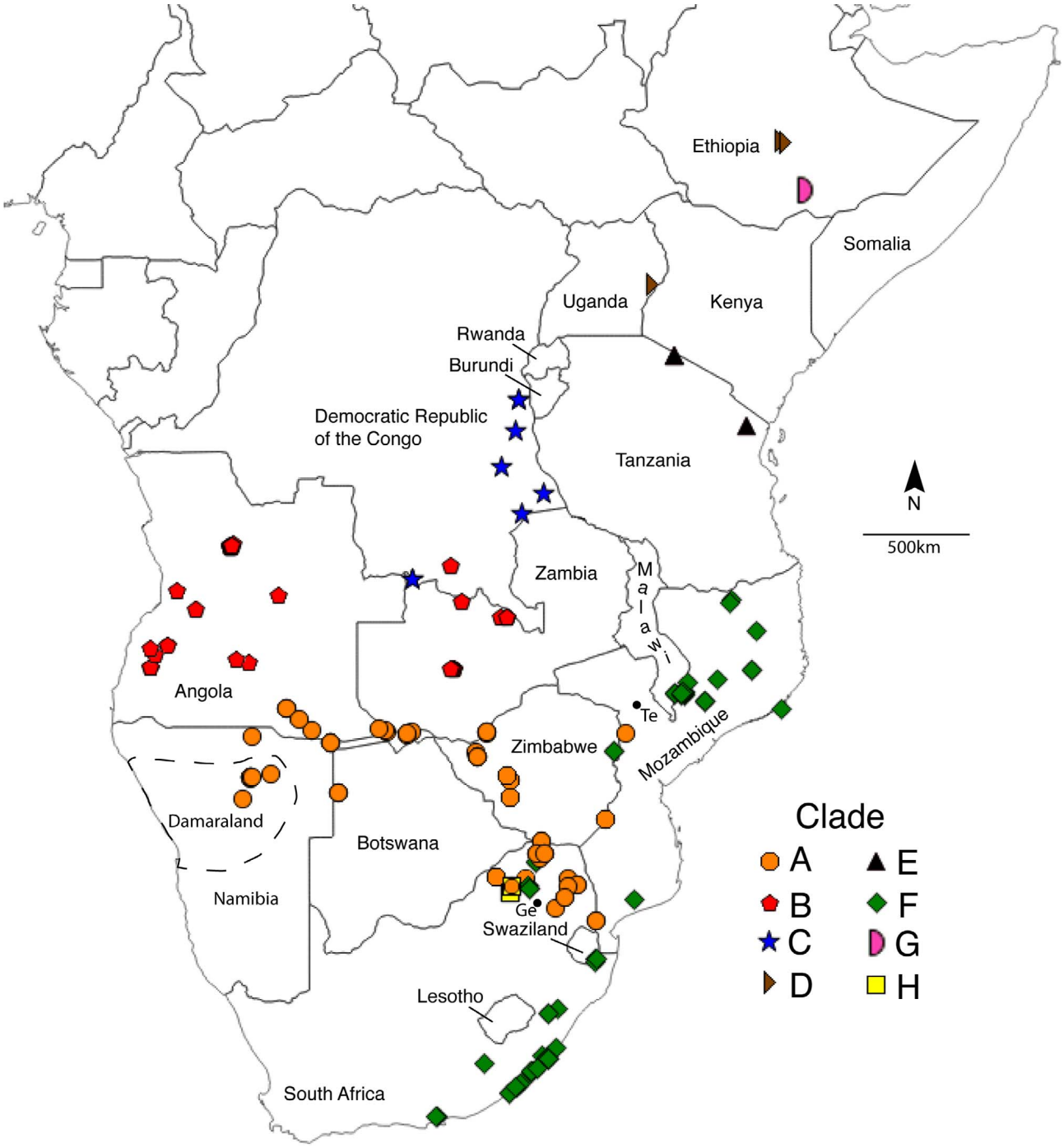

Fig. 3. Distribution of major clades of the *Trachylepis varia* complex. Clade A (orange circles; = *Trachylepis damarana*), clade B (red pentagons), clade C (blue stars), clade D (brown right-pointing triangles), clade E (black upwards-pointing triangles), clade F (green diamonds; = *Trachylepis varia* sensu stricto), clade G (pink semicircle), clade H (yellow squares; = *Trachylepis laevigata*). Clade IDs (A–H) correspond to the clades labeled on each of the gene trees and the multi-locus time-tree (Figs. 2 and S1–S5). Type localities are shown for the Subsaharan African species: *Trachylepis varia* (Te = Tete, Mozambique), *Trachylepis damarana* (Damaranaland, Namibia; outlined in black broken line), and *Trachylepis laevigata* (Ge = Gerlachshoop, South Africa). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

individuals removed from the training group (i.e., without specifying their clade membership *a priori*). One of the three DNA sequenced Bulawayo individuals (MCZ R 190457) was highly supported (membership probability > 0.95) as belonging to clade A and the other two individuals (MCZ R 190451 and MCZ R 190462) could not be confidently assigned to either clade A or F. Based on these results, additional genetic sampling of *Trachylepis varia* complex populations may reveal the presence of clade F near Bulawayo.

3.7. Niche models

Maximum entropy niche models suggest that *Trachylepis varia* clades A and F are sympatric or parapatric in northeastern South Africa and in western Mozambique and that both of these clades have allopatric populations in other parts of their ranges (Fig. 4). Clade A is predicted to occur in northern Namibia, southern Angola, Botswana, northeastern South Africa, southern Zimbabwe, and western Mozambique (Fig. 4a), whereas Clade F is predicted to occur in multiple, disjunct populations along the eastern mesic regions of the

Table 1
Standardized mensural characteristics of major clades in the *Trachylepis varia* complex.

Clade	TIVL/SVL	TVL/SVL	HL/SVL	HW/SVL	HH/SVL	AGL/SVL	L2AML/SVL	L2VML/SVL
A	0.115–0.169 $\bar{X}$ = 0.143 n = 38	0.074–0.116 $\bar{X}$ = 0.094 n = 38	0.184–0.229 $\bar{X}$ = 0.207 n = 40	0.12–0.159 $\bar{X}$ = 0.14 n = 40	0.091–0.109 $\bar{X}$ = 0.099 n = 44	0.377–0.655 $\bar{X}$ = 0.467 n = 40	0.010–0.016 $\bar{X}$ = 0.012 n = 40	0.018–0.031 $\bar{X}$ = 0.024 n = 40
C	0.111–0.142 $\bar{X}$ = 0.127 n = 3	0.068–0.082 $\bar{X}$ = 0.078 n = 3	0.191–0.233 $\bar{X}$ = 0.212 n = 3	0.137–0.151 $\bar{X}$ = 0.143 n = 3	0.099–0.109 $\bar{X}$ = 0.105 n = 3	0.438–0.569 $\bar{X}$ = 0.510 n = 3	0.014–0.015 $\bar{X}$ = 0.014 n = 3	0.016–0.022 $\bar{X}$ = 0.019 n = 3
D	0.109–0.151 $\bar{X}$ = 0.134 n = 3	0.080–0.099 $\bar{X}$ = 0.090 n = 3	0.183–0.249 $\bar{X}$ = 0.217 n = 4	0.126–0.150 $\bar{X}$ = 0.142 n = 4	0.090–0.110 $\bar{X}$ = 0.096 n = 4	0.460–0.521 $\bar{X}$ = 0.489 n = 4	0.014–0.019 $\bar{X}$ = 0.016 n = 4	0.011–0.018 $\bar{X}$ = 0.015 n = 4
F	0.118–0.143 $\bar{X}$ = 0.129 n = 6	0.076–0.085 $\bar{X}$ = 0.081 n = 6	0.183–0.203 $\bar{X}$ = 0.195 n = 6	0.125–0.139 $\bar{X}$ = 0.132 n = 6	0.092–0.100 $\bar{X}$ = 0.096 n = 6	0.476–0.555 $\bar{X}$ = 0.506 n = 6	0.011–0.017 $\bar{X}$ = 0.014 n = 6	0.016–0.022 $\bar{X}$ = 0.019 n = 6
H	0.134–0.151 $\bar{X}$ = 0.143 n = 2	0.083–0.096 $\bar{X}$ = 0.090 n = 2	0.198–0.221 $\bar{X}$ = 0.209 n = 2	0.142–0.143 $\bar{X}$ = 0.143 n = 2	0.093–0.097 $\bar{X}$ = 0.095 n = 2	0.454–0.522 $\bar{X}$ = 0.488 n = 2	0.013–0.018 $\bar{X}$ = 0.015 n = 2	0.017–0.020 $\bar{X}$ = 0.018 n = 2

Table 2
Meristic characteristics of major clades in the *Trachylepis varia* complex; values for ARD, SNC, and PC indicate number of individuals with character present/total number of individuals examined.

Clade	MSR	VS	SC	SL	AR	ARD	LT4	SNC	PC
A	30–36 $\bar{X}$ = 32.2; n = 43	46–56 $\bar{X}$ = 51; n = 41	4–6 $\bar{X}$ = 4.98; n = 44	4–5 $\bar{X}$ = 4.3; n = 44	2–4 $\bar{X}$ = 2.61; n = 23	2/36	19–25.5 $\bar{X}$ = 21.9; n = 40	42/44	23/44
B	–	–	4–6 $\bar{X}$ = 5.11; n = 9	4–5 $\bar{X}$ = 4.67; n = 9	3–4 $\bar{X}$ = 3.44; n = 9	9/9	19–20 $\bar{X}$ = 19.4; n = 9	1/8	5/9
C	34–36 $\bar{X}$ = 34.7; n = 3	52–61 $\bar{X}$ = 56; n = 3	5–6 $\bar{X}$ = 5.33; n = 3	4–5 $\bar{X}$ = 4.33; n = 3	3 n = 1	1/2	20.5–21.5 $\bar{X}$ = 21; n = 3	2/3	2/3
D	32–34 $\bar{X}$ = 33; n = 2	51–55 $\bar{X}$ = 53; n = 2	4–5 $\bar{X}$ = 4.67; n = 3	4–5 $\bar{X}$ = 4.5; n = 4	2 n = 1	–	18–19 $\bar{X}$ = 18.5; n = 4	3/4	4/4
E	32 n = 1	51 n = 1	4 n = 1	5 n = 1	–	–	22 n = 1	1/1	0/1
F	31–36 $\bar{X}$ = 32.9; n = 9	46–55 $\bar{X}$ = 51.8; n = 4	4–6 $\bar{X}$ = 4.92; n = 12	4–5 $\bar{X}$ = 4.14; n = 11	2–4 $\bar{X}$ = 2.5; n = 4	5/5	18.5–22.5 $\bar{X}$ = 20.4; n = 9	9/12	9/12
H	32 n = 2	50 n = 1	5 n = 2	5 n = 2	3 n = 2	1/2	19–20.5 $\bar{X}$ = 19.8; n = 2	2/2	2/2

Table 3
Color pattern characteristics of major clades in the *Trachylepis varia* complex; values indicate number of individuals with character present/total number of individuals examined.

Clade	VC	PVS	SBN	WSD	TBL	TBD	BLS	BSV
A	white (n = 43)	5/40	0/42	29/43	27/43	28/41	10/43	0/44
B	–	5/9	0/9	1/9	9/9	8/9	0/9	–
C	white (n = 3)	0/3	1/3	2/3	3/3	3/3	0/3	0/3
D	bluish-gray (n = 3)	4/4	2/4	2/4	2/4	2/4	0/4	0/4
E	white (n = 1)	0/1	0/1	1/1	1/1	1/1	0/1	0/1
F	white (n = 12)	8/12	0/11	3/12	8/11	8/12	1/12	3/12
H	white (n = 2)	0/2	1/1	1/2	0/2	0/2	0/2	0/2

subcontinent, including a broadly distributed population in South Africa. Additionally, separate clade F populations are predicted to occur in eastern Zimbabwe, southern Malawi, and northern Mozambique (Fig. 4b).

4. Discussion

4.1. Overview

We provide the first phylogenetic study of the *Trachylepis varia* complex incorporating both genetic and phenotypic data and we find strong support for our hypothesis that *T. varia* includes multiple species. Genetic data show that the *T. varia* complex is particularly diverse in northeastern South Africa, where at least three putative species occur in sympatry. Broadley (1966, 2000) synonymized *Euprepes damaranus* Peters, 1870 and *Euprepes laevigatus* Peters, 1869 with *Trachylepis varia*, but our results suggest that all three of these taxa should be recognized as distinct species considering that the type specimens correspond to deeply divergent clades that also exhibit phenotypic differences and are sympatric in some areas (Fig. 6). Jacobsen's (1989) putatively new species of *Trachylepis* warrants future investigation to determine whether it is in fact a distinct species; if true — this population needs to be re-described considering that the original description was part of Jacobsen's doctoral dissertation. Our data support the occurrence of at least three species belonging to the *T. varia* complex in northeastern South Africa, which increases the total number of *Trachylepis* species in this region to ten (Bates et al., 2014).

4.2. Phylogenetic relationships

We recovered a highly supported multilocus time-tree that resolves most relationships among the major clades (candidate species) of the *Trachylepis varia* complex, whereas individual gene trees poorly resolve deeper phylogenetic relationships and strongly conflict in the position of clade B. We find (1) strong support for the sister relationship between clade H and the rest of the *T. varia* complex, with divergence beginning ~15 Ma; (2) strong support for the sister relationship between clade A and the clade containing clades B–G, with divergence beginning ~9 Ma; (3) strong support for the sister relationship between clades E and G, with divergence beginning ~6 Ma; (4) and strong support for the sister relationship between clades C and D, with divergence beginning ~6 Ma. The position of clade B in the ND2 tree strongly conflicts with the position of clade B in the RAG1 gene tree and the multilocus time-tree and is likely the result of either incomplete lineage

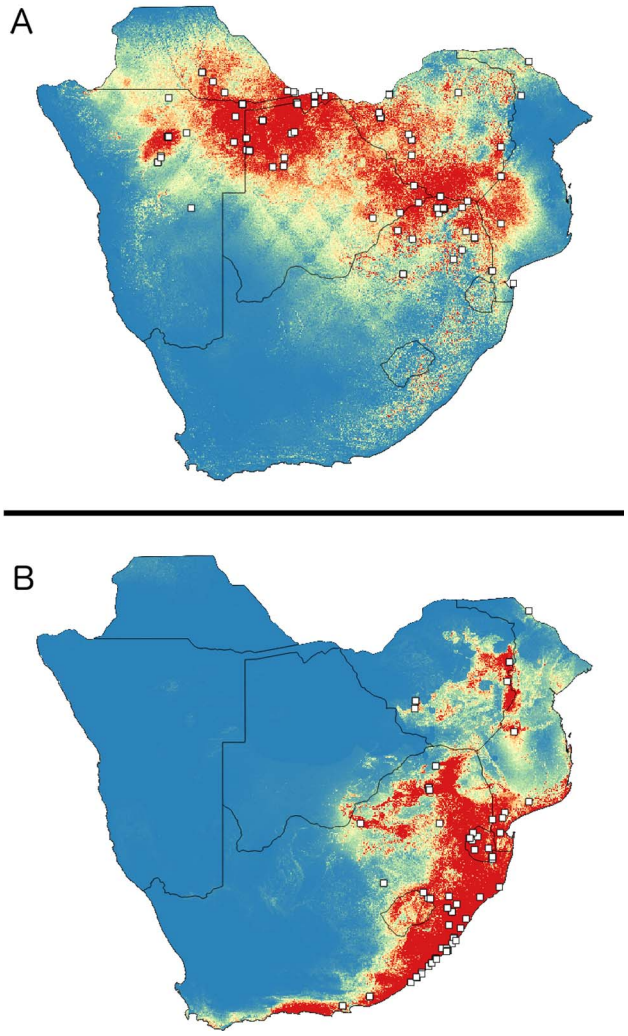

Fig. 4. Present day maximum entropy niche models for (A) clade A and (B) clade F of the *Trachylepis varia* complex. White squares indicate localities used for model training. Warmer colors indicate areas with higher predicted habitat suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sorting or historical gene flow between an ancestor of clade B and an ancestor of clade C, D, or F. Incomplete lineage sorting is expected to occur during rapid, successive diversification events. The presence of short internal branches 5–10 Ma in the time-tree (Fig. 2) is consistent with rapid diversification and suggests that incomplete lineage sorting may explain the gene tree discordance in this study. Future studies on the *T. varia* complex should employ a next generation DNA sequencing approach to distinguish incomplete lineage sorting from historical gene flow. Nevertheless, we recovered strong support for the monophyly of eight major clades in the *T. varia* complex and strong and congruent support for many of the deeper-level relationships in this group. Although we consider each of the eight *T. varia* clades to be distinct species, we limit the systematic discussion of this paper (Section 5) to the southern African clades (clades A, F, and H) and we will discuss the remaining clades in more detail in a paper that includes formal species descriptions.

4.3. Biogeographic hypotheses explaining diversification

This study provides a first look at diversification within the *Trachylepis varia* complex, but future studies are needed to determine which historical factors were most important for driving diversification

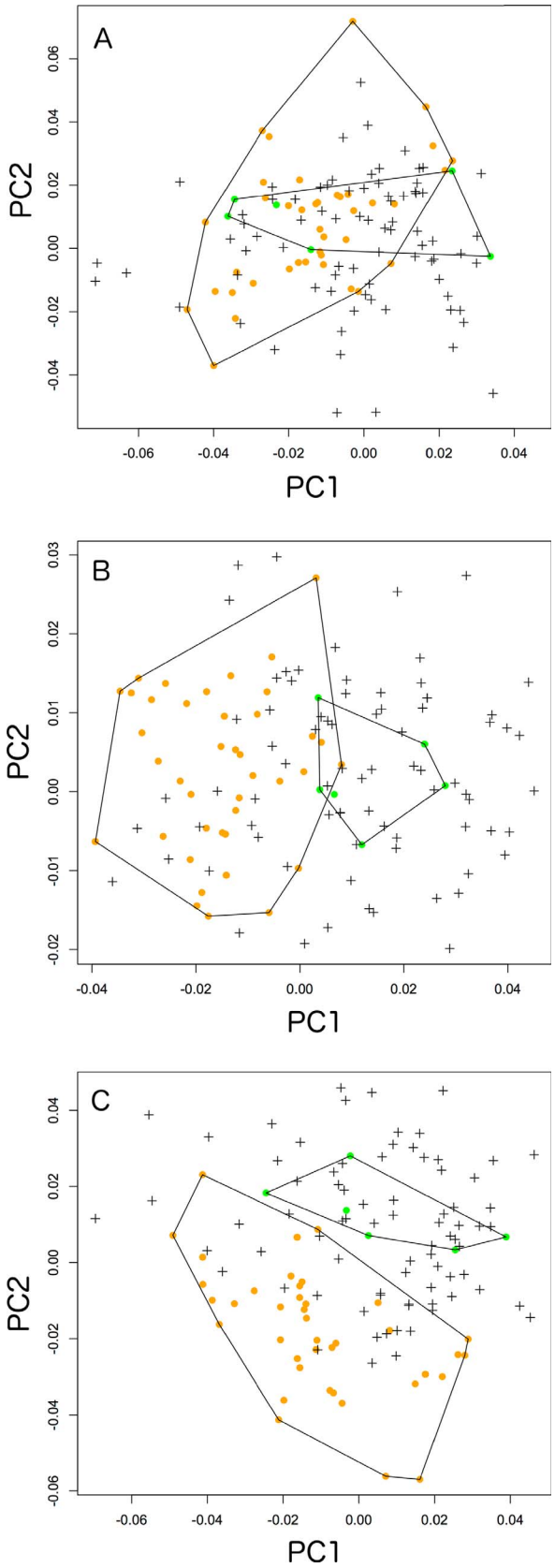

Fig. 5. Biplots of first and second principle components of two-dimensional head shape for clades A (orange) and F (green) of the *Trachylepis varia* complex. (A) Lateral view head shape; (B) dorsal view head shape, (C) combined lateral + dorsal PCA of head shape. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

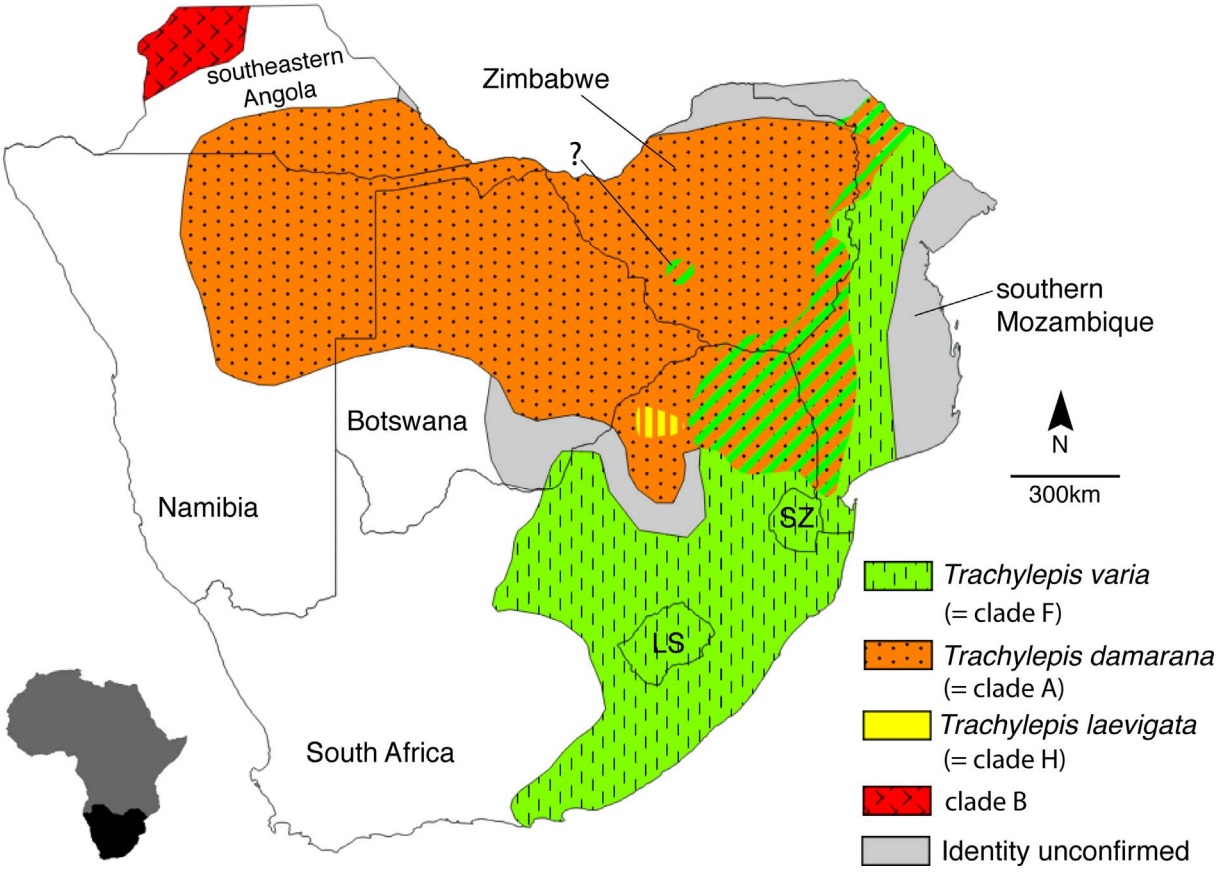

Fig. 6. Distribution of *Trachylepis damarana*, *Trachylepis laevigata*, *Trachylepis varia*, and clade B in southern Africa. Swaziland (SZ); Lesotho (LS).

Fig. 7. Lectotype of *Trachylepis damarana* (ZMB 6153) (Photo Frank Tillack).

in this group. Our data suggest that diversification in the *T. varia* complex occurred most rapidly during the middle Miocene through early Pliocene, a period when diversification rates were also high for other African groups, including grasses, grazing mammals, and agamid lizards (Strömberg, 2011; Leaché et al., 2014). Factors that may have driven diversification in some African taxa during the Miocene include the opening of the East African arid corridor (Leaché et al., 2014), expansion of new grassland habitat types, such as savannahs (Strömberg, 2011), or a warming climate combined with the presence of isolated mountain refugia (Travers et al., 2014).

The East African arid corridor hypothesis considers that diversification occurred following dispersal through an arid corridor linking southern Africa to the Horn of Africa region and this hypothesis has been used to explain Miocene diversification of xeric-adapted plants, mammals, and lizards (Verdcourt, 1969; Bobe, 2006; Leaché et al., 2014). In contrast, in situ diversification in the Drakensberg region of northeastern South Africa best explains Miocene diversification of geckos of the genus *Lygodactylus* (Travers et al., 2014). We find that the oldest *T. varia* complex lineages occur in northeastern South Africa, where putative species richness peaks for this group, favoring in situ diversification over dispersal-driven diversification. However, greater genetic sampling of *Trachylepis varia* populations in East Africa and in the Horn of Africa is needed before the arid corridor hypothesis can be confidently rejected.

In addition to the arid corridor hypothesis, the expansion of open-grasslands and the presence of mountain refugia are two factors that may also explain Miocene diversification in Africa (Strömberg, 2011). The grassland expansion hypothesis considers that the appearance of novel types of open-grasslands, such as savannahs, drove diversification during the Miocene in Africa (Strömberg, 2011). Members of the *Trachylepis varia* complex occur in a wide variety of grass-dominated ecosystems, including arid and mesic savannahs, montane grasslands, and grassland-forest mosaics (Branch, 1998; Spawls et al., 2004; Largen and Spawls, 2010), suggesting that grassland expansion could have been an important driver of diversification in this group. Alternatively, the mountain refugia hypothesis considers that warming temperatures shifted populations to higher elevations where they became isolated and eventually speciated. Three of the four oldest lineages in the *T. varia* complex (clades A, F, and H) are occur in the highland regions of northeastern South Africa, suggesting a possible role for mountain refugia during the earliest divergence events of the *T. varia* complex. However, the *Lygodactylus ocellatus* complex is a rupicolous group, whereas the *Trachylepis varia* complex is a grassland-adapted group, and, therefore, it may be more appropriate to compare the evolutionary history of the *Trachylepis varia* complex to those of other grassland lizards (e.g., *Chamaesaura* or *Tetradactylus*), but, at present, little is known about the evolutionary history of other grassland-specialist lizards that co-occur with *Trachylepis varia* group. Furthermore, future studies that reconstruct Miocene climates and ecosystems may be able to infer the relative influence of different ecological and climactic factors on diversification in the *T. varia* complex.

5. Systematics

5.1. Prelude

Three of the eight major *Trachylepis varia* clades recovered in this study occur in southern Africa and will be discussed in greater detail below. Nevertheless, it is worth briefly mentioning that clade B, which occurs primarily in Angola and Zambia, likely corresponds to either one or both of two taxa previously described by Bocage (1867, 1872). Namely, *Trachylepis albopunctatus* (Bocage, 1867) and *Trachylepis angolensis* (Bocage, 1872) both likely correspond to clade B. The name *angolensis* is also sometimes used for a different, poorly understood species, *Trachylepis angolensis* (Monard, 1937) that is likely closely related to *Trachylepis striata*. Unfortunately, Bocage's type specimens of *T. albopunctatus* and *T. angolensis* were lost in the 1978 fire that destroyed most of the zoology collection of the Museu Nacional de História Natural e da Ciência, Lisbon, and neotypes will likely need to be chosen to stabilize the taxonomy of this group (Almaça, 1993). The taxonomy of Angolan *Trachylepis* will be reviewed in a forthcoming paper. The following systematic sections (Sections 5.2–5.4) focus on the primarily southern African members of the *T. varia* species complex: *Trachylepis varia* (Peters, 1867), *Trachylepis laevigata* (Peters, 1869), and *Trachylepis damarana* (Peters, 1870).

5.2. *Trachylepis varia* (Peters, 1867)

Euprepes varius Peters, 1867

Lectotype: ZMB 64341 (Fig. 9) here designated. *Type locality:* "Tette" [Tete, Mozambique, ca. −16.145S, 33.61E]. *Distribution in southern Africa:* eastern South Africa, eastern and southern Zimbabwe, Malawi, and Mozambique; possibly southeastern Botswana (Fig. 6).

Description: A medium-sized skink (max. SVL 66 mm, TM 57625) with fully developed, pentadactyl limbs; dorsal scales tricarinate; ventral scales smooth; 46–55 gular + ventral scales before the row of anal scales; 31–36 scale rows around midbody; lamellae beneath fingers and toes keeled and spinose; scales on palms and soles spinose; 18–23 lamellae beneath the fourth toe; supranasals in contact or separated; parietals in contact or separated; prefrontals usually separated, rarely in slight contact; one pair of enlarged nuchal scales present; ear opening vertically ovoid and smaller than the eye; 2–4 subtriangular auricular scales (shorter than the diameter of ear) extend posteriorly and usually slightly upwards from the anterior margin of the ear opening; anterior margin of the second loreal scale is longer or slightly shorter than the ventral margin.

Comparisons: This species is most likely to be confused with *Trachylepis damarana*, *Trachylepis laevigata*, or *Trachylepis variegata*, but can usually be distinguishable from these species based on color pattern or lepidosis. In *T. damarana*, the relative length of the ventral margin of the second loreal scale is usually much longer than in *T. varia*, whereas the relative length of the anterior margin of the second loreal is usually longer in *T. varia* than in *T. damarana*. *Trachylepis laevigata* has thin, dark longitudinal stripes on the dorsum that begin a few scale rows behind the nuchal scales, whereas the region behind the nuchal scales is usually uniformly colored (without stripes and matching the dorsal color of the head) in *T. varia*. *Trachylepis variegata* has the nostrils situated anterior to the rostrolabial suture, whereas *T. varia* has the nostrils situated in line with or posterior to the rostrolabial suture. Furthermore, the nostrils are situated more dorsally in *T. variegata* compared to *T. varia*. Furthermore, *T. variegata* frequently lacks a pale lateral stripe and often occurs in arid habitats (including deserts), whereas *T. varia* virtually always has a pale lateral stripe and is found in grassland-dominated habitats.

Remarks: The syntype series of *Euprepes varius* Peters, 1867 includes three individuals: ZMB 1231, ZMB 64341 (formerly ZMB 1231a), and ZMB 64342 (formerly ZMB 1231b), but is likely composed of individuals from both clade A and clade F. The compound nature of the type series and the recognition of the distinctiveness of several other taxa previously considered as synonyms of *T. varia* require the designation of a lectotype in order to stabilize the application of names to members of the species complex as a whole. We chose ZMB 64341 as the lectotype because this individual has a head shape that falls within the morphospace of clade F, whereas ZMB 64342 and ZMB 1231 head shapes fall within the morphospace of clade A. Consequently, we do not treat ZMB 64342 or ZMB 1231 as paralectotypes. Fixing the name *Euprepes varius* to clade F leaves the name *Euprepes damaranus* available for clade A and avoids the necessity of establishing a new name.

5.3. *Trachylepis laevigata* (Peters, 1869)

Euprepes laevigatus Peters, 1869

Fig. 8. Holotype of *Trachylepis laevigata* (ZMB 6224) (Photo Frank Tillack).

Holotype: ZMB 6224 (Fig. 8) here designated. *Type locality:* "Gerlachshoop" [25.2S, 29.4E, Limpopo Province, South Africa]. *Distribution:* presently only known from the type locality and from the Waterberg Massif, South Africa, but may occur elsewhere (Fig. 6).

Description: A medium-sized skink with fully developed, pentadactyl limbs; tricarinate dorsal scales; smooth ventral scales; 32 scale rows around midbody; keeled and spinose lamellae beneath fingers and toes; scales on palms and soles spinose; 19–21 lamellae beneath the fourth toe; supranasals in contact; parietals in contact; prefrontals separated; one pair of enlarged nuchal scales; ear opening vertically ovoid and smaller than the eye; three subtriangular auricular scales (shorter than the diameter of ear) extend posteriorly from the anterior margin of the ear; seven thin, dark longitudinal stripes begin within five scale rows behind the nuchal scales and extend posteriorly to the base of the tail.

Comparisons: Within its range, this species is most likely to be confused with *Trachylepis varia* or *Trachylepis damarana*, but differs from these species primarily in color pattern. The presence of dark longitudinal dorsal stripes beginning within five scale rows behind the nuchal scales and extending onto the base of the tail is characteristic of *T. laevigata* but not *T. varia* or *T. damarana*.

Remarks: Morphological and geographic distribution data suggest that *Euprepes laevigatus* Peters, 1869, corresponds to Clade H of the

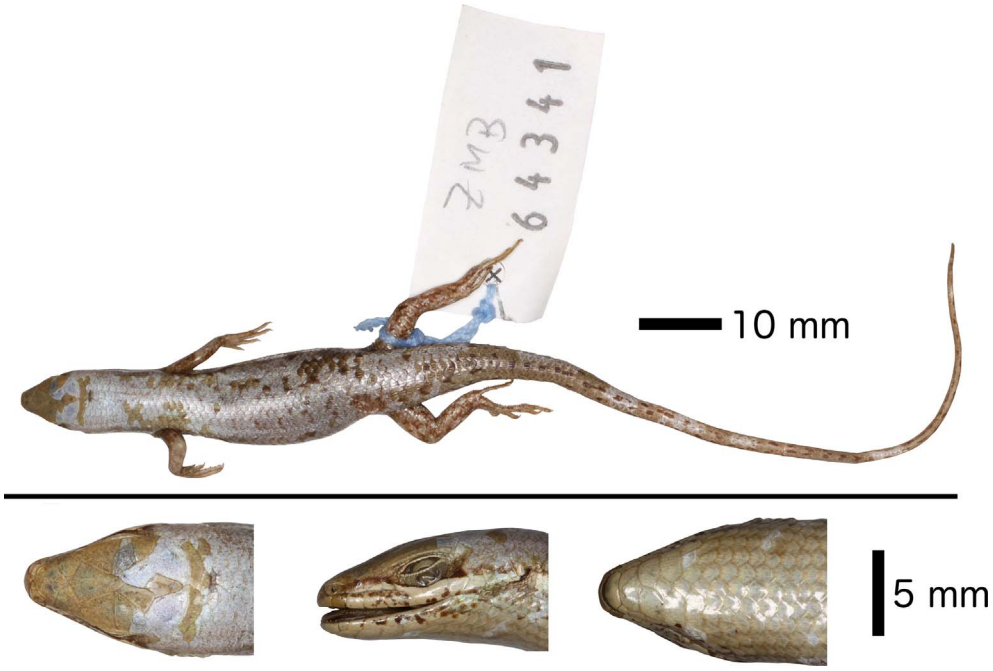

Fig. 9. Lectotype of *Trachylepis varia* (ZMB 64341) (Photo Frank Tillack).

Trachylepis varia complex. Although *T. laevigata* can be distinguished from the other members of the *T. varia* complex based on color pattern, the members of the *T. varia* complex are nevertheless similar in appearance, and, therefore, a lectotype must be chosen for *T. laevigata* to ensure taxonomic stability within the *T. varia* complex as a whole. Phylogenetic data suggest that clade H shared a common ancestor with the rest of the *T. varia* complex 17–12 Ma, which strong supports the hypothesis that clade H is a distinct species. Although clade H is phenotypically similar to other members of the *varia* complex, it has a more olive-bluish coloration, especially on the supralabials, and it also has a relatively long frontal scale, three auricular scales, and feebly tricarinate dorsal scales (becoming smooth laterally). Additionally, clade H has dark longitudinal stripes between each dorsal scale row, beginning just behind the nuchal scales and extending onto the tail, whereas other clades of the *T. varia* complex either lack dark longitudinal stripes on the dorsum or have dark longitudinal stripes beginning near the insertion of the forelimbs and extending to the tail. The *E. laevigatus* holotype (ZMB 6224) agrees in color pattern and in morphology with the individuals genetically assigned to clade H. Additionally, the type locality of *E. laevigatus* is relatively close (~150 km) to where the DNA sequenced clade H individuals were collected. Therefore, we formally resurrect the name *Euprepes laevigatus* Peters, 1869, as *Trachylepis laevigata*, for clade H.

5.4. *Trachylepis damarana* (Peters, 1870)

Euprepes damaranus Peters, 1870

Lectotype: ZMB 6153 (Fig. 7) here designated. *Type locality:* "Damaraland" [north-central Namibia]. *Distribution:* northern Namibia, southeastern Angola, northern and eastern Botswana, Zimbabwe, northeastern South Africa, and western Mozambique (Fig. 6).

Description: A medium-sized skink (max. SVL 67.7 mm, CAS 248617) with fully developed, pentadactyl limbs; tricarinate dorsal scales; smooth ventral scales; lamellae beneath fingers and toes keeled and spinose; scales on palms and soles spinose; 19–26 lamellae beneath the fourth toe; 30–34 scale rows around midbody; 46–56 ventral + gular scales before the row of anal scales; supranasals usually in contact, rarely separated; parietals in contact or separated; prefrontals usually separated, rarely in slight contact; one pair of enlarged nuchal scales; ear opening vertically ovoid and smaller than the eye; 2–4 subtriangular auricular scales (shorter than the diameter of ear) extend posteriorly and usually slightly downwards from the anterior margin of the ear opening; ventral margin of the second loreal scale is much longer than the anterior margin.

Comparisons: This species is most likely to be confused with *Trachylepis varia* sensu stricto, *Trachylepis laevigata*, *Trachylepis variegata*, and *Trachylepis bayonii*, but usually differs from these taxa in several ways. *Trachylepis damarana* is sympatric with *T. varia* in northeastern South Africa, western Mozambique, and possibly southern Botswana, where it can usually be distinguished from *T. varia* by having a relatively longer second loreal scale. *Trachylepis laevigata* has thin, dark longitudinal stripes between each of the medial six dorsal scale rows and these stripes begin within a few scales rows behind the nuchal scales, whereas in *T. damarana*, the first 10 dorsal scale rows behind the nuchal scales are uniformly colored and of the same color as the dorsal surface of the head. *Trachylepis damarana* differs from *T. variegata* in the position of the nostril, which is even with or posterior to the rostrolabial suture in *T. damarana* and is anterior to the rostrolabial suture in *T. variegata*; the nostrils are also situated more dorsally in *T. variegata* compared to *T. damarana*, which have the nostrils situated more laterally. *Trachylepis damarana* has keeled subdigital lamellae and paired frontoparietal scales, whereas *T. bayonii* has smooth or tuberculose subdigital lamellae and usually has a single frontoparietal scale.

Remarks: The syntype series of *Euprepes damaranus* Peters, 1870 includes two individuals: ZMB 6135 and NRM 2149. We were only able to examine individual ZMB 6135, which corresponds to clade A (Fig. 2) of the *T. varia* species complex (see remarks in Section 5.2). Although *T. damarana* are morphologically distinct from the other members of the *T. varia* complex, the differences are subtle, which requires us to designate a lectotype (ZMB 6153) for *T. damarana* to ensure taxonomic stability within the *T. varia* complex as a whole. We did not examine the other syntype of *Euprepes damaranus* (i.e., NRM 2149), and, therefore, we do not designate this individual as a paralectotype of *Trachylepis damarana*. Additionally, *T. damarana* should not be confused with *Mabuya damarana rhodesiana* Broadley, 1960, which is a synonym of *Trachylepis lacertiformis* (Peters, 1954), following Broadley (1975, 2000).

6. Conclusions

We find strong evidence that *Trachylepis varia*, *T. damarana*, and *T. laevigata* are distinct species that occur in southern Africa and that five additional, species-level clades occur north of the Zambezi and Kunene rivers, although future studies are needed to determine whether *Trachylepis nyikae* and *Trachylepis isellii* should also be recognized. The allopatric distribution and morphological distinctiveness of *T. isellii* (Largen and Spawls, 2010) suggests that this species is probably valid and the presence of multiple endemic species on the Nyika Plateau (Poynton, 1997; Burrows and Willis, 2005) suggests that *T. nyikae* may also be a valid species. Additionally, little is known about the distribution or natural history of the undescribed species sampled in Ethiopia, Democratic Republic of the Congo, or Tanzania. Lastly, next generation DNA sequencing may be useful in resolving deeper phylogenetic relationships within the *T. varia* complex and for distinguishing historical gene flow from incomplete lineage sorting. This study is the first to use genetic data to address species diversity, phylogenetic history, and taxonomic issues for the *T. varia* complex and is an example of how both genetic and phenotypic data can be used to resolve taxonomic problems and to estimate species ranges.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ympev.2017.11.014.

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