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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 Bayâo 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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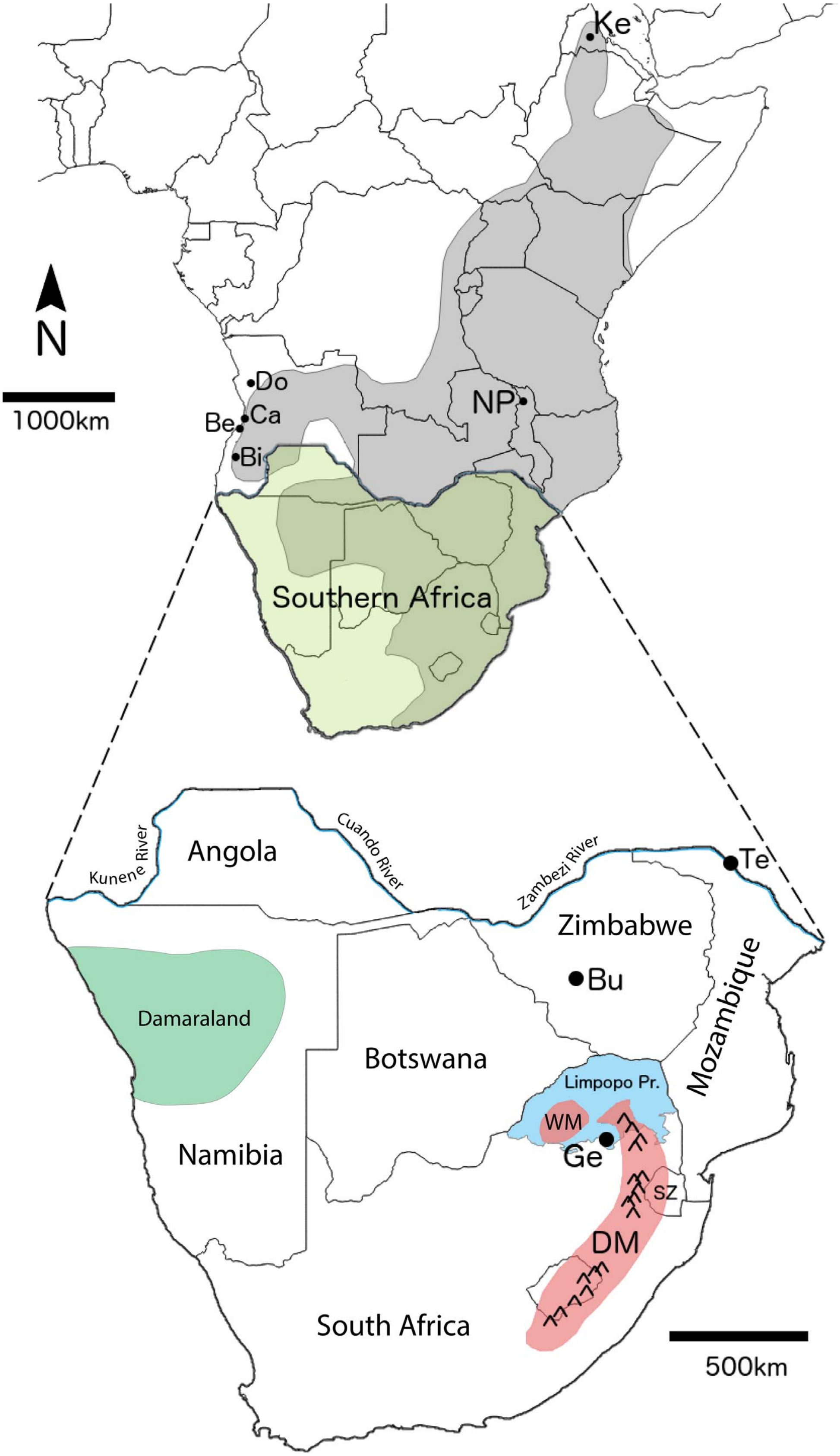

Fig. 1. Map of the study area. Gray shading indicates the distribution of the *Trachylepis varia* complex, based on occurrences reported by Bates et al. (2014), Broadley (1966), Jacobsen (1989), Largen and Spawls (2010), Parker (1942), Pietersen et al. (2013), Pietersen (2014), Spawls et al. (2004), 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:

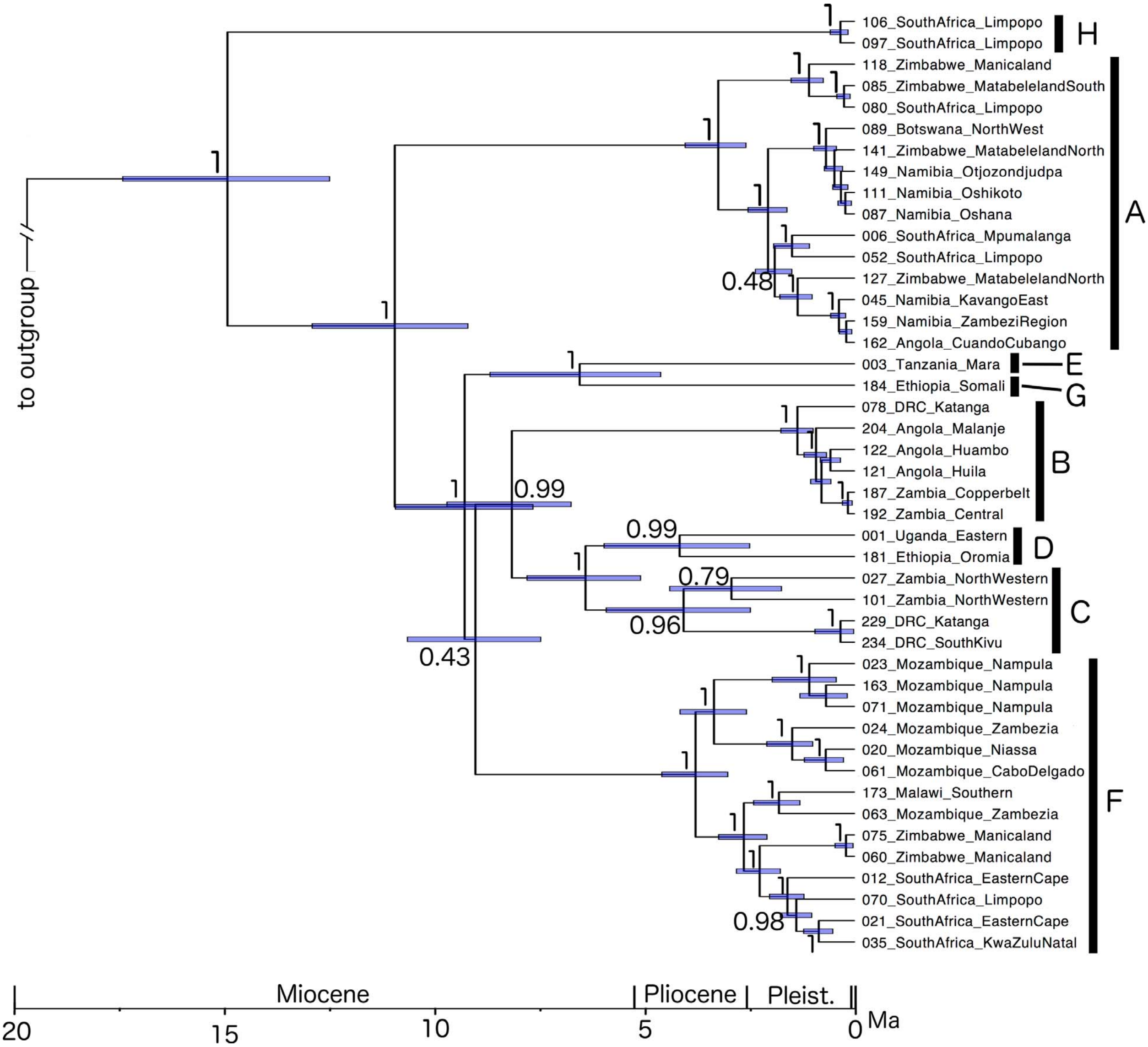

Fig. 2. Multilocus time-tree of the *Trachylepis varia* complex. Major clades (A–H) are indicated to the right of black vertical after tip names. Values at internal nodes are posterior probabilities. Shallow, unlabeled nodes have low (PP < 0.95) support. ID numbers shown at tips correspond to those shown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

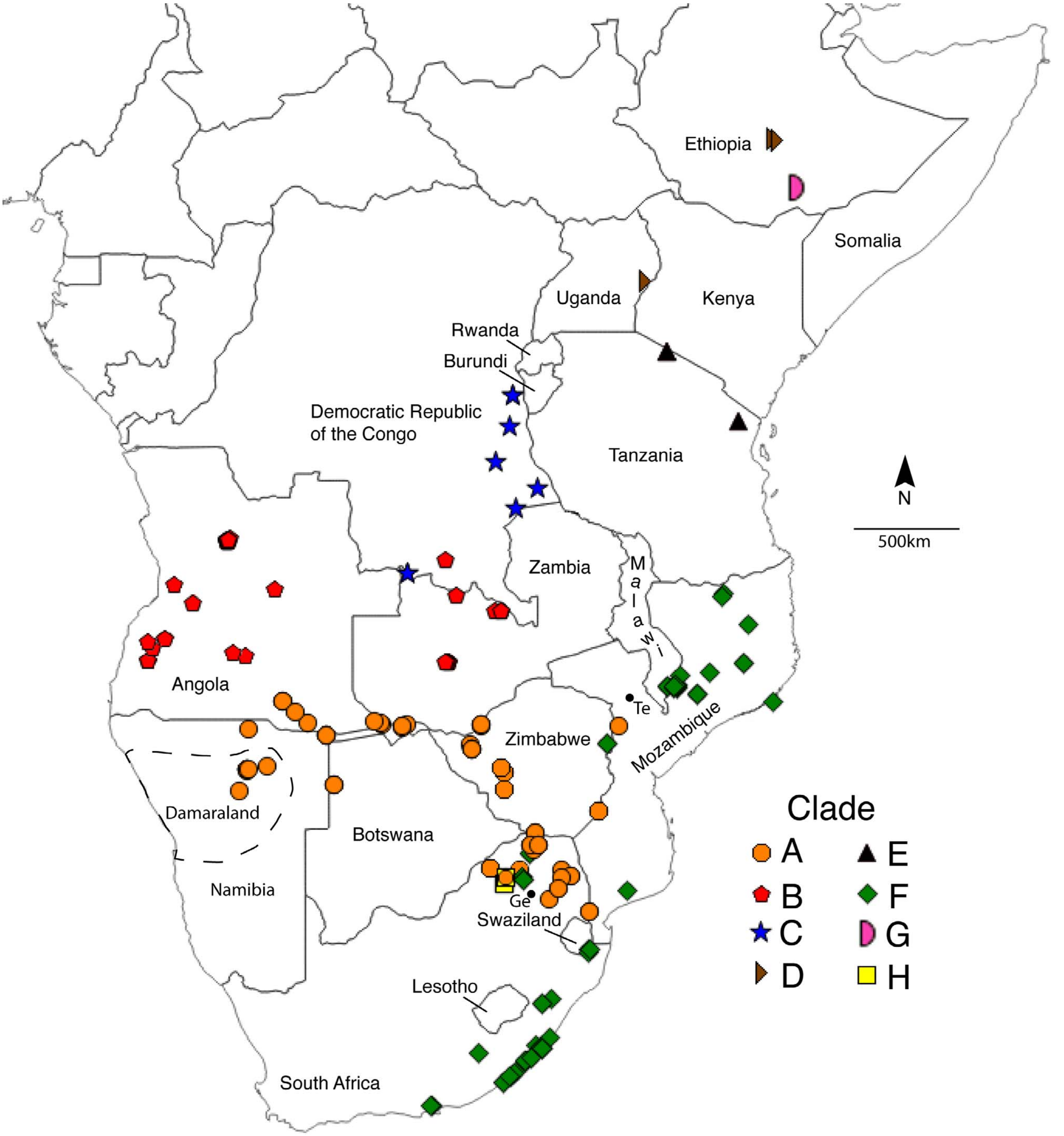

Fig. 3. Distribution of major clades of the *Trachylepis varia* complex. Clade A (orange circles; = *Trachylepis damarana*), clade B (red pentagons), clade C (blue stars), clade D (brown right-pointing triangles), clade E (black upwards-pointing triangles), clade F (green diamonds; = *Trachylepis varia* 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 *X* = 0.143 n = 38	0.074–0.116 *X* = 0.094 n = 38	0.184–0.229 *X* = 0.207 n = 40	0.12–0.159 *X* = 0.14 n = 40	0.091–0.109 *X* = 0.099 n = 44	0.377–0.655 *X* = 0.467 n = 40	0.010–0.016 *X* = 0.012 n = 40	0.018–0.031 *X* = 0.024 n = 40
C	0.111–0.142 *X* = 0.127 n = 3	0.068–0.082 *X* = 0.078 n = 3	0.191–0.233 *X* = 0.212 n = 3	0.137–0.151 *X* = 0.143 n = 3	0.099–0.109 *X* = 0.105 n = 3	0.438–0.569 *X* = 0.510 n = 3	0.014–0.015 *X* = 0.014 n = 3	0.016–0.022 *X* = 0.019 n = 3
D	0.109–0.151 *X* = 0.134 n = 3	0.080–0.099 *X* = 0.090 n = 3	0.183–0.249 *X* = 0.217 n = 4	0.126–0.150 *X* = 0.142 n = 4	0.090–0.110 *X* = 0.096 n = 4	0.460–0.521 *X* = 0.489 n = 4	0.014–0.019 *X* = 0.016 n = 4	0.011–0.018 *X* = 0.015 n = 4
F	0.118–0.143 *X* = 0.129 n = 6	0.076–0.085 *X* = 0.081 n = 6	0.183–0.203 *X* = 0.195 n = 6	0.125–0.139 *X* = 0.132 n = 6	0.092–0.100 *X* = 0.096 n = 6	0.476–0.555 *X* = 0.506 n = 6	0.011–0.017 *X* = 0.014 n = 6	0.016–0.022 *X* = 0.019 n = 6
H	0.134–0.151 *X* = 0.143 n = 2	0.083–0.096 *X* = 0.090 n = 2	0.198–0.221 *X* = 0.209 n = 2	0.142–0.143 *X* = 0.143 n = 2	0.093–0.097 *X* = 0.095 n = 2	0.454–0.522 *X* = 0.488 n = 2	0.013–0.018 *X* = 0.015 n = 2	0.017–0.020 *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 *X* = 32.2; n = 43	46–56 *X* = 51; n = 41	4–6 *X* = 4.98; n = 44	4–5 *X* = 4.3; n = 44	2–4 *X* = 2.61; n = 23	2/36	19–25.5 *X* = 21.9; n = 40	42/44	23/44
B	–	–	4–6 *X* = 5.11; n = 9	4–5 *X* = 4.67; n = 9	3–4 *X* = 3.44; n = 9	9/9	19–20 *X* = 19.4; n = 9	1/8	5/9
C	34–36 *X* = 34.7; n = 3	52–61 *X* = 56; n = 3	5–6 *X* = 5.33; n = 3	4–5 *X* = 4.33; n = 3	3 n = 1	1/2	20.5–21.5 *X* = 21; n = 3	2/3	2/3
D	32–34 *X* = 33; n = 2	51–55 *X* = 53; n = 2	4–5 *X* = 4.67; n = 3	4–5 *X* = 4.5; n = 4	2 n = 1	–	18–19 *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 *X* = 32.9; n = 9	46–55 *X* = 51.8; n = 4	4–6 *X* = 4.92; n = 12	4–5 *X* = 4.14; n = 11	2–4 *X* = 2.5; n = 4	5/5	18.5–22.5 *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 *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

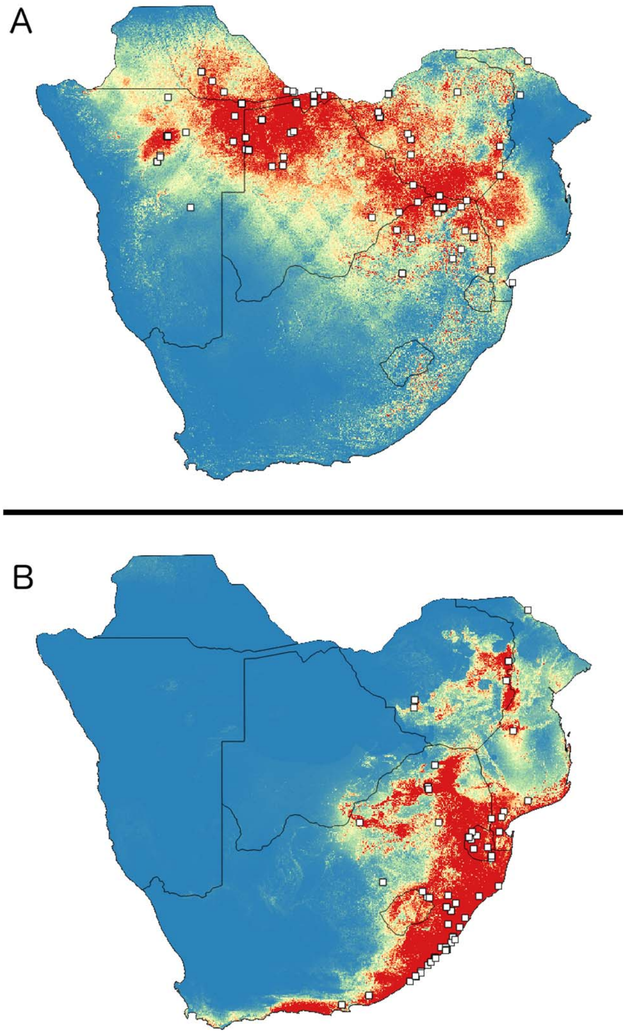

Fig. 4. Present day maximum entropy niche models for (A) clade A and (B) clade F of the *Trachylepis varia* complex. White squares indicate localities used for model training. Warmer colors indicate areas with higher predicted habitat suitability. (For interpretation of the references to colour in this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

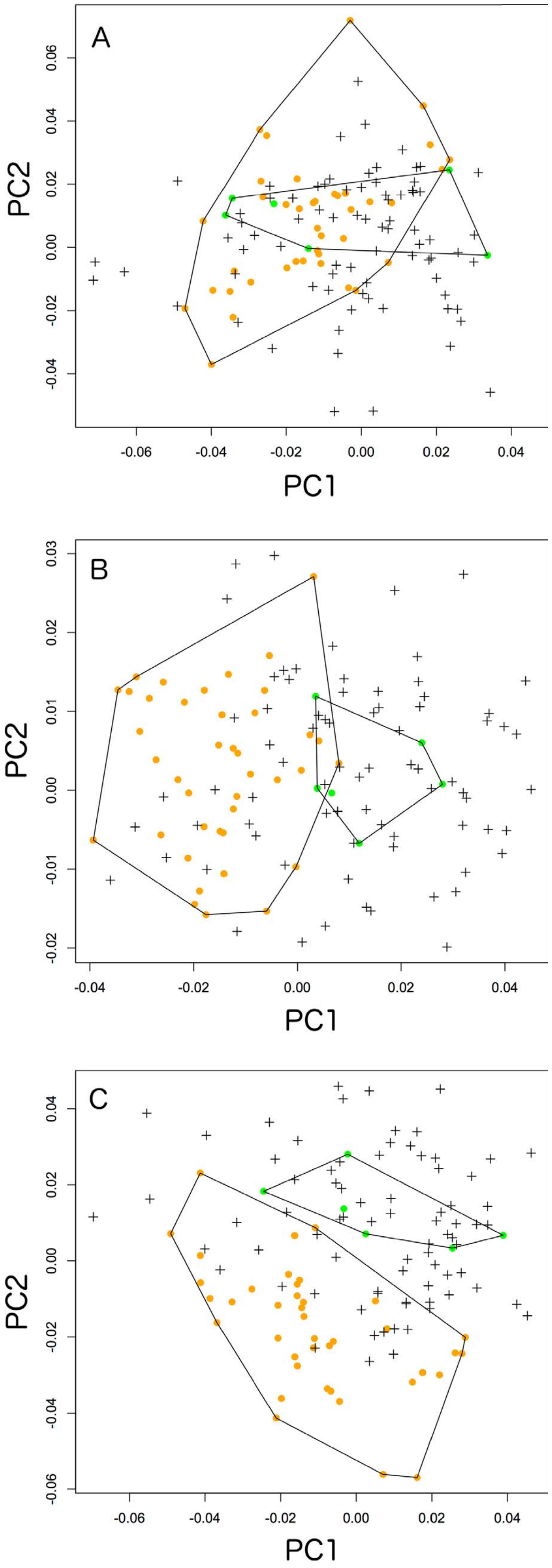

Fig. 5. Biplots of first and second principle components of two-dimensional head shape for clades A (orange) and F (green) of the *Trachylepis varia* complex. (A) Lateral view head shape; (B) dorsal view head shape, (C) combined lateral + dorsal PCA of head shape. (For interpretation of the references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

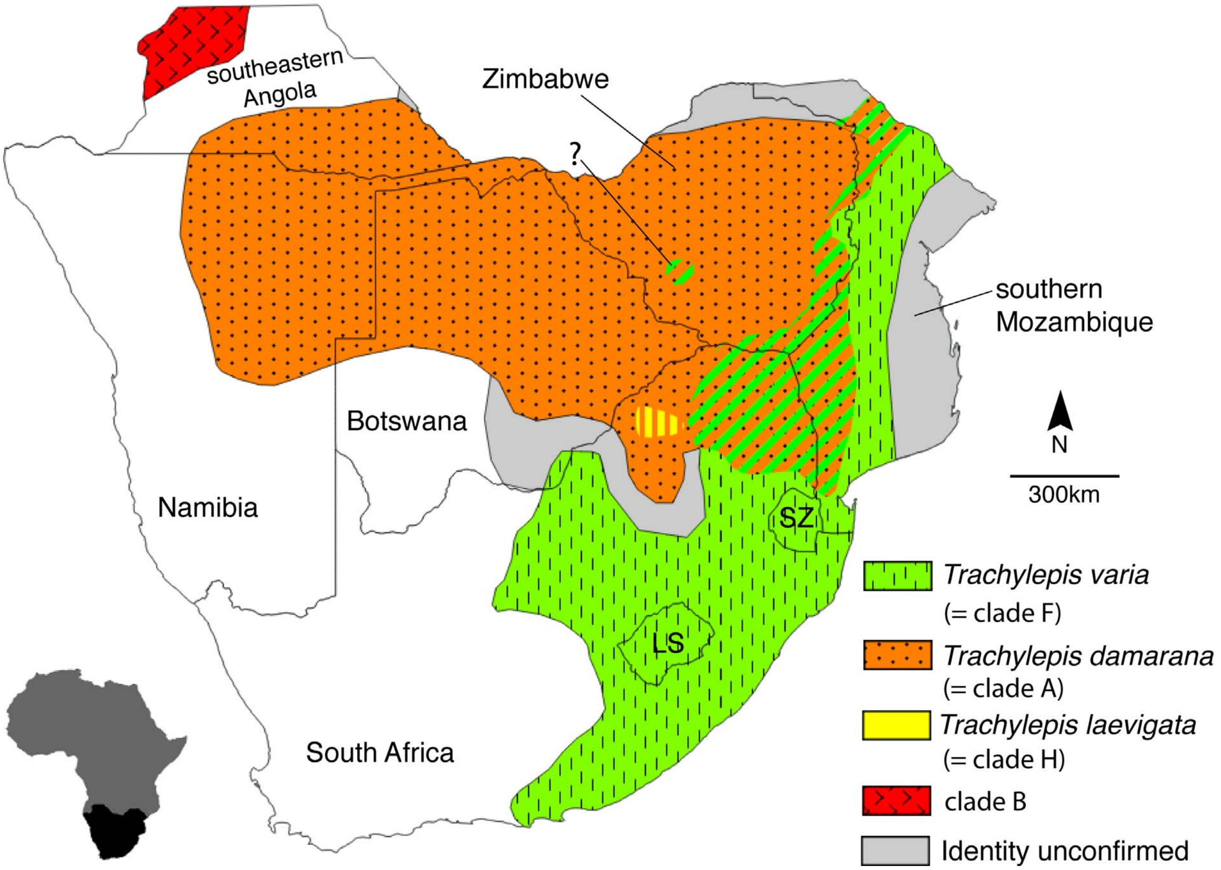

Fig. 6. Distribution of *Trachylepis damarana*, *Trachylepis laevigata*, *Trachylepis varia*, and clade B in southern Africa. Swaziland (SZ); Lesotho (LS).

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

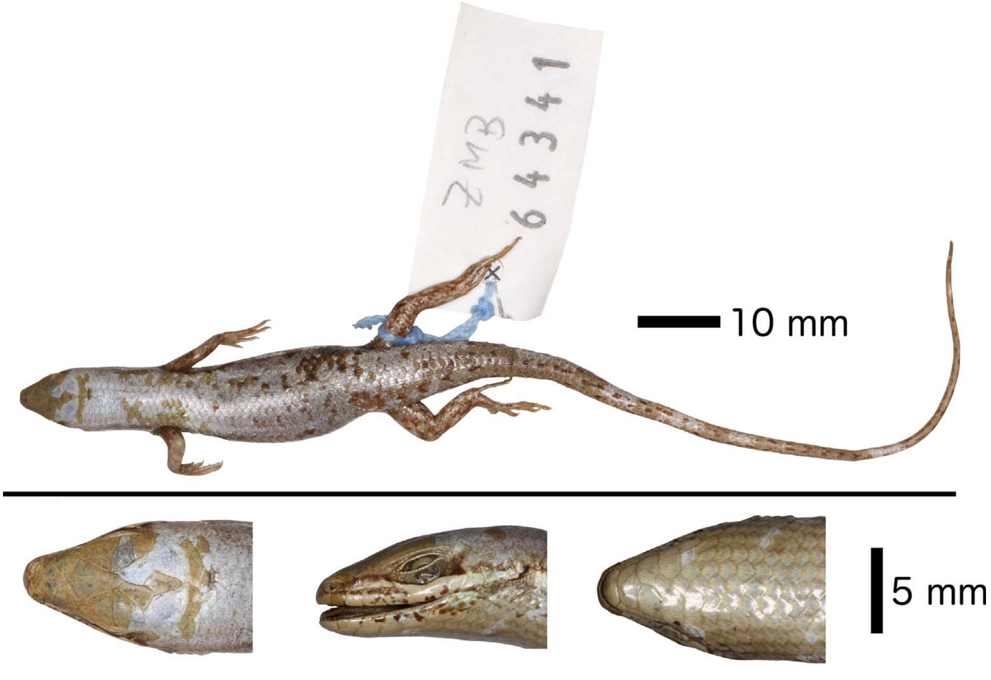

Fig. 9. Lectotype of *Trachylepis varia* (ZMB 64341) (Photo Frank Tillack).

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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Table S1. Polymerase chain reaction (PCR) and sequencing (Seq.) primers used in this study.

Locus	**Primer Name**	**Primer Sequence**	**Direction & Type**
16S	[6]16sA-L	CGCCTGTTTATCAAAAACAT	forward (PCR & Seq.)
16S	[6]16sB-H	CCGGTCTGAACTCAGATCACGT	reverse (PCR & Seq.)
ND2	[4]MetF1	AAGCTTTCGGGCCCATACC	forward (PCR & Seq.
ND2	[1]COIR1	AGRGTGCCAATGTCTTTGTGRTT	reverse (PCR & Seq.)
ND2	[2]TrpR3a	TTTAGGGCTTTGAAGGC	reverse (Seq.)
KIF24	[5]KIF24F1	SAAACGTRTCTCCMAAACGCATCC	forward (PCR & Seq.)
KIF24	[7]Kif24R1zebra	GCTGCTGRARCTGGTGATAAAGRCG	reverse (PCR & Seq.)
RAG1	[5]RAG1skinkF2	TTCAAAGTGAGATCGCTTGAAA	forward (PCR & Seq.)
RAG1	[5]RAG1skinkR1200	CCCTTCTTCTTTCTCAGCAAAA	reverse (PCR & Seq.)
RAG1	[5]RAG1skinkF370	GCCAAGGTTTTTAAGATTGACG	forward (Seq.)
RAG1	[5]RAG1skinkR2	AACATCACAGCTTGATGAATGG	reverse (Seq.)
BRCA2	[3]Skink984F	AACAGGTAGTCAGTTTGAMTTYACAC	forward (PCR & Seq.)
BRCA2	[3]Skink2315R	RTTGAAGYYTGAATGCYAGGTTTGAC	reverse (PCR & Seq.)

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Table S2. Genbank numbers for sequences generated or used in this study.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Chioninia delalandii	BMNH2000.18	—	KX231461	MG605667	KX231532	KX231373	KX231519
Trachylepis cf. *varia* clade B	AMB9329	191	MG605284	MG605656	—	MG605381	—
Trachylepis cf. *varia* clade B	CAS258377	211	MG605292	—	—	MG605388	MG605450
Trachylepis cf. *varia* clade B	CAS258378	212	MG605293	—	—	MG605389	CAS258378
Trachylepis cf. *varia* clade B	CAS258379	213	MG605294	—	—	MG605390	MG605452
Trachylepis cf. *varia* clade B	CAS258382	216	MG605295	—	—	MG605391	MG605453
Trachylepis cf. *varia* clade B	CAS258385	218	MG605296	—	—	MG605392	MG605454
Trachylepis cf. *varia* clade B	CAS258386	219	MG605297	—	—	MG605393	MG605455
Trachylepis cf. *varia* clade B	CAS258389	222	MG605298	—	—	MG605394	MG605456
Trachylepis cf. *varia* clade B	CAS258390	224	MG605300	—	—	MG605396	MG605458
Trachylepis cf. *varia* clade B	CAS258392	226	MG605301	—	—	MG605397	MG605459
Trachylepis cf. *varia* clade B	CAS258393	228	MG605303	—	—	MG605399	MG605460
Trachylepis cf. *varia* clade B	DQ234811	38	—	DQ234811	—	—	—
Trachylepis cf. *varia* clade B	JVV9091	209	MG605291	—	—	—	MG605449
Trachylepis cf. *varia* clade B	JVV9174	204	MG605289	MG605660	MG605521	MG605386	—
Trachylepis cf. *varia* clade B	JVV9212	205	MG605290	—	—	MG605387	MG605448
Trachylepis cf. *varia* clade B	JVV9305	223	MG605299	—	—	MG605395	MG605457
Trachylepis cf. *varia* clade B	JVV9449	227	MG605302	—	—	MG605398	—
Trachylepis cf. *varia* clade B	MCZR193550	186	MG605279	MG605651	—	MG605376	—
Trachylepis cf. *varia* clade B	MCZR193582	189	MG605282	MG605654	—	MG605379	—

Table S2 *continued*.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Trachylepis cf. *varia* clade B	MCZR193588	190	MG605283	MG605655	—	MG605380	—
Trachylepis cf. *varia* clade B	MCZR193589	192	MG605285	MG605657	—	MG605382	MG605447
Trachylepis cf. *varia* clade B	MCZR193590	193	MG605286	MG605658	—	MG605383	—
Trachylepis cf. *varia* clade B	MCZR193591	194	MG605287	—	—	MG605384	—
Trachylepis cf. *varia* clade B	MCZR193592	195	MG605288	MG605659	—	MG605385	—
Trachylepis cf. *varia* clade B	MCZR193788	188	MG605281	MG605653	—	MG605378	MG605446
Trachylepis cf. *varia* clade B	MCZR193901	187	MG605280	MG605652	—	MG605377	MG605445
Trachylepis cf. *varia* clade B	PEMR17447	78	GU931597	MG605587	MG605485	GU931666	GU931528
Trachylepis cf. *varia* clade B	PEMR17940	77	—	MG605586	—	—	—
Trachylepis cf. *varia* clade B	WC1809	121	MG605224	MG605608	MG605496	MG605366	—
Trachylepis cf. *varia* clade B	WC1832	122	MG605225	MG605609	MG605497	MG605367	MG605435
Trachylepis cf. *varia* clade B	WC1838	84	MG605205	—	—	—	MG605427
Trachylepis cf. *varia* clade B	WRB0020	113	MG605218	MG605604	—	—	—
Trachylepis cf. *varia* clade C	MB20429	25	—	MG605545	—	—	—
Trachylepis cf. *varia* clade C	MB20430	26	—	MG605546	—	—	—
Trachylepis cf. *varia* clade C	EBG2256	229	—	MG605661	—	—	—
Trachylepis cf. *varia* clade C	EBG2893	232	—	MG605664	—	—	—
Trachylepis cf. *varia* clade C	ELI61	231	—	MG605663	—	—	—
Trachylepis cf. *varia* clade C	ELI378	230	—	MG605662	—	—	—
Trachylepis cf. *varia* clade C	ELI712	233	—	MG605665	—	—	—

Table S2 *continued*.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Trachylepis cf. *varia* clade C	ELI713	234	—	MG605666	—	—	—
Trachylepis cf. *varia* clade C	PW7	101	—	MG605595	MG605490	MG605359	MG605431
Trachylepis cf. *varia* clade C	PW88	27	MG605168	MG605547	—	—	MG605407
Trachylepis cf. *varia* clade D	AMNHR145452	79	—	MG605588	—	—	—
Trachylepis cf. *varia* clade D	TJC1335	181	MG605275	MG605647	MG605519	MG605373	MG605442
Trachylepis cf. *varia* clade D	TJC1336	182	MG605276	MG605648	MG605520	MG605374	—
Trachylepis cf. *varia* clade D	TJC1337	183	MG605277	MG605649	—	—	MG605443
Trachylepis cf. *varia* clade D	ZFMK66631	1	—	AF153571	—	—	—
Trachylepis cf. *varia* clade E	PEMR16789	28	—	MG605548	—	MG605323	—
Trachylepis cf. *varia* clade E	PEMR16768	3	—	MG605525	—	MG605308	MG605403
Trachylepis cf. *varia* clade G	TJC1409	184	MG605278	MG605650	—	MG605375	MG605444
Trachylepis damarana	AMB8337	94	—	—	—	MG605355	—
Trachylepis damarana	AMB8737	109	—	MG605600	MG605493	—	—
Trachylepis damarana	AMB8738	110	MG605215	MG605601	—	—	—
Trachylepis damarana	AMB8739	8	MG605160	MG605528	—	MG605310	—
Trachylepis damarana	AMB8928	112	MG605217	MG605603	—	—	—
Trachylepis damarana	CAS234102	47	MG605177	MG605564	—	—	MG605413
Trachylepis damarana	CAS234126	65	MG605194	MG605576	—	MG605342	—
Trachylepis damarana	CAS234133	41	MG605174	MG605558	—	MG605326	MG605411

Table S2 *continued*.

Species	Catalog #	ID# at tree tips	ND2	16S	BRCA2	RAG1	KIF24
Trachylepis damarana	CAS234154	155	MG605255	—	—	—	—
Trachylepis damarana	CAS234158	91	MG605207	—	—	MG605353	MG605429
Trachylepis damarana	CAS234159	50	MG605180	MG605567	—	MG605332	—
Trachylepis damarana	CAS234215	80	MG605204	MG605589	MG605486	MG605349	MG605425
Trachylepis damarana	CAS248329	124	MG605226	MG605610	—	—	—
Trachylepis damarana	CAS248617	55	MG605185	MG605572	MG605476	MG605337	—
Trachylepis damarana	CAS248757	54	MG605184	MG605571	—	MG605336	—
Trachylepis damarana	CAS248760	53	MG605183	MG605570	—	MG605335	—
Trachylepis damarana	JM1720	52	MG605182	MG605569	MG605463	MG605334	MG605415
Trachylepis damarana	JM1721	51	MG605181	MG605568	—	MG605333	—
Trachylepis damarana	Mab98	42	—	MG605559	—	—	—
Trachylepis damarana	MCZA27892	85	MG605206	—	MG605487	MG605352	MG605428
Trachylepis damarana	MCZA28787	148	MG605249	—	—	—	—
Trachylepis damarana	MCZA28791	151	MG605252	MG605624	—	—	—
Trachylepis damarana	MCZR184437	49	MG605179	MG605566	—	MG605306	MG605414
Trachylepis damarana	MCZR184438	48	MG605178	MG605565	—	MG605331	—
Trachylepis damarana	MCZR184449	44	—	MG605561	—	MG605328	—
Trachylepis damarana	MCZR184450	93	MG605208	—	—	MG605354	—
Trachylepis damarana	MCZR184452	98	—	—	—	MG605358	—

Table S2 *continued*.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Trachylepis damarana	MCZR184460	95	MG605209	—	—	MG605356	—
Trachylepis damarana	MCZR184873	87	GU931604	MG605592	MG605488	GU931671	GU931535
Trachylepis damarana	MCZR188205	107	MG605213	MG605598	—	MG605362	—
Trachylepis damarana	MCZR188206	45	MG605175	MG605562	MG605475	MG605329	MG605412
Trachylepis damarana	MCZR188207	108	MG605214	MG605599	MG605492	MG605363	—
Trachylepis damarana	MCZR188225	111	MG605216	MG605602	MG605494	MG605364	MG605433
Trachylepis damarana	MCZR190185	104	MG605211	MG605596	—	MG605360	—
Trachylepis damarana	MCZR190378	133	MG605235	—	—	—	—
Trachylepis damarana	MCZR190412	134	MG605236	—	—	—	—
Trachylepis damarana	MCZR190414	135	MG605237	—	—	—	—
Trachylepis damarana	MCZR190451	136	MG605238	MG605615	—	—	—
Trachylepis damarana	MCZR190457	137	MG605239	MG605616	—	—	—
Trachylepis damarana	MCZR190462	138	MG605240	MG605617	—	—	—
Trachylepis damarana	MCZR190487	74	MG605202	MG605584	—	—	—
Trachylepis damarana	MCZR190488	139	MG605241	MG605618	—	—	—
Trachylepis damarana	MCZR190489	140	MG605242	MG605619	—	—	—
Trachylepis damarana	MCZR190490	141	MG605243	MG605620	MG605499	—	MG605437
Trachylepis damarana	MCZR190491	142	MG605244	MG605621	—	—	—
Trachylepis damarana	MCZR190492	143	MG605245	—	—	—	—
Trachylepis damarana	MCZR190504	72	MG605200	MG605582	—	—	MG605423

Table S2 *continued*.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Trachylepis damarana	MCZR190538	126	MG605228	MG605612	—	—	—
Trachylepis damarana	MCZR190539	127	MG605229	MG605613	MG605498	—	MG605436
Trachylepis damarana	MCZR190540	128	MG605230	MG605614	—	—	—
Trachylepis damarana	MCZR190569	125	MG605227	MG605611	—	—	—
Trachylepis damarana	MCZR193225	145	MG605246	—	—	—	—
Trachylepis damarana	MCZR193227	146	MG605247	—	MG605500	—	—
Trachylepis damarana	MCZR193228	147	MG605248	—	—	—	—
Trachylepis damarana	MCZR193241	149	MG605250	MG605622	MG605501	MG605368	MG605438
Trachylepis damarana	MCZR193243	150	MG605251	MG605623	—	—	—
Trachylepis damarana	MCZR193244	152	MG605253	MG605625	—	—	—
Trachylepis damarana	MCZR193255	153	MG605254	MG605626	—	—	—
Trachylepis damarana	NMZB17900	118	MG605222	MG605607	MG605495	MG605365	MG605434
Trachylepis damarana	NMZB17909	119	MG605223	—	—	—	—
Trachylepis damarana	PEMR17361	43	—	MG605560	—	MG605327	—
Trachylepis damarana	PEMR17574	6	MG605159	MG605527	MG605464	MG605309	MG605402
Trachylepis damarana	PEMR17575	46	MG605176	MG605560	—	MG605330	—
Trachylepis damarana	PEMR20508	56	MG605186	MG605573	MG605477	MG605338	—
Trachylepis damarana	PEMR20509	62	MG605192	MG605575	MG605480	—	MG605419
Trachylepis damarana	PEMR20510	161	MG605258	MG605628	—	—	—
Trachylepis damarana	PEMR20511	159	MG605256	MG605627	MG605502	MG605369	—

Table S2 *continued*.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Trachylepis damarana	PEMR20512	73	MG605201	MG605583	—	MG605347	—
Trachylepis damarana	PEMR20514	162	MG605259	MG605629	MG605503	MG605370	MG605439
Trachylepis damarana	PEMR20515	68	MG605196	MG605578	—	MG605344	—
Trachylepis damarana	PEMR20516	57	MG605187	MG605574	—	MG605339	—
Trachylepis damarana	TNHC68769	89	GU931603	MG605593	—	GU931670	GU931534
Trachylepis damarana	TNHC68770	90	GU931601	—	—	GU931669	GU931532
Trachylepis damarana	TNHC68771	88	GU931602	—	—	GU931668	GU931533
Trachylepis damarana	WCANG322	67	MG605195	MG605577	—	MG605343	—
Trachylepis damarana	WCANG362	160	MG605257	—	—	—	—
Trachylepis damarana	ZFMK68413	7	—	AF153584	—	—	—
Trachylepis hoeschi	MCZR184257	—	MG605305	MG605668	—	MG605401	MG605462
Trachylepis laevigata	MCZR184495	106	MG605212	MG605597	MG605491	MG605361	MG605432
Trachylepis laevigata	MCZR184536	97	MG605210	MG605594	MG605489	MG605357	MG605430
Trachylepis megalura	CAS258401	—	MG605304	MG605669	MG605522	MG605400	MG605461
Trachylepis varia	CAS234199	81	—	MG605590	—	MG605350	—
Trachylepis varia	CAS234208	82	—	MG605591	—	MG605351	MG605426
Trachylepis varia	CAS248607	70	MG605198	MG605580	MG605482	MG605345	MG605421
Trachylepis varia	CAS248611	69	MG605197	MG605579	—	—	—
Trachylepis varia	DGB737	75	MG605203	MG605585	MG605484	MG605348	MG605424
Trachylepis varia	DGB738	60	MG605190	—	—	MG605340	—

Table S2 *continued*.

Species	Catalog #	ID# at tree tips	ND2	16S	BRCA2	RAG1	KIF24
Trachylepis varia	JM1600	36	MG605172	MG605556	—	—	—
Trachylepis varia	JM1602	35	MG605171	MG605555	MG605473	MG605324	MG605410
Trachylepis varia	LIZARD#2	116	MG605220	MG605605	—	—	—
Trachylepis varia	LIZARD#4	117	MG605221	MG605606	—	—	—
Trachylepis varia	Mab91	19	—	MG605539	—	MG605318	—
Trachylepis varia	Mab193	31	MG605169	MG605551	—	—	—
Trachylepis varia	Mab198	32	—	MG605552	—	—	—
Trachylepis varia	Mab199	30	—	MG605550	—	—	MG605409
Trachylepis varia	MCZR190354	129	MG605231	—	—	—	—
Trachylepis varia	MCZR190356	130	MG605232	—	—	—	—
Trachylepis varia	MCZR190368	131	MG605233	—	—	—	—
Trachylepis varia	MCZR190369	132	MG605234	—	—	—	—
Trachylepis varia	NAMULI1	24	MG605167	MG605544	MG605471	MG605322	MG605406
Trachylepis varia	PEMR5413	21	MG605166	MG605541	MG605470	MG605320	—
Trachylepis varia	PEMR5418	34	—	MG605554	—	—	—
Trachylepis varia	PEMR5542	20	MG605165	MG605540	MG605469	MG605319	MG605405
Trachylepis varia	PEMR9708	4	—	MG605526	—	—	—
Trachylepis varia	PEMR9761	18	—	MG605538	—	—	—
Trachylepis varia	PEMR12205	17	—	MG605537	—	MG605317	—
Trachylepis varia	PEMR15544	22	—	MG605542	—	MG605321	—

Table S2 *continued*.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Trachylepis varia	PEMR15639	23	—	MG605543	—	—	—
Trachylepis varia	PEMR16197	13	—	MG605533	—	—	—
Trachylepis varia	PEMR16636	37	—	MG605557	—	—	—
Trachylepis varia	Uncataloged	2	MG605158	MG605524	—	MG605307	—
Trachylepis varia	PEMR17478	15	—	MG605535	—	—	—
Trachylepis varia	PEMR17589	11	MG605163	MG605531	MG605467	MG605313	MG605404
Trachylepis varia	PEMR17592	9	MG605161	MG605529	MG605465	MG605311	—
Trachylepis varia	PEMR17743	10	MG605162	MG605530	MG605466	MG605312	—
Trachylepis varia	PEMR18537	176	MG605270	—	MG605515	—	—
Trachylepis varia	PEMR18538	173	MG605268	MG605640	MG605512	MG605371	MG605440
Trachylepis varia	PEMR19158	178	MG605272	MG605644	—	—	MG605441
Trachylepis varia	PEMR19159	177	MG605271	MG605643	MG605516	—	—
Trachylepis varia	PEMR19160	180	MG605274	MG605646	MG605518	—	—
Trachylepis varia	PEMR19161	179	MG605273	MG605645	MG605517	—	—
Trachylepis varia	PEMR19428	165	MG605260	MG605632	MG605504	—	—
Trachylepis varia	PEMR19434	166	MG605261	MG605633	MG605505	—	—
Trachylepis varia	PEMR19452	167	MG605262	MG605634	MG605506	—	—
Trachylepis varia	PEMR19788	40	MG605173	—	MG605474	MG605325	—
Trachylepis varia	PEMR19801	164	—	MG605631	—	—	—
Trachylepis varia	PEMR19875	168	MG605263	MG605635	MG605507	—	—

Table S2 *continued*.

Species	**Catalog #**	**ID# at tree tips**	**ND2**	**16S**	**BRCA2**	**RAG1**	**KIF24**
Trachylepis varia	PEMR19876	169	MG605264	MG605636	MG605508	—	—
Trachylepis varia	PEMR20149	171	MG605266	MG605638	MG605510	—	—
Trachylepis varia	PEMR20150	58	MG605188	—	—	—	MG605416
Trachylepis varia	PEMR20206	59	MG605189	—	MG605478	—	MG605417
Trachylepis varia	PEMR20207	172	MG605267	MG605639	MG605511	—	—
Trachylepis varia	PEMR20250	175	MG605269	MG605642	MG605514	—	—
Trachylepis varia	PEMR20301	170	MG605265	MG605637	MG605509	—	—
Trachylepis varia	PEMR20302	12	MG605164	MG605532	MG605468	MG605314	—
Trachylepis varia	PEMR20363	14	—	MG605534	—	MG605315	—
Trachylepis varia	PEMR20364	16	—	MG605536	—	MG605316	—
Trachylepis varia	PEMR20366	29	—	MG605549	—	—	MG605408
Trachylepis varia	WCDNA1020	71	MG605199	MG605581	MG605483	MG605346	MG605422
Trachylepis varia	WCDNA1058	61	MG605191	—	MG605479	—	MG605418
Trachylepis varia	WCDNA1123	163	—	MG605630	—	—	—
Trachylepis varia	WCQQ0645	174	—	MG605641	MG605513	MG605372	—
Trachylepis varia	WRB0029	33	MG605170	MG605553	MG605472	—	—
Trachylepis varia	WRB0030-MM3	63	MG605193	—	MG605481	MG605341	MG605420
Trachylepis varia	WRB0030-MM4	114	MG605219	—	—	—	—

Catalog number	ID number (at tree tips)	Species	DNA	Morphology	Country	Lat.	Lon.
ZFMK66631	1	*Trachylepis* cf. *varia* clade D	yes	no	UG	1.167	34.53
Uncataloged	2	*Trachylepis varia*					
PEMR16768	3	*Trachylepis* cf. *varia* clade E	yes	yes	TZ	-1.85	35.3
PEMR9708	4	*Trachylepis varia*	yes	no	ZA	-31.16	29.75
PEMR17574	6	*Trachylepis damarana*	yes	no	ZA	-25.48	31.97
ZFMK68413	7	*Trachylepis damarana*	yes	no	NA	-20.42	17.23
AMB8739	8	*Trachylepis damarana*	yes	no	NA	-18.03	20.86
PEMR17592	9	*Trachylepis varia*	yes	no	ZA	-27.10	31.98
PEMR17743	10	*Trachylepis varia*	yes	no	ZA	-27.20	31.98
PEMR17589	11	*Trachylepis varia*	yes	no	ZA	-27.10	31.99
PEMR20302	12	*Trachylepis varia*	yes	no	ZA	-32.48	28.65
PEMR16197	13	*Trachylepis varia*	yes	no	MZ	-12.09	37.67
PEMR20363	14	*Trachylepis varia*	yes	no	MW	-16.03	35.65
PEMR17478	15	*Trachylepis varia*	yes	no	MW	-15.97	35.53
PEMR20364	16	*Trachylepis varia*	yes	no	MW	-15.99	35.56
PEMR12205	17	*Trachylepis varia*	yes	no	MW	-16.03	35.65
PEMR9761	18	*Trachylepis varia*	yes	no	MW	-16.02	35.3
Mab91	19	*Trachylepis varia*	yes	no	MW	-15.96	35.65
PEMR5542	20	*Trachylepis varia*	yes	yes	MZ	-12.18	37.55
PEMR5413	21	*Trachylepis varia*	yes	no	ZA	-31.19	29.94

PEMR15544	22	*Trachylepis varia*	yes	no	MZ	-24.63	33.60
PEMR15639	23	*Trachylepis varia*	yes	yes	MZ	-16.6	39.7
NAMULI1	24	*Trachylepis varia*	yes	no	MZ	-15.37	37.03
MB20429	25	*Trachylepis* cf. *varia* clade C	yes	no	ZM	—	—
MB20430	26	*Trachylepis* cf. *varia* clade C	yes	no	ZM	—	—
PW88	27	*Trachylepis* cf. *varia* clade C	yes	no	ZM	-11.236	24.272
PEMR16789	28	*Trachylepis* cf. *varia* clade E	yes	no	TZ	-1.836	35.259
PEMR20366	29	*Trachylepis varia*	yes	no	MW	-15.938	35.670
Mab199	30	*Trachylepis varia*	yes	no	MW	-16.017	35.3
Mab193	31	*Trachylepis varia*	yes	no	MW	-15.89	35.698
Mab198	32	*Trachylepis varia*	yes	no	MW	-16.017	35.3
WRB0029	33	*Trachylepis varia*	yes	no	MZ	-16.29	36.51
PEMR5418	34	*Trachylepis varia*	yes	no	ZA	-29.209	30.402
JM1602	35	*Trachylepis varia*	yes	no	ZA	-29.369	29.974
JM1600	36	*Trachylepis varia*	yes	no	ZA	-29.369	29.974
PEMR16636	37	*Trachylepis varia*	yes	no	ZA	-30.837	30.347
DQ234811	38	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-12.169	26.392
PEMR19788	40	*Trachylepis varia*	yes	no	ZA	-32.246	28.849
CAS234133	41	*Trachylepis damarana*	yes	yes	ZA	-22.7	29.8
Mab98	42	*Trachylepis damarana*	yes	no	MZ	-17.669	33.255
PEMR17361	43	*Trachylepis damarana*	yes	no	ZA	-22.687	29.8
MCZR184449	44	*Trachylepis damarana*	yes	yes	ZA	-22.705	29.828
MCZR188206	45	*Trachylepis damarana*	yes	yes	NAM	-18	20.9

PEMR17575	46	*Trachylepis damarana*	yes	no	ZA	-25.477	31.971
CAS234102	47	*Trachylepis damarana*	yes	yes	ZA	-23.7	30.8
MCZR184438	48	*Trachylepis damarana*	yes	yes	ZA	-25	30.3
MCZR184437	49	*Trachylepis damarana*	yes	yes	ZA	-24.5	30.6
CAS234159	50	*Trachylepis damarana*	yes	yes	ZA	-21.7	28.5
JM1721	51	*Trachylepis damarana*	yes	no	ZA	-22.170	29.673
JM1720	52	*Trachylepis damarana*	yes	no	ZA	-22.170	29.673
CAS248760	53	*Trachylepis damarana*	yes	yes	ZA	-24	31.2
CAS248757	54	*Trachylepis damarana*	yes	yes	ZA	-24	31.2
CAS248617	55	*Trachylepis damarana*	yes	yes	ZA	-22.7	29.8
PEMR20508	56	*Trachylepis damarana*	yes	no	AO	-16.623	19.054
PEMR20516	57	*Trachylepis damarana*	yes	no	AO	-17.573	23.227
PEMR20150	58	*Trachylepis varia*	yes	no	ZA	-31.653	29.508
PEMR20206	59	*Trachylepis varia*	yes	no	ZA	-33.715	25.315
DGB738	60	*Trachylepis varia*	yes	no	ZW	-18.431	32.763
WCDNA1058	61	*Trachylepis varia*	yes	no	MZ	-13.345	38.690
PEMR20509	62	*Trachylepis damarana*	yes	no	AO	-16.623	19.054
WRB0030-MM3	63	*Trachylepis varia*	yes	no	MZ	-16.29	36.51
CAS234126	65	*Trachylepis damarana*	yes	yes	ZA	-22.672	29.496
WCANG322	67	*Trachylepis damarana*	yes	no	AO	-17.512	20.060
PEMR20515	68	*Trachylepis damarana*	yes	no	AO	-17.496	23.134
CAS248611	69	*Trachylepis varia*	yes	yes	ZA	-24.1	29.2
CAS248607	70	*Trachylepis varia*	yes	yes	ZA	-24.1	29.2
WCDNA1020	71	*Trachylepis varia*	yes	no	MZ	-14.98	38.505
MCZR190504	72	*Trachylepis damarana*	yes	yes	ZW	-18.4	26.9
PEMR20512	73	*Trachylepis damarana*	yes	no	NAM	-17.678	24.074
MCZR190487	74	*Trachylepis damarana*	yes	yes	ZW	-18.6	27
DGB737	75	*Trachylepis varia*	yes	no	ZW	-18.431	32.763

PEMR17940	77	*Trachylepis* cf. *varia* clade B	yes	no	AO	-14.927	13.336
PEMR17447	78	*Trachylepis* cf. *varia* clade B	yes	no	DRC	-10.650	25.927
AMNHR145452	79	*Trachylepis* cf. *varia* clade D	yes	yes	ET	7.14	39.9
CAS234215	80	*Trachylepis damarana*	yes	yes	ZA	-23.7	29
CAS234199	81	*Trachylepis varia*	yes	yes	ZA	-23	29.4
CAS234208	82	*Trachylepis varia*	yes	yes	ZA	-23	29.4
WC1838	84	*Trachylepis* cf. *varia* clade B	yes	no	AO	-13.972	14.047
MCZA27892	85	*Trachylepis damarana*	yes	no	ZW	-20.331	28.379
MCZR184873	87	*Trachylepis damarana*	yes	yes	NAM	-17.8	17.6
TNHC68771	88	*Trachylepis damarana*	yes	no	BW	-20.133	21.167
TNHC68769	89	*Trachylepis damarana*	yes	no	BW	-20.133	21.167
TNHC68770	90	*Trachylepis damarana*	yes	no	BW	-20.133	21.167
CAS234158	91	*Trachylepis damarana*	yes	yes	ZA	-22.9	29.6
MCZR184450	93	*Trachylepis damarana*	yes	yes	ZA	-22.7	29.8
AMB8337	94	*Trachylepis damarana*	yes	no	ZA	—	—
MCZR184460	95	*Trachylepis damarana*	yes	yes	ZA	-22.7	29.5
MCZR184536	97	*Trachylepis laevigata*	yes	yes	ZA	-24.3	28.4
MCZR184452	98	*Trachylepis damarana*	yes	yes	ZA	-22.7	29.8
PW7	101	*Trachylepis* cf. *varia* clade C	yes	no	ZM	-11.236	24.272
MCZR190185	104	*Trachylepis damarana*	yes	yes	NAM	-18	20.9
MCZR184495	106	*Trachylepis laevigata*	yes	yes	ZA	-24.1	28.4
MCZR188205	107	*Trachylepis damarana*	yes	yes	NAM	-17.567	24.265
MCZR188207	108	*Trachylepis damarana*	yes	yes	NAM	-18.035	20.861

AMB8737	109	*Trachylepis damarana*	yes	no	NAM	-18.035	20.861
AMB8738	110	*Trachylepis damarana*	yes	no	NAM	-18.035	20.861
MCZR188225	111	*Trachylepis damarana*	yes	yes	NAM	-19.325	18.391
AMB8928	112	*Trachylepis damarana*	yes	no	NAM	-17.687	24.062
WRB0020	113	*Trachylepis* cf. *varia* clade B	yes	no	AO	-14.916	13.374
WRB0030-MM4	114	*Trachylepis varia*	yes	no	MZ	-16.29	36.51
LIZARD#2	116	*Trachylepis varia*	yes	no	—	—	—
LIZARD#4	117	*Trachylepis varia*	yes	no	MW	-15.550	35.833
NMZB17900	118	*Trachylepis damarana*	yes	no	ZW	-21.250	32.351
NMZB17909	119	*Trachylepis damarana*	yes	no	ZW	-21.250	32.351
WC1809	121	*Trachylepis* cf. *varia* clade B	yes	no	AO	-13.972	14.047
WC1832	122	*Trachylepis* cf. *varia* clade B	yes	no	AO	-12.503	15.225
CAS248329	124	*Trachylepis damarana*	yes	yes	ZA	-24.1	28.4
MCZR190569	125	*Trachylepis damarana*	yes	yes	ZW	-17.6	27.4
MCZR190538	126	*Trachylepis damarana*	yes	yes	ZW	-17.6	27.4
MCZR190539	127	*Trachylepis damarana*	yes	yes	ZW	-17.6	27.4
MCZR190540	128	*Trachylepis damarana*	yes	yes	ZW	-17.6	27.4
MCZR190354	129	*Trachylepis varia*	yes	yes	ZA	-24	29.1
MCZR190356	130	*Trachylepis varia*	yes	yes	ZA	-24	29.1
MCZR190368	131	*Trachylepis varia*	yes	yes	ZA	-24.1	29.2
MCZR190369	132	*Trachylepis varia*	yes	yes	ZA	-24.1	29.2
MCZR190378	133	*Trachylepis damarana*	yes	yes	ZA	-23.7	27.8
MCZR190412	134	*Trachylepis damarana*	yes	yes	ZA	-24	30.8
MCZR190414	135	*Trachylepis damarana*	yes	yes	ZA	-24.5	30.6
MCZR190451	136	*Trachylepis damarana*	yes	yes	ZW	-19.6	28.4

MCZR190457	137	*Trachylepis damarana*	yes	yes	ZW	-19.6	28.4
MCZR190462	138	*Trachylepis damarana*	yes	yes	ZW	-19.410	28.245
MCZR190488	139	*Trachylepis damarana*	yes	yes	ZW	-18.6	27
MCZR190489	140	*Trachylepis damarana*	yes	yes	ZW	-18.6	27
MCZR190490	141	*Trachylepis damarana*	yes	yes	ZW	-18.6	27
MCZR190491	142	*Trachylepis damarana*	yes	yes	ZW	-18.6	27
MCZR190492	143	*Trachylepis damarana*	yes	yes	ZW	-18.6	27
MCZR190508	144	*Trachylepis damarana*	yes	yes	ZW	-18.4	26.9
MCZR193225	145	*Trachylepis damarana*	yes	yes	NAM	-19.5	17.6
MCZR193227	146	*Trachylepis damarana*	yes	yes	NAM	-19.5	17.6
MCZR193228	147	*Trachylepis damarana*	yes	yes	NAM	-19.5	17.6
MCZA28787	148	*Trachylepis damarana*	yes	no	NAM	-19.496	17.559
MCZR193241	149	*Trachylepis damarana*	yes	yes	NAM	-19.5	17.6
MCZR193243	150	*Trachylepis damarana*	yes	yes	NAM	-19.5	17.6
MCZA28791	151	*Trachylepis damarana*	yes	no	NAM	-19.496	17.559
MCZR193244	152	*Trachylepis damarana*	yes	yes	NAM	-19.5	17.6
MCZR193255	153	*Trachylepis damarana*	yes	no	NAM	-19.504	17.571
CAS234154	155	*Trachylepis damarana*	yes	yes	ZA	-22.7	29.8
PEMR20511	159	*Trachylepis damarana*	yes	no	NAM	-17.678	24.074
WCANG362	160	*Trachylepis damarana*	yes	no	AO	-16.623	19.054
PEMR20510	161	*Trachylepis damarana*	yes	no	AO	-17.049	19.534
PEMR20514	162	*Trachylepis damarana*	yes	no	AO	-17.463	22.866
WCDNA1123	163	*Trachylepis varia*	yes	no	MZ	-14.98	38.505
PEMR19801	164	*Trachylepis varia*	yes	no	ZA	-32.310	28.827
PEMR19428	165	*Trachylepis varia*	yes	no	ZA	-31.825	29.303
PEMR19434	166	*Trachylepis varia*	yes	no	ZA	-31.823	29.308
PEMR19452	167	*Trachylepis varia*	yes	no	ZA	-31.821	29.298
PEMR19875	168	*Trachylepis varia*	yes	no	ZA	-32.701	28.359

PEMR19876	169	*Trachylepis varia*	yes	no	ZA	-32.701	28.359
PEMR20301	170	*Trachylepis varia*	yes	no	ZA	-32.441	28.604
PEMR20149	171	*Trachylepis varia*	yes	no	ZA	-31.660	29.499
PEMR20207	172	*Trachylepis varia*	yes	no	ZA	-33.72	25.314
PEMR18538	173	*Trachylepis varia*	yes	yes	MW	-15.9	35.6
WCQQ0645	174	*Trachylepis varia*	yes	no	MZ	—	—
PEMR20250	175	*Trachylepis varia*	yes	no	MW	-16.019	35.519
PEMR18537	176	*Trachylepis varia*	yes	no	MW	-15.979	35.555
PEMR19159	177	*Trachylepis varia*	yes	no	ZA	-31.304	29.992
PEMR19158	178	*Trachylepis varia*	yes	no	ZA	-31.269	30.014
PEMR19161	179	*Trachylepis varia*	yes	no	ZA	-31.277	29.988
PEMR19160	180	*Trachylepis varia*	yes	no	ZA	-31.315	29.966
TJC1335	181	*Trachylepis* cf. *varia* clade D	yes	yes	ET	7.08	40.2
TJC1336	182	*Trachylepis* cf. *varia* clade D	yes	yes	ET	7.08	40.2
TJC1337	183	*Trachylepis* cf. *varia* clade D	yes	yes	ET	7.08	40.2
TJC1409	184	*Trachylepis* cf. *varia* clade G	yes	no	ET	5.16865	40.503
MCZR193550	186	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-12.808	28.244
MCZR193901	187	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-12.808	28.244
MCZR193788	188	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-12.829	27.991
MCZR193582	189	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-12.808	28.244

MCZR193588	190	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-14.985	26.023
AMB9329	191	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-14.985	26.023
MCZR193589	192	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-14.994	26.020
MCZR193590	193	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-14.994	26.020
MCZR193591	194	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-14.973	25.994
MCZR193592	195	*Trachylepis* cf. *varia* clade B	yes	no	ZM	-14.961	25.928
JVV9174	204	*Trachylepis* cf. *varia* clade B	yes	no	AO	-9.855	16.710
JVV9212	205	*Trachylepis* cf. *varia* clade B	yes	no	AO	-9.845	16.721
JVV9091	209	*Trachylepis* cf. *varia* clade B	yes	no	AO	-9.819	16.655
CAS258377	211	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.869	16.691
CAS258378	212	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.855	16.710
CAS258379	213	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.8546	16.710
CAS258382	216	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.8446	16.721
CAS258385	218	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.873	16.701

CAS258386	219	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.850	16.679
CAS258389	222	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.828	16.667
JVV9305	223	*Trachylepis* cf. *varia* clade B	yes	no	AO	-9.821	16.667
CAS258390	224	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.759	16.802
CAS258392	226	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.812	16.691
JVV9449	227	*Trachylepis* cf. *varia* clade B	yes	no	AO	-9.786	16.765
CAS258393	228	*Trachylepis* cf. *varia* clade B	yes	yes	AO	-9.776	16.755
EBG2256	229	*Trachylepis* cf. *varia* clade C	yes	no	DRC	-5.03	28.6
ELI378	230	*Trachylepis* cf. *varia* clade C	yes	no	DRC	-6.51	28
ELI61	231	*Trachylepis* cf. *varia* clade C	yes	yes	DRC	-8.48	28.9
EBG2893	232	*Trachylepis* cf. *varia* clade C	yes	yes	DRC	-7.62	29.8
ELI712	233	*Trachylepis* cf. *varia* clade C	yes	no	DRC	-3.7	28.7
ELI713	234	*Trachylepis* cf. *varia* clade C	yes	yes	DRC	-3.7	28.7
PEMR21820	235	*Trachylepis* cf. *varia* clade B	yes	no	AO	-11.59	18.47

PEMR21821	236	*Trachylepis* cf. *varia* clade B	yes	no	AO	-11.59	18.47
PEMR21824	237	*Trachylepis* cf. *varia* clade B	yes	no	AO	-11.59	18.47
PEMR21823	239	*Trachylepis* cf. *varia* clade B	yes	no	AO	-11.59	18.47
PEMR21841	241	*Trachylepis* cf. *varia* clade B	yes	no	AO	-14.70	17.38
PEMR21825	242	*Trachylepis* cf. *varia* clade B	yes	no	AO	-14.59	16.91
AG13	243	*Trachylepis* cf. *varia* clade B	yes	no	AO	-14.54	13.524
AG37	244	*Trachylepis* cf. *varia* clade B	yes	no	AO	-14.21	13.406
PEMR21814	245	*Trachylepis* cf. *varia* clade B	yes	no	AO	-11.73	14.449
MCZR184257	—	*Trachylepis hoeschi*	yes	no	NAM	-20.78	14.08
BMNH2000.18	—	*Chioninia delalandii*	yes	no	—	—	—
CAS258401	—	*Trachylepis megalura*	yes	no	AO	-9.846	16.722
CAS234198	—	*Trachylepis* cf. *varia*	no	yes	ZA	-23	29.4
PEMR15640	—	*Trachylepis* cf. *varia*	no	yes	MZ	-16.6	39.7
DFH217	—	*Trachylepis* cf. *varia*	no	yes	UG	2.51	34.7
TM21536	—	*Trachylepis damarana*	no	yes	ZW	-17.536	30.456
TM66966	—	*Trachylepis* cf. *varia*	no	yes	BW	-24.200	26.200
TM47578	—	*Trachylepis* cf. *varia*	no	yes	BW	-21.174	27.512
TM41460	—	*Trachylepis* cf. *varia*	no	yes	BW	-23.341	24.501
TM27321	—	*Trachylepis varia*	no	yes	ZA	-28.283	27.160
TM64931	—	*Trachylepis damarana*	no	yes	BW	-22.883	27.867

TM64932	—	*Trachylepis* cf. *varia*	no	yes	BW	-22.883	27.867
TM79697	—	*Trachylepis damarana*	no	yes	BW	-23.117	26.667
TM62688	—	*Trachylepis damarana*	no	yes	ZA	-22.567	30.85
TM62689	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.567	30.85
TM62692	—	*Trachylepis damarana*	no	yes	ZA	-22.367	30.883
TM78585	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.2	29.817
TM78596	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.567	30.85
TM78600	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.417	30.867
TM18622	—	*Trachylepis damarana*	no	yes	ZW	-19.946	32.370
TM85075	—	*Trachylepis* cf. *varia*	no	yes	ZA	-25.690	28.117
TM82396	—	*Trachylepis damarana*	no	yes	ZA	-25.614	28.025
TM82397	—	*Trachylepis damarana*	no	yes	ZA	-25.614	28.025
TM82398	—	*Trachylepis* cf. *varia*	no	yes	ZA	-24.732	28.274
TM82400	—	*Trachylepis* cf. *varia*	no	yes	ZA	-24.732	28.274
TM82401	—	*Trachylepis damarana*	no	yes	ZA	-25.614	28.025
TM82403	—	*Trachylepis* cf. *varia*	no	yes	ZA	-24.281	31.302
TM82404	—	*Trachylepis* cf. *varia*	no	yes	ZA	-24.281	31.302
TM82407	—	*Trachylepis* cf. *varia*	no	yes	ZA	-25.614	28.025
TM42880	—	*Trachylepis damarana*	no	yes	BW	-22.423	28.704
TM1839	—	*Trachylepis* cf. *varia*	no	yes	ZA	-26.909	27.467
TM39343	—	*Trachylepis* cf. *varia*	no	yes	NAM	-17.996	24.073
TM39339	—	*Trachylepis damarana*	no	yes	NAM	-17.996	24.073
TM31107	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.823	22.706
TM31108	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.823	22.706
TM83253	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.593	23.695
TM63100	—	*Trachylepis damarana*	no	yes	NAM	-20.633	17.083
TM63101	—	*Trachylepis* cf. *varia*	no	yes	NAM	-20.633	17.083
TM63102	—	*Trachylepis* cf. *varia*	no	yes	NAM	-20.633	17.083

TM30772	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.090	21.040
TM30775	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.134	21.167
TM30786	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.134	21.167
TM31020	—	*Trachylepis damarana*	no	yes	BW	-18.770	21.754
TM31021	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.770	21.754
TM79747	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.600	21.817
TM83404	—	*Trachylepis* cf. *varia*	no	yes	ZA	-27.399	30.404
TM69668	—	*Trachylepis* cf. *varia*	no	yes	MW	-11.266	33.878
TM69733	—	*Trachylepis* cf. *varia*	no	yes	MW	-11.015	33.939
TM69761	—	*Trachylepis* cf. *varia*	no	yes	MW	-10.450	34.269
TM69767	—	*Trachylepis* cf. *varia*	no	yes	MW	-13.621	34.471
TM26644	—	*Trachylepis varia*	no	yes	ZA	-31.669	29.482
TM52368	—	*Trachylepis varia*	no	yes	ZA	-30.273	30.585
TM71815	—	*Trachylepis* cf. *varia*	no	yes	SW	-26.956	31.335
TM37533	—	*Trachylepis* cf. *varia*	no	yes	ZA	-31.638	29.479
TM37535	—	*Trachylepis* cf. *varia*	no	yes	ZA	-31.638	29.479
TM69764	—	*Trachylepis* cf. *varia*	no	yes	MW	-10.450	34.269
TM40940	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-15.317	13.533
TM45208	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.741	15.058
TM79698	—	*Trachylepis laevigata*	no	yes	BW	-23.117	26.667
TM79699	—	*Trachylepis laevigata*	no	yes	BW	-23.117	26.667
TM79701	—	*Trachylepis laevigata*	no	yes	BW	-23.117	26.667
TM78617	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.367	30.883
TM39165	—	*Trachylepis damarana*	no	yes	NAM	-17.983	23.286
TM39166	—	*Trachylepis damarana*	no	yes	NAM	-17.983	23.286
TM39344	—	*Trachylepis* cf. *varia*	no	yes	NAM	-17.996	24.073

TM39348	—	*Trachylepis* cf. *varia*	no	yes	NAM	-17.649	24.163
TM39169	—	*Trachylepis damarana*	no	yes	NAM	-18.043	23.322
TM39176	—	*Trachylepis* cf. *varia*	no	yes	NAM	-18.043	23.322
TM39295	—	*Trachylepis damarana*	no	yes	NAM	-17.712	24.531
TM39322	—	*Trachylepis* cf. *varia*	no	yes	NAM	-17.501	24.268
TM39337	—	*Trachylepis* cf. *varia*	no	yes	NAM	-17.996	24.073
TM39376	—	*Trachylepis damarana*	no	yes	NAM	-17.501	24.268
TM14481	—	*Trachylepis damarana*	no	yes	BW	-20.446	22.744
TM26953	—	*Trachylepis damarana*	no	yes	BW	-20.833	22.217
TM38338	—	*Trachylepis* cf. *varia*	no	yes	NAM	-17.926	19.749
TM44812	—	*Trachylepis damarana*	no	yes	BW	-19.346	23.028
TM55117	—	*Trachylepis damarana*	no	yes	BW	-19.283	23.183
TM30932	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.739	22.173
TM30933	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.739	22.173
TM31091	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.369	21.845
TM31109	—	*Trachylepis damarana*	no	yes	BW	-20.823	22.706
TM31110	—	*Trachylepis damarana*	no	yes	BW	-20.823	22.706
TM31111	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.823	22.706
TM31112	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.823	22.706
TM16901	—	*Trachylepis damarana*	no	yes	NAM	-20.633	17.083
TM16935	—	*Trachylepis* cf. *varia*	no	yes	NAM	-22.367	17.383
TM26884	—	*Trachylepis* cf. *varia*	no	yes	NAM	-19.789	20.957
TM38289	—	*Trachylepis* cf. *varia*	no	yes	NAM	-20.646	17.100
TM38290	—	*Trachylepis damarana*	no	yes	NAM	-20.646	17.100
TM41415	—	*Trachylepis damarana*	no	yes	NAM	-22.678	18.582
TM63116	—	*Trachylepis damarana*	no	yes	NAM	-20.367	17.233
TM30665	—	*Trachylepis* cf. *varia*	no	yes	BW	-19.662	22.191
TM30666	—	*Trachylepis* cf. *varia*	no	yes	BW	-19.662	22.191

TM30773	—	*Trachylepis damarana*	no	yes	BW	-20.090	21.040
TM30774	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.134	21.167
TM30776	—	*Trachylepis damarana*	no	yes	BW	-20.134	21.167
TM30787	—	*Trachylepis* cf. *varia*	no	yes	BW	-20.134	21.167
TM30831	—	*Trachylepis damarana*	no	yes	BW	-19.567	21.033
TM30832	—	*Trachylepis* cf. *varia*	no	yes	BW	-19.567	21.033
TM30833	—	*Trachylepis* cf. *varia*	no	yes	BW	-19.567	21.033
TM30834	—	*Trachylepis damarana*	no	yes	BW	-19.567	21.033
TM30835	—	*Trachylepis* cf. *varia*	no	yes	BW	-19.567	21.033
TM30836	—	*Trachylepis* cf. *varia*	no	yes	BW	-19.567	21.033
TM31018	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.770	21.754
TM31019	—	*Trachylepis damarana*	no	yes	BW	-18.770	21.754
TM31022	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.770	21.754
TM31023	—	*Trachylepis damarana*	no	yes	BW	-18.770	21.754
TM31024	—	*Trachylepis damarana*	no	yes	BW	-18.770	21.754
TM79746	—	*Trachylepis* cf. *varia*	no	yes	BW	-18.600	21.817
TM38388	—	*Trachylepis* cf. *varia*	no	yes	NAM	-19.742	20.477
TM38389	—	*Trachylepis damarana*	no	yes	NAM	-19.742	20.477
TM38390	—	*Trachylepis* cf. *varia*	no	yes	NAM	-19.742	20.477
TM38391	—	*Trachylepis* cf. *varia*	no	yes	NAM	-19.742	20.477
TM38392	—	*Trachylepis* cf. *varia*	no	yes	NAM	-19.742	20.477
TM38397	—	*Trachylepis damarana*	no	yes	NAM	-18.585	20.566
TM38399	—	*Trachylepis* cf. *varia*	no	yes	NAM	-18.585	20.566
TM38409	—	*Trachylepis* cf. *varia*	no	yes	NAM	-18.683	20.283
TM82286	—	*Trachylepis* cf. *varia*	no	yes	NAM	-19.118	20.117
TM29761	—	*Trachylepis varia*	no	yes	ZA	-28.287	27.135
TM741	—	*Trachylepis varia*	no	yes	ZA	-33.314	26.518
TM756	—	*Trachylepis varia*	no	yes	ZA	-33.314	26.518

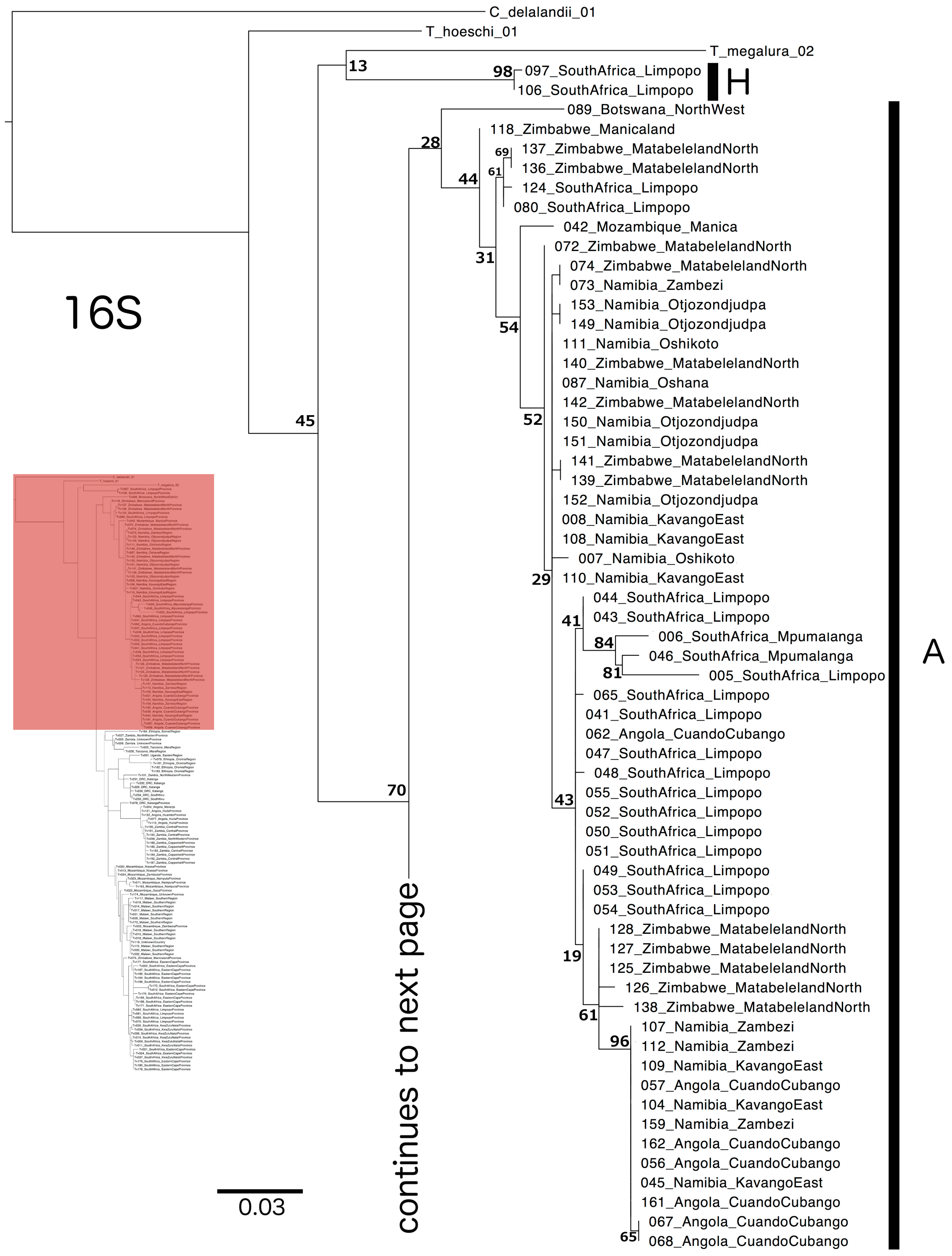
TM37607	—	*Trachylepis* cf. *varia*	no	yes	ZA	-29.477	30.058
TM20806	—	*Trachylepis* cf. *varia*	no	yes	ZA	-28.850	30.067
TM20972	—	*Trachylepis* cf. *varia*	no	yes	ZA	-28.850	30.067
TM20974	—	*Trachylepis varia*	no	yes	ZA	-28.850	30.067
TM20975	—	*Trachylepis* cf. *varia*	no	yes	ZA	-28.850	30.067
TM50735	—	*Trachylepis varia*	no	yes	ZA	-28.925	29.134
TM51612	—	*Trachylepis varia*	no	yes	ZA	-28.961	29.231
TM51682	—	*Trachylepis* cf. *varia*	no	yes	ZA	-30.273	30.585
TM52371	—	*Trachylepis varia*	no	yes	ZA	-28.895	31.452
TM47576	—	*Trachylepis varia*	no	yes	ZA	-31.984	29.148
TM53430	—	*Trachylepis varia*	no	yes	ZA	-30.691	30.292
TM54145	—	*Trachylepis varia*	no	yes	ZA	-29.862	30.809
TM54593	—	*Trachylepis varia*	no	yes	ZA	-30.733	30.267
TM55149	—	*Trachylepis varia*	no	yes	ZA	-30.983	30.183
TM55427	—	*Trachylepis* cf. *varia*	no	yes	ZA	-27.502	31.293
TM57504	—	*Trachylepis* cf. *varia*	no	yes	ZA	-28.683	29.493
TM57625	—	*Trachylepis* cf. *varia*	no	yes	ZA	-30.483	30.633
TM65045	—	*Trachylepis varia*	no	yes	ZA	-28.450	32.283
TM65212	—	*Trachylepis varia*	no	yes	ZA	-30.150	30.050
TM76475	—	*Trachylepis* cf. *varia*	no	yes	ZA	-29.565	30.318
TM79361	—	*Trachylepis varia*	no	yes	ZA	-29.538	30.208
TM79363	—	*Trachylepis varia*	no	yes	ZA	-29.538	30.207
TM79570	—	*Trachylepis* cf. *varia*	no	yes	ZA	-27.325	30.485
TM70975	—	*Trachylepis varia*	no	yes	SW	-26.362	31.104
TM70978	—	*Trachylepis varia*	no	yes	SW	-26.732	31.813
TM70979	—	*Trachylepis varia*	no	yes	SW	-26.277	30.949
TM70981	—	*Trachylepis* cf. *varia*	no	yes	SW	-26.127	31.126
TM70983	—	*Trachylepis* cf. *varia*	no	yes	SW	-26.040	31.407

TM70985	—	*Trachylepis varia*	no	yes	SW	-26.212	31.334
TM71109	—	*Trachylepis varia*	no	yes	SW	-26.793	31.200
TM80017	—	*Trachylepis varia*	no	yes	SW	-26.016	31.128
TM80035	—	*Trachylepis* cf. *varia*	no	yes	SW	-26.028	31.241
TM80810	—	*Trachylepis varia*	no	yes	SW	-26.275	30.997
TM37534	—	*Trachylepis* cf. *varia*	no	yes	ZA	-31.638	29.479
TM37536	—	*Trachylepis varia*	no	yes	ZA	-31.638	29.479
TM37537	—	*Trachylepis varia*	no	yes	ZA	-31.638	29.479
TM37539	—	*Trachylepis varia*	no	yes	ZA	-31.638	29.479
TM69019	—	*Trachylepis* cf. *varia*	no	yes	ZA	-31.645	29.520
TM62647	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.983	29.933
TM62687	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.567	30.85
TM62694	—	*Trachylepis* cf. *varia*	no	yes	ZA	-25.683	31.183
TM83961	—	*Trachylepis* cf. *varia*	no	yes	SW	-27.089	31.154
TM688706	—	*Trachylepis varia*	no	yes	ZA	-28.683	28.917
TM78584	—	*Trachylepis* cf. *varia*	no	yes	ZA	-26.317	26.817
TM38063	—	*Trachylepis* cf. *varia*	no	yes	DRC	-9.138	26.501
TM38064	—	*Trachylepis* cf. *varia*	no	yes	DRC	-9.138	26.501
TM71031	—	*Trachylepis* cf. *varia*	no	yes	ZM	-8.768	31.119
TM71032	—	*Trachylepis* cf. *varia*	no	yes	ZM	-8.768	31.119
TM40129	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.733	13.345
TM40833	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.940	13.512
TM45302	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-8.345	20.212
TM45465	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-9.074	16.0

TM45466	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-9.074	16.0
TM45480	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-9.074	16.0
TM46465	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-10.223	14.811
TM46479	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-10.839	14.629
TM46552	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-12.163	13.877
TM46591	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-12.388	13.883
TM46607	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-12.252	14.266
TM46643	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-11.901	15.450
TM46666	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.184	14.428
TM46695	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.638	13.928
TM45196	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.769	14.808
TM45197	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.769	14.808
TM45198	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.769	14.808
TM45205	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.741	15.058

TM45206	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.741	15.058
TM45207	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.741	15.058
TM45209	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-14.741	15.058
TM45264	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-13.650	21.426
TM45265	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-13.650	21.426
TM45285	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-13.786	14.643
TM45286	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-13.786	14.643
TM45292	—	*Trachylepis* cf. *varia* clade B	no	yes	AO	-8.346	20.212
TM2769	—	*Trachylepis damarana*	no	yes	MZ	-23.383	32.367
TM26767	—	*Trachylepis varia*	no	yes	MZ	-25.456	31.993
TM29466	—	*Trachylepis varia*	no	yes	MZ	-25.382	32.436
TM47601	—	*Trachylepis* cf. *varia*	no	yes	ZA	-25.556	30.993
TM78974	—	*Trachylepis* cf. *varia*	no	yes	ZA	-28.235	31.931
TM78633	—	*Trachylepis* cf. *varia*	no	yes	ZA	-22.35	31.083
TM22390	—	*Trachylepis* cf. *varia*	no	yes	ZW	-18.25	32.767
TM18512	—	*Trachylepis varia*	no	yes	ZW	-19.297	32.640
TM16402	—	*Trachylepis* cf. *varia*	no	yes	UG	1.127	34.518
TM16403	—	*Trachylepis* cf. *varia*	no	yes	UG	1.127	34.518
TM16405	—	*Trachylepis* cf. *varia*	no	yes	UG	1.127	34.518
TM27542	—	*Trachylepis* cf. *varia*	no	yes	ZA	-24.447	31.699

TM30229	—	*Trachylepis damarana*	no	yes	MZ	-16.145	33.610
TM30247	—	*Trachylepis* cf. *varia*	no	yes	MZ	-16.145	33.610
TM57979	—	*Trachylepis* cf. *varia*	no	yes	ZA	-28.708	29.508
TM29170	—	*Trachylepis varia*	no	yes	MZ	-26.041	32.328
TM29192	—	*Trachylepis* cf. *varia*	no	yes	MZ	-21.547	32.952
TM29193	—	*Trachylepis varia*	no	yes	MZ	-21.547	32.952
TM29416	—	*Trachylepis* cf. *varia*	no	yes	MZ	-25.033	32.65
TM29418	—	*Trachylepis varia*	no	yes	MZ	-25.033	32.65
TM3995	—	*Trachylepis damarana*	no	yes	MZ	-26.012	32.913
TM80314	—	*Trachylepis* cf. *varia*	no	yes	NAM	-19.302	20.665
TM62637	—	*Trachylepis* cf. *varia*	no	yes	ZA	-23.2	28.833
TM66453	—	*Trachylepis varia*	no	yes	ZW	-20.151	28.584
TM16400	—	*Trachylepis* cf. *varia*	no	yes	TZ	-9.025	33.442
TM16401	—	*Trachylepis* cf. *varia*	no	yes	TZ	-9.025	33.442
TM12423	—	*Trachylepis* cf. *varia*	no	yes	TZ	-3.167	33.767
TM69667	—	*Trachylepis* cf. *varia*	no	yes	MW	-15.90	34.749
ZMB64341$^{\text{Lect.}}$	—	*Trachylepis varia*	no	yes	MZ	-16.145	33.610
ZMB64342	—	*Trachylepis* cf. *varia*	no	yes	MZ	-16.145	33.610
TM66450	—	*Trachylepis varia*	no	yes	ZW	-20.151	28.584
TM66459	—	*Trachylepis varia*	no	yes	ZW	-20.503	28.523
TM80924	—	*Trachylepis* cf. *varia*	no	yes	MZ	-17.073	38.745
TM80925	—	*Trachylepis* cf. *varia*	no	yes	MZ	-17.073	38.745
TM80999	—	*Trachylepis* cf. *varia*	no	yes	MZ	-17.042	38.838
ZMB1231	—	*Trachylepis damarana*	no	yes	MZ	-16.145	33.610
TM34442	—	*Trachylepis* cf. *varia*	no	yes	ZW	-17.93	25.83
ZMB6224$^{\text{Hol.}}$	—	*Trachylepis laevigata*	no	yes	ZA	—	—
ZMB6153$^{\text{Lect.}}$	—	*Trachylepis damarana*	no	yes	NAM	—	—



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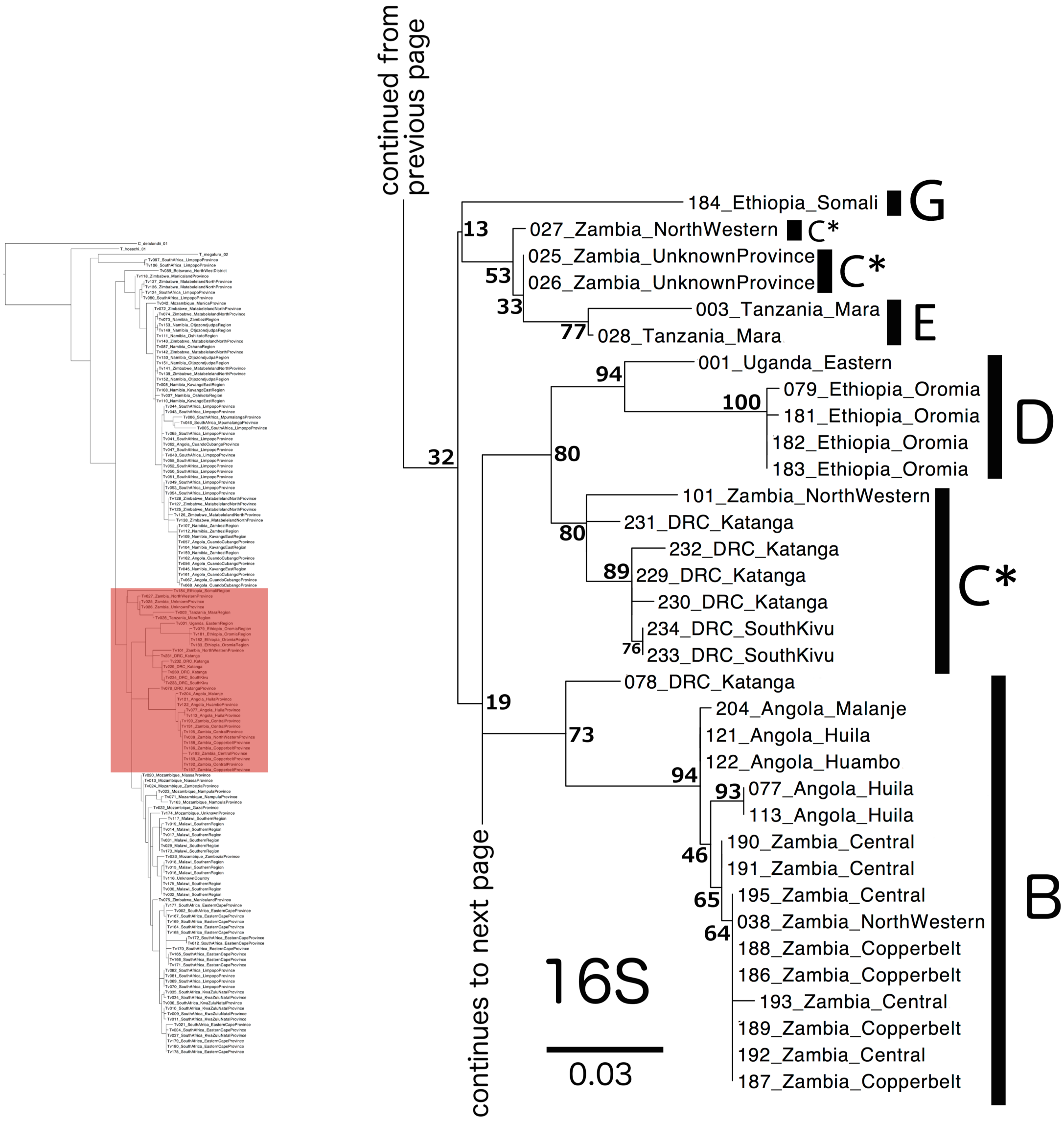
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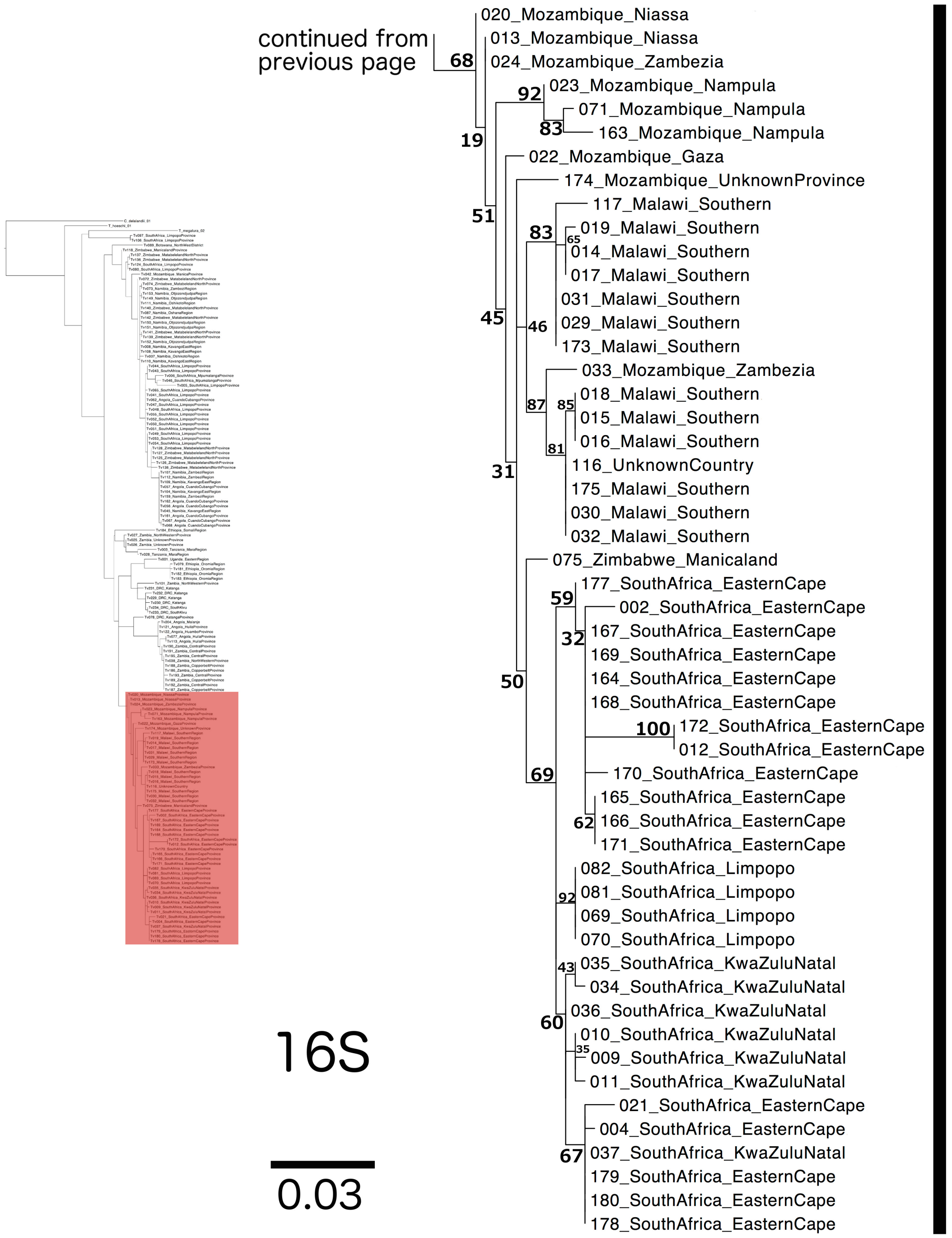
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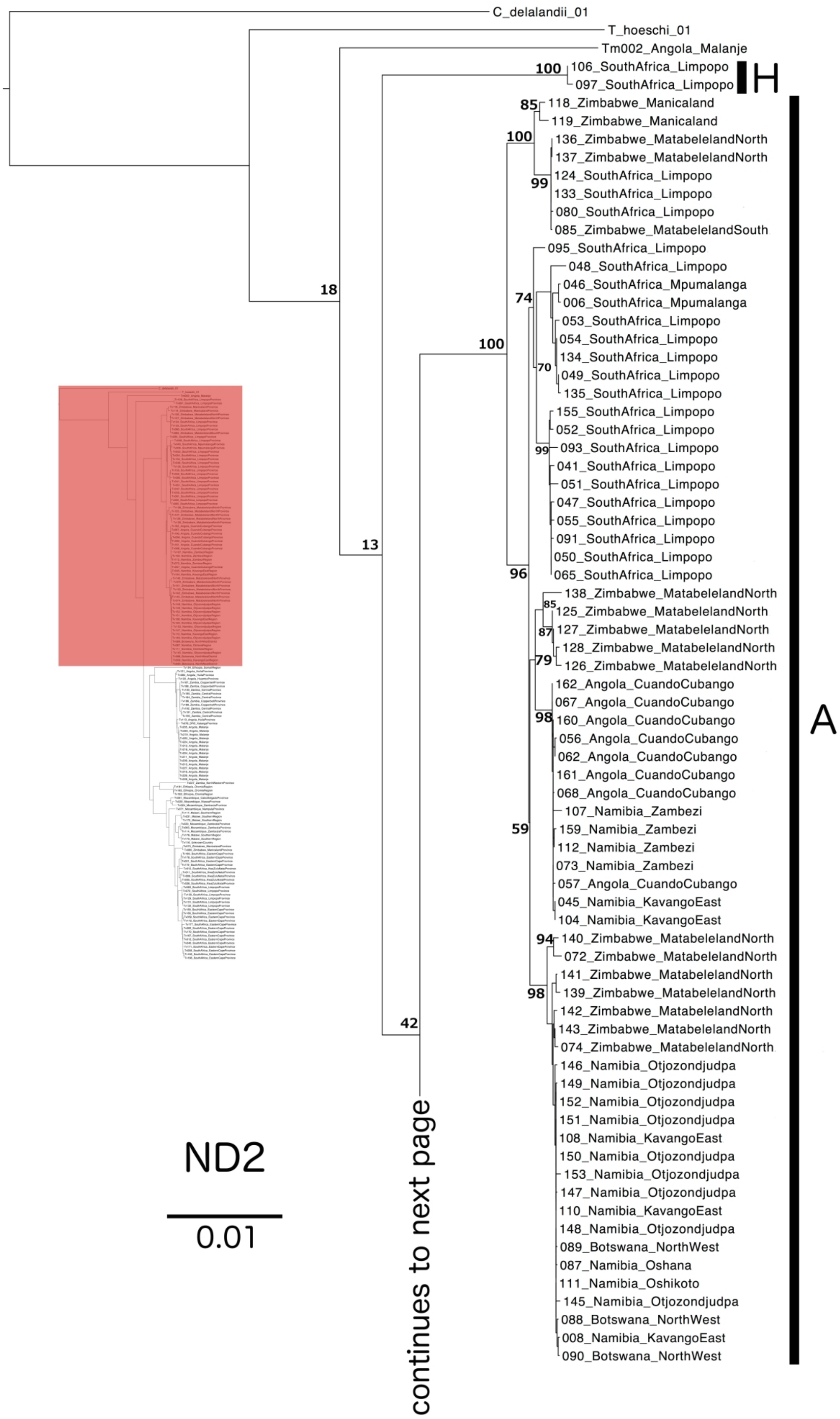
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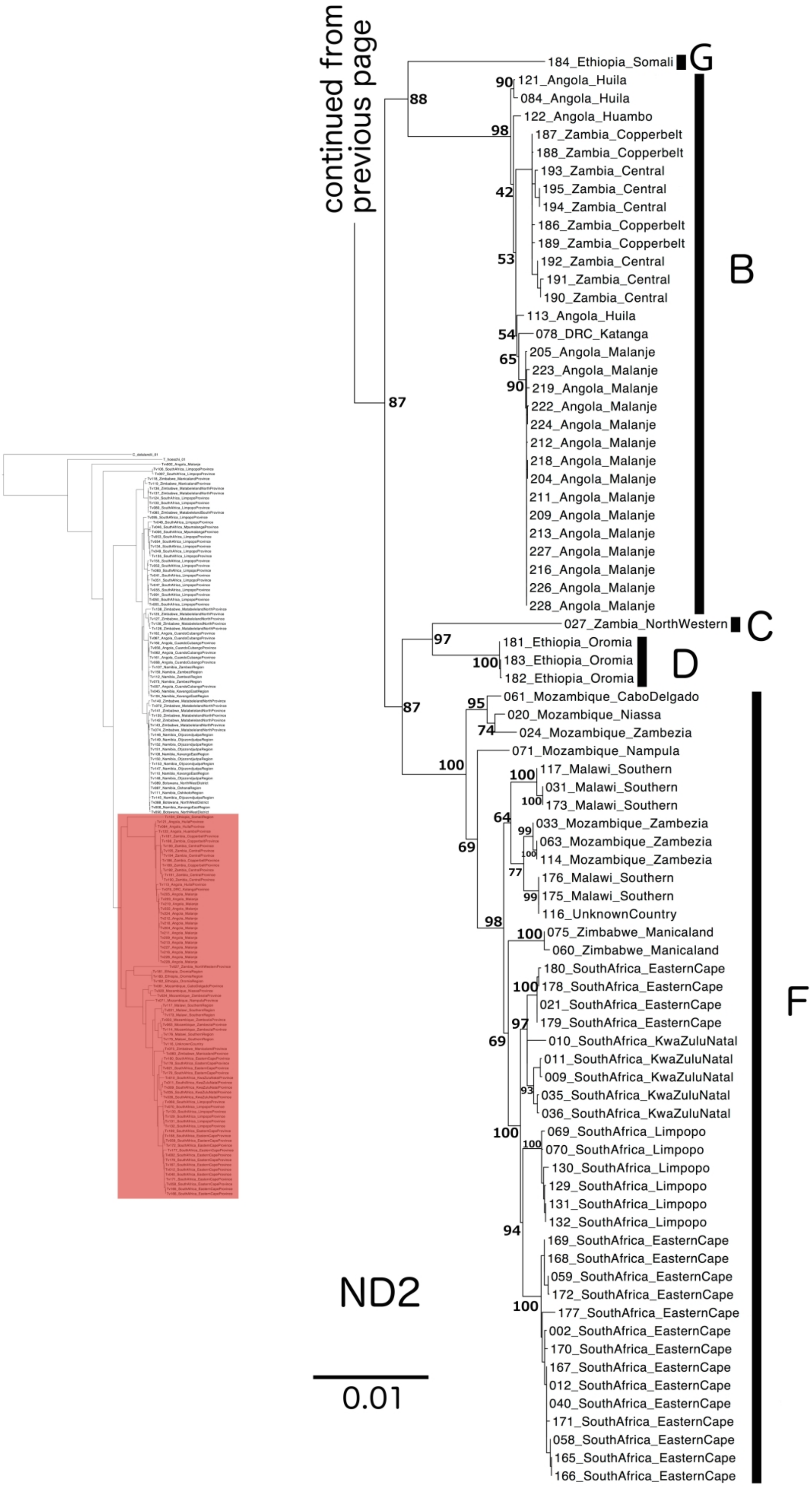
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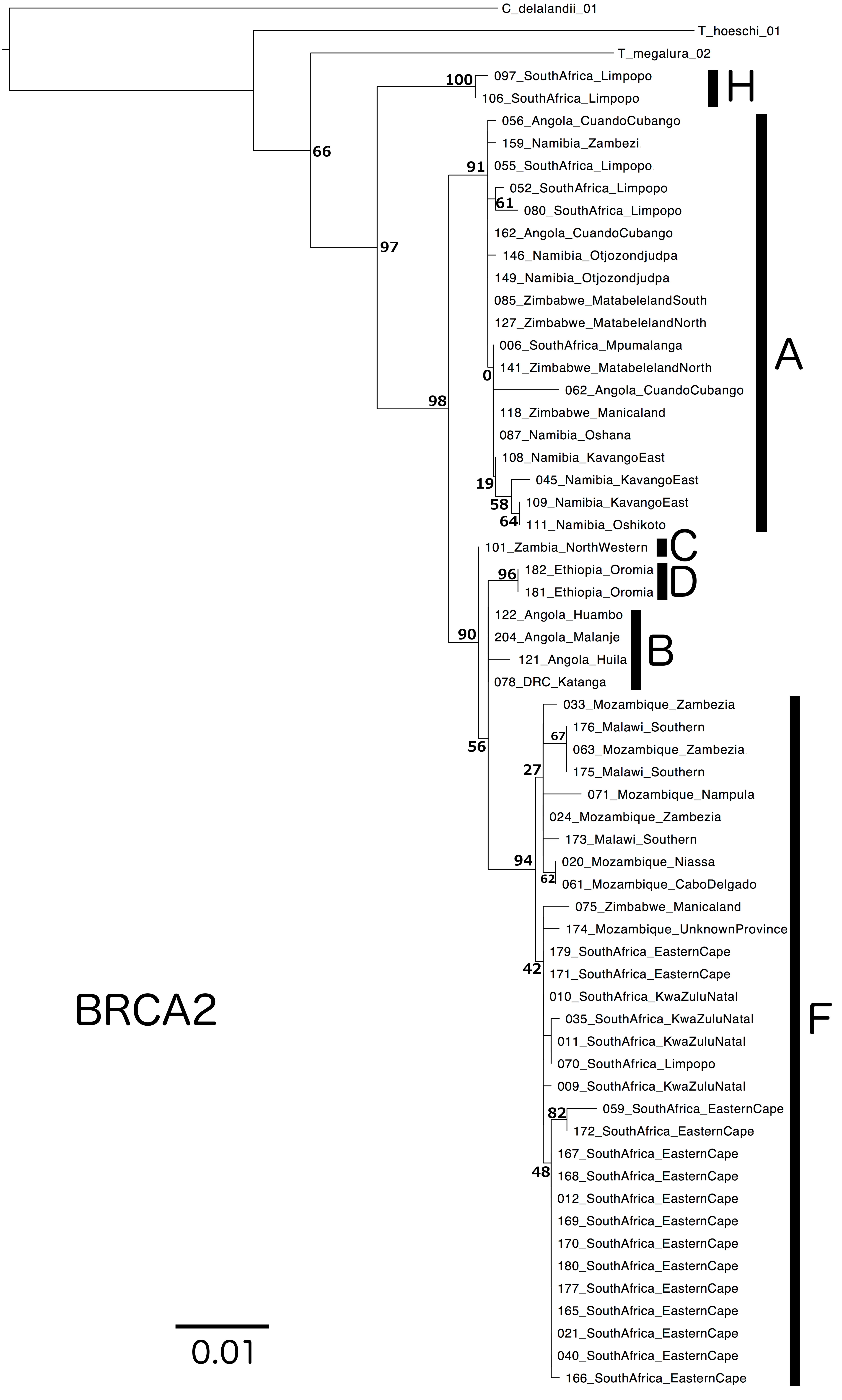
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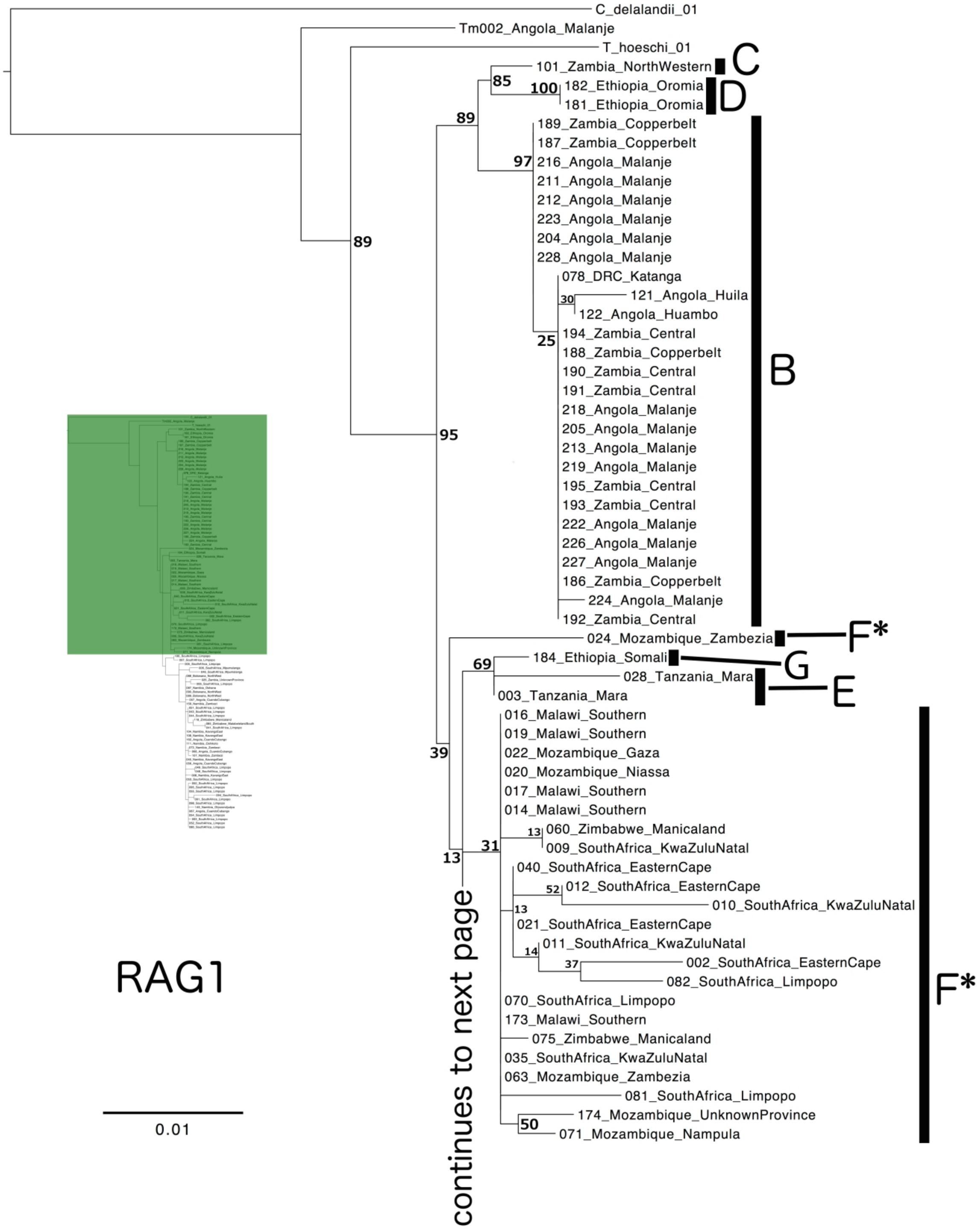
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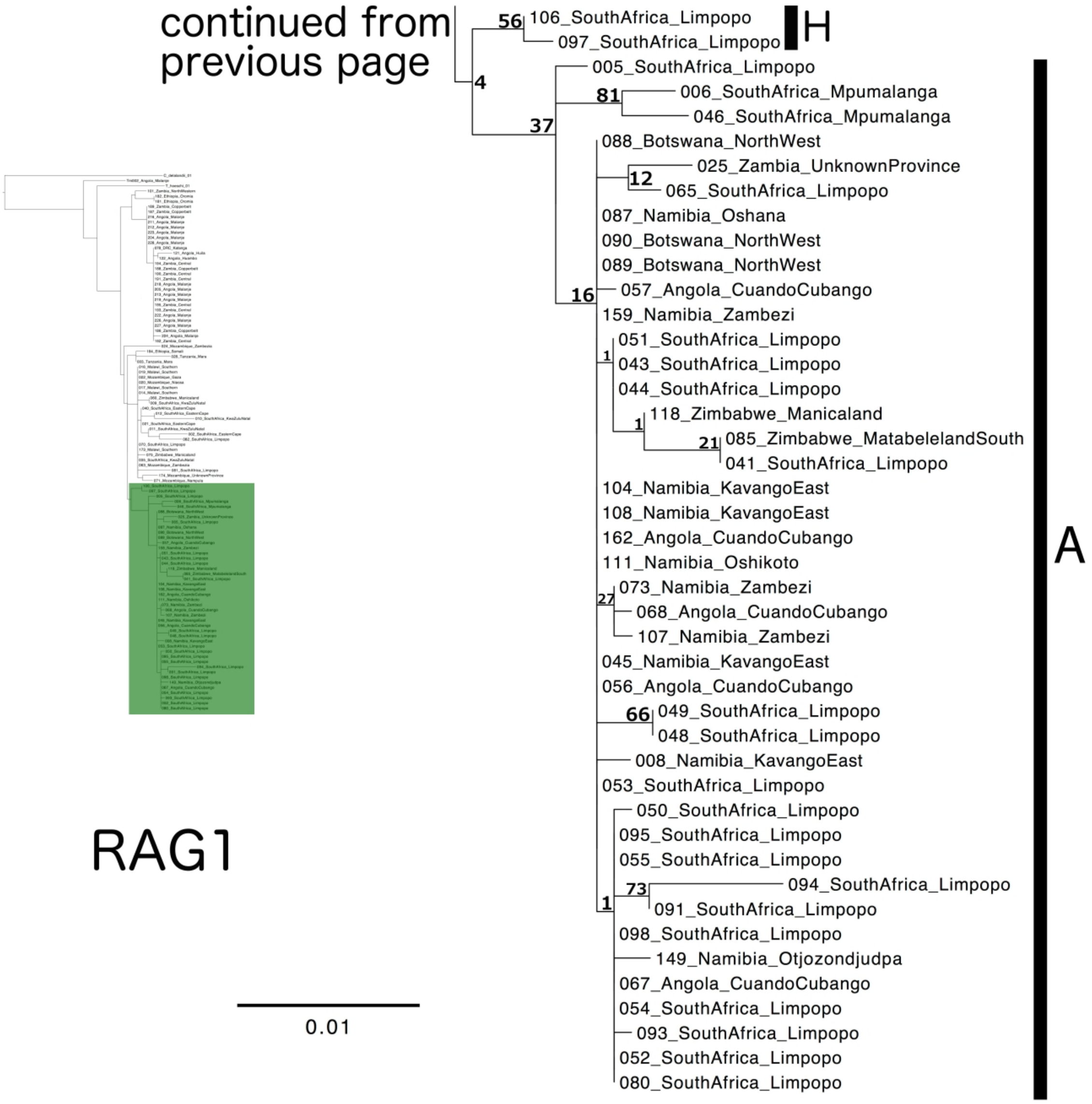
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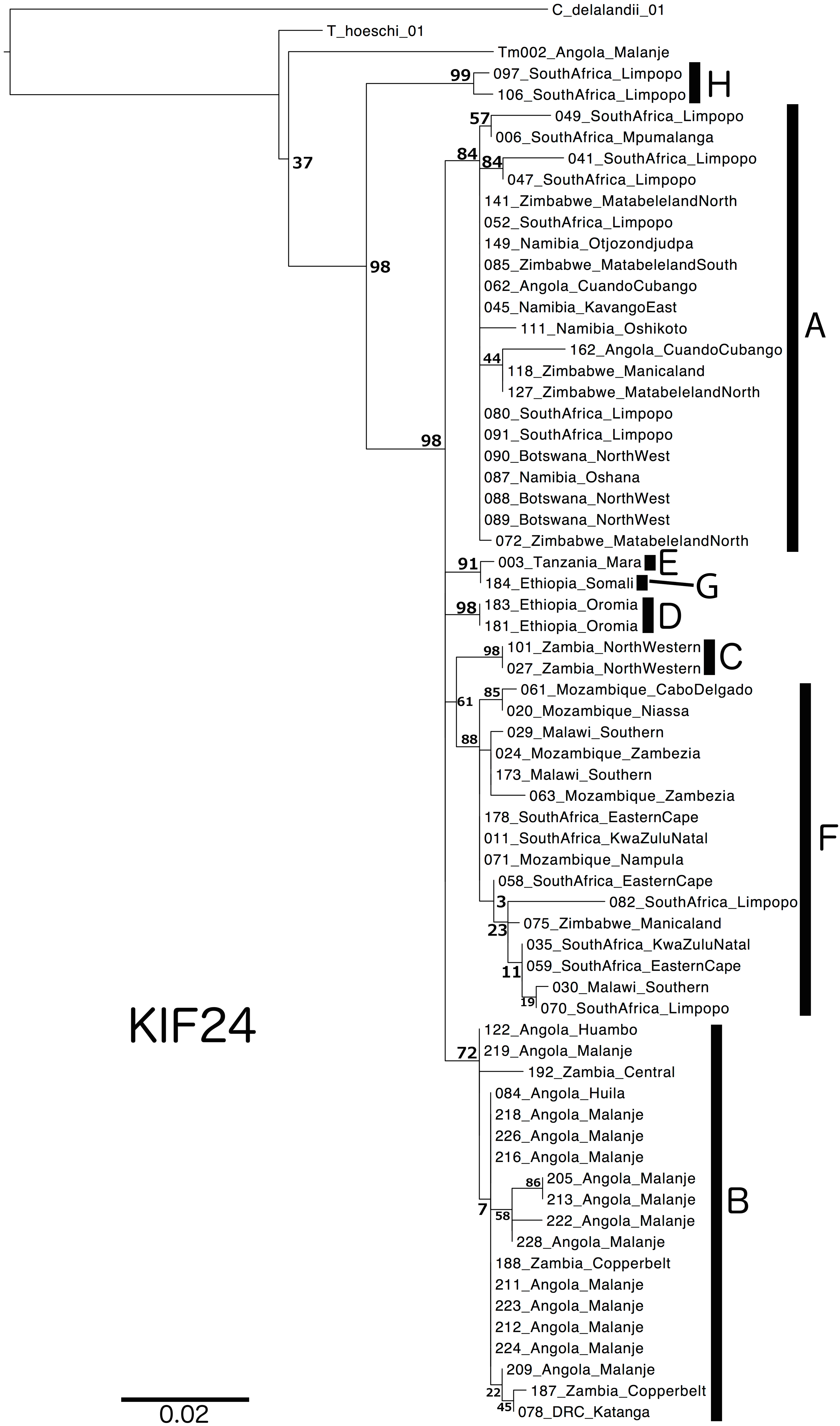
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