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A species-level phylogeny of *Trachylepis* (Scincidae: Mabuyinae) provides insight into their reproductive mode evolution

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ABSTRACT

Trachylepis (Mabuyinae) includes ~80 species of fully-limbed skinks found primarily in Africa and Madagascar, but a robust species-level phylogeny for this genus is lacking and this impedes studies on a wide-range of topics from biogeography to character evolution. *Trachylepis* and its close relatives (which together form the *Mabuya* group or Mabuyinae) are notable in that they have undergone multiple transitions and remarkable specializations in their reproductive modes. A *Trachylepis* phylogeny will be particularly useful for investigating reproductive evolution, because it includes species that exhibit oviparity, viviparity, and bimodal parity (species with both oviparous and viviparous populations). We sequenced DNA at four mitochondrial and five nuclear loci for 67 (~84% of) *Trachylepis* species to infer a phylogeny for this genus. We performed stochastic character mapping of parity mode under a variety of parity mode transition models to infer ancestral parity mode states and the number and type of parity mode transitions. We recovered a strongly supported phylogeny of *Trachylepis* that is generally consistent with earlier phylogenetic studies. The best-fit model of reproductive mode evolution supports an oviparous ancestor for *Trachylepis*, and supports at least three viviparity to oviparity transitions. We compared parity mode evolution under the overall best-fit model (no constraints on parity mode transitions) to the best-fit model among the subset of models that assume viviparity to oviparity transitions are impossible. Our results support a model of reproductive evolution that allows for reversibility from viviparity to oviparity, a process that is not generally accepted. Alternatively, the best-fit model of evolution among the set of models that eliminate reversals from viviparity to oviparity suggests that bimodal reproduction may have persisted for millions of years within multiple lineages.

1. Introduction

The genus *Trachylepis* comprises ~80 species of mostly African and Malagasy skinks in the *Mabuya* group (a member of Lygosominae *sensu* Greer (1970), Mabuyinae *sensu* Mittleman (1952), or Mabuyidae Hedges and Conn (2012)), and the systematics and taxonomy of this group have a convoluted history. Historically, *Trachylepis* species were placed in the genus *Mabuya*, but Mausfeld et al. (2002) restricted *Mabuya* to incorporate only the Neotropical taxa and resurrected *Eutropis* for the Asian members, *Euprepis* for the African, Mediterranean, and Malagasy species, and *Chioninia* for the Cape Verde clade. Subsequently, Bauer (2003) showed that *Trachylepis*, rather than *Euprepis*, is the name applicable to the African and allied species. Karin et al. (2016) resurrected *Heremites* for the three Mediterranean/Middle Eastern species formerly assigned to *Trachylepis*, and restricted *Trachylepis* to only include the species in the clade sister to *Chioninia*. Metallinou et al. (2016) resurrected *Lubuya* for *T. ivensii*, which was recovered as sister to *Eumecia*, and confirmed the sister relationship between *Chioninia* and

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the remaining *Trachylepis*.

Phylogenetic studies of *Trachylepis* have primarily focused on insular species, including *Trachylepis* from the Gulf of Guinea islands, Madagascar, Seychelles, Comoros, and Socotra (Jesus et al., 2005; Ceríaco et al., 2016; Lima et al., 2013; Rocha et al., 2010; Sindaco et al., 2012). Continental African *Trachylepis* that have been studied using molecular data include species in the *T. affinis*, *T. striata*, *T. sulcata*, *T. variegata*, and *T. varia* species groups (Allen et al., 2017; Castiglia et al., 2006; Portik et al., 2010; Portik and Bauer, 2012; Weinell and Bauer, 2018). Several African species have occasionally been placed in monotypic genera, e.g., *Oelofsia laevis* (Steyn and Mitchell, 1965) and *Labuya ivensii* (Horton, 1972), and although the latter genus has been revived and its phylogenetic relationships studied (Metallinou et al., 2016), sampling of potentially cryptic taxa associated with the discovery of new populations of *L. ivensii* is required (Broadley and Willems, 2015). Moreover, a broadly-sampled phylogeny of *Trachylepis* is still lacking, limiting not only assessment of the monophyly of *Lubuya* and the status of *Oelofsia*, but also future work on a wide array of topics, ranging from biogeographic histories to phenotypic character evolution within *Trachylepis*.

Mabuyine skinks are emerging as a powerful model system for studying reproductive mode transitions and specialization (Cornelis et al., 2017; Blackburn and Vitt, 1992). The genera *Eumecia* and *Labuya*, and members of the Neotropical clade are viviparous, and exhibit advanced forms of matrotrophy (Flemming and Branch, 2001; Flemming and Blackburn, 2003; Blackburn and Vitt, 1992), whereas only oviparity is known to occur in the Asian genus *Dasia*. Both viviparity and oviparity occur in *Chioninia*, *Eutropis*, *Heremites*, and *Trachylepis*, with bimodal parity (i.e., species that have viviparous and oviparous populations) also occurring in *Trachylepis* and *Heremites* (Broadley, 2000; Brown-Wessels, 1989; Jacobsen, 1989; Greer, pers. comm.). Information on placentation is lacking for virtually all of the viviparous *Trachylepis* species, although most or all species are probably lecithotrophic considering that the oviductal eggs of viviparous *Trachylepis* contain a large amount of yolk (pers. obs.). The lack of a well-supported *Trachylepis* phylogeny impedes studies on reproductive mode transitions in this group.

For this study, we analyzed mitochondrial and nuclear DNA sequences sampled from 67 *Trachylepis* species and 11 other mabuyine species spanning eight genera, in addition to two eugongyline species, which we used to infer maximum-likelihood (ML) and Bayesian inference (BI) phylogenies for this group. Our sampling included 11 *Trachylepis* species that have not previously been included in any phylogenetic study. We compiled information from the literature and provide new data on reproductive (parity) mode for most of the *Trachylepis* species included in this study. We used parity mode data, our estimated phylogenies, and stochastic mapping to reconstruct parity mode evolution in *Trachylepis* under a variety of models. Lastly, we provide an estimate for the number and type of parity mode transitions as well as their phylogenetic placement in order to discuss the reversibility of parity mode evolution in a phylogenetic context.

2. Methods

2.1. Tissue sampling, DNA extraction, sequencing, and alignment

We obtained new DNA sequence data for 48 *Trachylepis* species, from tissue samples that we collected or obtained on loan from museums and private collections. We also obtained DNA sequence data from GenBank for 19 of these 48 species, and for an additional 19 *Trachylepis* species. To confirm the monophyly of *Trachylepis*, we included GenBank sequence data for 11 species sampled from eight other mabuyine genera, and two species in the subfamily Eugongylinae that were used as outgroup taxa (Table S2).

We extracted genomic DNA from tissues by using a salt DNA extraction protocol (Aljanabi and Martinez, 1997), and we performed polymerase chain reactions (PCR) for four mitochondrial and five nuclear loci. We used a magnetic-bead solution (Rohland and Reich, 2012) to clean PCR product prior to sequencing DNA with Big-Dye v3.1 chemistry, additional magnetic-bead cleanup, and analysis of cycle sequencing product on an ABI3730xl. PCR reactions included an initial 2 min denaturation step at 95 °C, 34 cycles of DNA denaturation at 95 °C for 35 s, primer annealing at 50–52 °C for 35 s, and extension at 72 °C for 1 min 35 s. See Table S1 for PCR and sequencing primers.

Mitochondrial genes included 16S ribosomal RNA (16S), 12S ribosomal RNA (12S), cytochrome oxidase subunit C (Cyt-b), and NADH dehydrogenase subunit 2 (ND2), and nuclear genes included recombination activation protein 1 (RAG1), brain-derived neurotrophic factor (BDNF), kinesin family member 24 (KIF24), oocyte maturation factor Mos (C-MOS), and breast cancer 2 early onset (BRCA2). We used genes useful for resolving species-level phylogenetic relationships within the *Mabuya* group skinks (Portik et al., 2012; Karin et al., 2016; Metallinou et al., 2016; Weinell and Bauer, 2018). We used Muscle (Edgar, 2004) implemented in Geneious v6.1 to generate DNA sequence alignments. See Table S2 for GenBank accession codes of individuals included in this study.

2.2. Phylogenetic inference

To produce a robust phylogeny, we used Bayesian inference (BI) and our multilocus dataset in the program BEAST v2.2.0 (Drummond and Rambaut, 2007) under a yule tree process. We included DNA sequences from 67 *Trachylepis* species or subspecies, plus the mabuyine species *Eutropis longicuadata*, *E. multifasciata*, *Lubuya ivensii*, *Heremites septemtaeniata*, *Toenayar novemcarinata*, *Mabuya aurae* (sometimes called *Copeoglossum aurae*, *sensu* Hedges and Conn (2012)), *Eumecia anchietae*, *Dasia vittata*, *D. olivacea*, *Chioninia delalandii*, and *C. vaillanti*. Furthermore, we included the eugongyline species *Cryptoblepharus novocaledonicus* and *Caledoniscincus austrocaledonicus* as outgroups (Zheng and Wiens, 2016; Pyron et al., 2013). We enforced monophyly on Mabuyinae and Eugongylinae, which was necessary to assign a secondary time-calibration on the age of Mabuyinae. In particular, we used a normal distribution prior (mean = 51.21 Ma; SD = 1) for the crown-node age of Mabuyinae, following the time-tree of Squamata results of Zheng and Wiens (2016). For each gene partition of the concatenated BEAST2 analysis, we assigned a relaxed lognormal clock and we used the reversible-jump model to explore multiple substitution models during phylogenetic inference. During the BEAST2 analysis, we sampled from the posterior distribution every 10,000 generations for 200 million generations, we used Tracer v1.5 (Rambaut et al., 2014a; Rambaut et al., 2018) to check that all posteriors converged, which we considered true if the estimated sample size (ESS) of each posterior was ≥250. We omitted the first 10 million generations as burnin, and we used TreeAnnotator v1.8.1 (Rambaut et al., 2014b) to generate a maximum clade-credibility tree with median divergence times. We used FigTree v1.4.0 (Rambaut, 2012) to visualize trees. We considered posterior probability (PP) values ≥0.95 to be strong support for the monophyly of a group (Huelsenbeck and Rannala, 2004).

To infer a ML tree for *Trachylepis*, we used IQ-TREE v1.6.4 (Nguyen et al., 2014) implemented on the web server W-IQ-TREE (Trifinopoulos et al., 2016). Taxon and gene sampling was identical as in the BI analysis. We treated each locus as a separate partition, and we used the automatic model-selection feature (Chernomor et al., 2016) to identify and assign the best-fit substitution model for each partition during tree inference. We performed 1,000 ultrafast bootstraps to assess clade heuristic support for inferred clades, and we considered ultrafast bootstrap support values (UFboot) ≥95 to be strong support for the monophyly of a group (Minh et al., 2013). To assess gene tree topological heterogeneity, we also ran IQ-TREE separately for each locus, and for an alignment that included only the mitochondrial loci.

2.3. Parity evolution

We collected data on parity mode for *Trachylepis* and outgroup species by reviewing previously published literature, and in some cases by examining previously dissected specimens, to check for the presence of nearly fully-developed embryos (which we considered evidence for viviparity), or large, opaque eggs (which we considered evidence for oviparity), following Blackburn (1993). If different females from the same species contained highly developed embryos and large, opaque eggs, then we considered that species to have bimodal parity.

To estimate the historical pattern of parity mode evolution in *Trachylepis*, we performed ML and maximum parsimony (MP) ancestral state reconstruction analyses of parity mode. For parsimony ancestral state reconstruction, we used Mesquite v3.2, with parity mode states treated as unordered (Maddison and Maddison, 2017). For maximum likelihood ancestral state reconstruction, we performed model-fitting, model comparison, and stochastic character mapping using SIMMAP (Bollback, 2006), implemented in the R package phytools (Revell, 2012). The simplest, least-restrictive model examined was the equal-rates model, which uses a single parameter for the transition rates between three parity mode states (six transition types). The transition types include (1) oviparity to viviparity, (2) viviparity to oviparity, (3) oviparity to bimodal parity, (4) bimodal parity to oviparity, (5) viviparity to bimodal parity, and (6) bimodal parity to viviparity. More complex transition-rate models included additional transition-rate parameters assigned to one or more of the transition types. More restrictive models prevented one or more types of transitions from occurring (e.g., some models prevented transitions from viviparity to oviparity). In total, we modelled all possible ($n = 870$) combinations of transition type restrictions (0–4 restricted transition types) and transition rate parameter assignments (1–6 transition rate parameters). For each model, we ran SIMMAP using three different priors on the ancestral (= root, π) parity mode state: (1) oviparity (O), viviparity (V), and bimodal (B) parity equally probable (i.e., $\pi \in \{O, V, B\}$), (2) oviparity and viviparity equally probable (bimodal parity prevented) (i.e., $\pi \in \{O, V\}$), and (3) only oviparity possible at the root (i.e., $\pi \in \{O\}$).

We used the estimated BEAST2 tree (Fig. 1), pruned to include only one branch per species, as the input tree for all SIMMAP analyses. For species in which reproductive mode is unknown we used a uniform prior across all possible reproductive modes for the tip state of the species. Additionally, we reran all SIMMAP analyses after pruning species for which parity mode was unknown, to assess the effect of missing data on ancestral state estimates. See Table S3 for reproductive mode data for the species included in this study.

We used Akaike Index Criterion (AIC) scores to determine the best-fit transition-rate model for each root-state prior probability scheme. Additionally, we identified the best-fit transition-rate model for each root-state prior probability scheme for the subset of transition-rate models that restrict transitions from viviparity to oviparity. For these six best-fit transition-rate model + prior probability schemes, we performed stochastic mapping using SIMMAP (1000 simulations per run) to infer the ancestral parity mode states and the number, types, and phylogenetic locations of parity mode transitions.

3. Results

3.1. DNA sequence and parity mode data

We obtained DNA sequences for 167 individuals (up to 7,122 base pairs [bp]; total missing data = 59.5%), from 67 *Trachylepis* species and 11 other mabuyine species, and 2 outgroup species from Eugongylinae (Table S2). Specifically, we obtained DNA sequences at the mitochondrial genes 16S (562 bp), 12S (881 bp), ND2 (1,451 bp), and Cyt-b (1,018 bp) for 76 (95%), 64 (80%), 55 (68.75%), and 39 (48.75%) of species, respectively. Additionally, we obtained DNA sequences at the nuclear genes RAG1 (566 bp), CMOS (566 bp), BDNF (684 bp), KIF24 (568 bp), and BRCA2 (818 bp), for 55 (68.75%), 50 (62.5%), 52 (65%), 46 (57.5%), and 22 (27.5%) of the sampled species, respectively. New sequence data generated for this study can be found on GenBank (Table S2).

Previous studies contained information on reproductive mode for 49 of the 67 *Trachylepis* species that we included in this study, and we obtained new information on the reproductive mode of three species: *Trachylepis albopunctata*, *T. damarana*, and *T. gonwouoi* (Table S3). We captured *T. albopunctata* females in Zambia that gave birth to be fully-developed young, and, therefore, we consider this species to be viviparous. Jacobsen (1989) reported that in northeastern South Africa, bushveld populations of what were then called *T. varia* — now *T. damarana sensu* Weinell and Bauer (2018) — lay 6–12 eggs from December to October, although some specimens of *T. damarana* contained fully developed embyros, indicative of viviparity. Therefore, we consider this species to have bimodal parity. Specimens of *T. gonwouoi* from Cameroon contained eggs (Tapondjou, pers. comm.), and eggs from this species have been collected beneath logs where an adult female *T. gonwouoi* was also found guarding her clutch (Tapondjou, pers. comm.). Additionally, we compiled parity mode data from the literature for 12 of the 13 non-*Trachylepis* species that we sampled (Table S3). Among the taxa that we sampled for this study, we were unable to obtain reliable information on reproductive mode for 21 species or subspecies, including: *Trachylepis albotaeniata*, *T. bayonii huilensis*, *T. casuarinae*, *T. chimbana*, *T. cristinae*, *T. homalocephala peringueyi*, *T. infralineata*, *T. laevigata*, *T. laevis*, *T. ozorii*, *T. paucisquamis*, *T. sulcata ansorgi*, *T. tandrefana*, *T. tavaratra*, *T.* cf. *varia* (clades 1–4), *T. vato*, *T. vezo*, and *Toenayar novemcarinata*.

3.2. Reversible-jump substitution model estimates

The best-fit substitution models included HKY85 (for CMOS and KIF24), TN93 (for RAG1), EVS (for ND2 and BDNF), and GTR (for 12S, 16S, Cyt-b, and BRCA2). The EVS substitution model is not available to set *a priori*, and, therefore, we used the reversible-jump substitution model for ND2 and BDNF during subsequent BEAST runs, whereas we restricted model space to the best-fit substitution model for each of the remaining genes.

3.3. Phylogenetic relationships

Phylogenetic relationships are summarized in Fig. 1 (BI tree) and Figs. S1–S11 (ML trees). The multilocus BI and ML analyses both recovered *Trachylepis* to be monophyletic, and to contain three main clades: clades A, B, and C, and both analyses recovered clade B sister to clade C (Fig. 1). Additionally, the BI analysis supports the crown age of *Trachylepis* to be approximately 36 million years old (Ma) (95% highest posterior density 30.5–36.8 Ma), which is consistent with earlier estimates for the crown age of *Trachylepis* (Zheng and Wiens, 2016; Karin et al., 2016). The monophyly of clade C was strongly supported in both BI and ML concatenated analyses (PP = 1, UFboot = 96), whereas the monophyly of clade A was not strongly supported in either analysis (PP = 0.54, UFboot = 84), and the monophyly of clade B was only strongly supported in the BI analysis (PP = 0.95, UFboot = 55) (Fig. 1). Species-level relationships within each of these major groups sometimes differs between BI and ML analyses, but there were no cases of hard discordance (i.e., different strongly supported relationships) between multilocus BI and ML analyses. Furthermore, the concatenated mitochondrial-only ML analysis supports similar relationships to the multilocus (i.e., concatenated mitochondrial and nuclear loci) BI and ML analyses (Fig. S2). Single-locus ML gene trees received low support at most nodes (Figs. S3–S11), especially for the nuclear loci, but strongly supported relationships were usually consistent with the relationships inferred from the multilocus analyses, with the exception of the position of *T. brauni*, which we mention later in this section.

Clade A comprises *T. tessellata*, *T. socotrana*, and the *brevicollis*

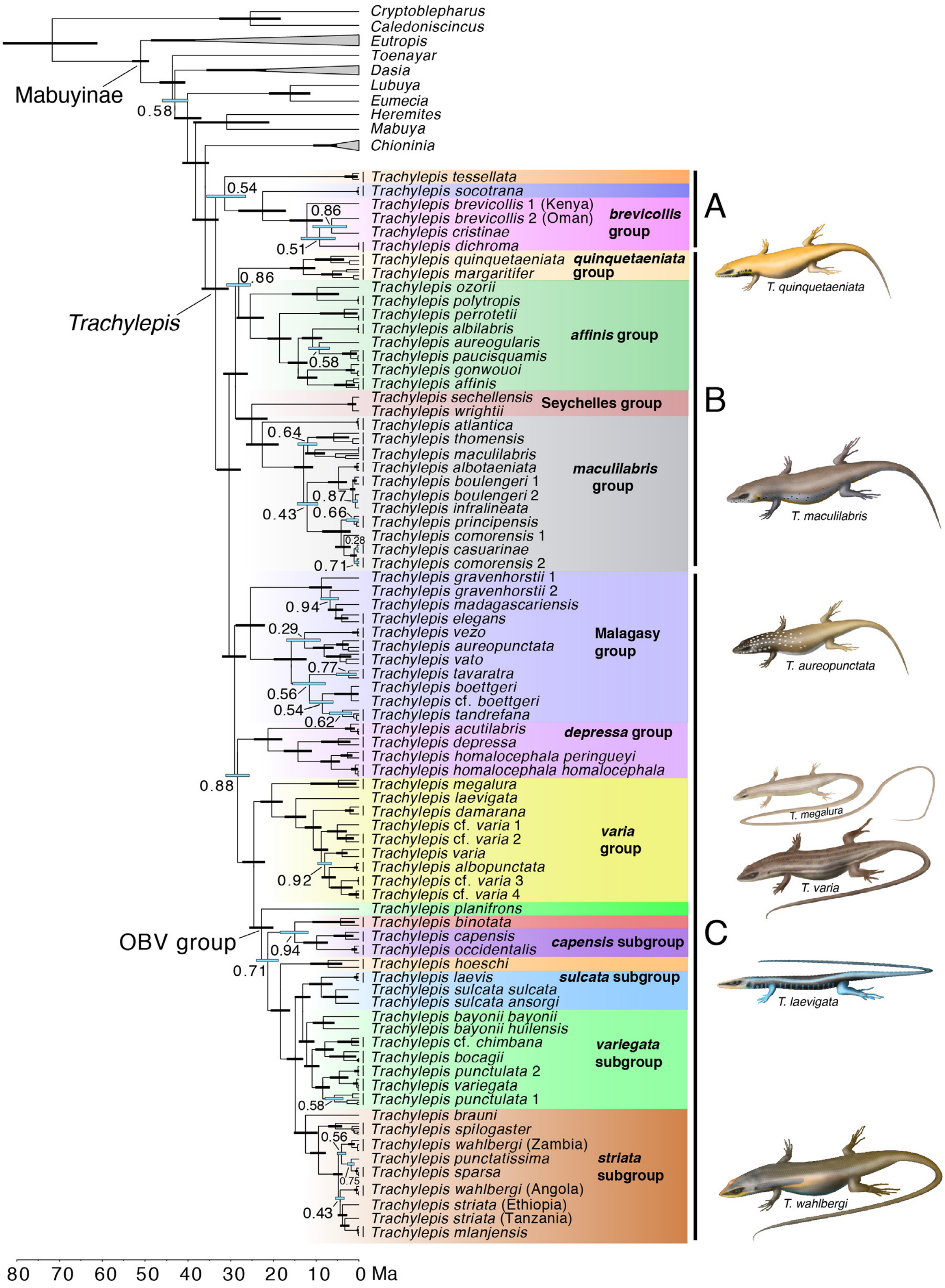

Fig. 1. Multilocus BEAST phylogeny of *Trachylepis*. Loci include five mitochondrial and four nuclear genes. Bars at internal nodes indicate 95% highest posterior density clade ages; black bars are used for clades with posterior probability (PP) ≥0.95, and blue bars are used for clades with < 0.95 PP (values indicate PP at these nodes). OBV group = the clade that includes all descendents of the most recent common ancestor of *T. planifrons* and *T. striata*; this clade includes species with oviparity, bimodal, and viviparous reproduction. *Trachylepis albopunctata* and *T.* cf. *varia* 1–4 correspond to *T.* cf. *varia* clades B, G, E, D, and C, respectively, *sensu* Weinell and Bauer (2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species group, each of which are strongly supported as monophyletic, and *T. socotrana* is strongly supported as sister to the *brevicollis* group. The *brevicollis* group includes three species: *T. brevicollis*, *T. cristinae*, and *T. dichroma*, with the latter two species embedded within *T. brevicollis* (Fig. 1).

Clade B includes four species groups: the *quinquetaeniata*, *affinis*, Seychelles, and *maculilabris* groups, each of which is strongly supported as monophyletic. The Seychelles and *maculilabris* groups are strongly supported as sister groups; the *quinquetaeniata* and *affinis* groups were recovered as sister groups, but with low values of support (PP = 0.86, UFboot = 51). Within the *quinquetaeniata* group, *T. quinquetaeniata* and *T. margaritifer* were each strongly supported as monophyletic. The *affinis* group includes *T. ozorii*, *T. polytropis*, *T. paucisquamis*, *T. perrotetti*, *T. albilabris*, *T. aureogularis*, *T. gonwouoi*, and *T. affinis*, each of which were strongly recovered as monophyletic. Relationships among species in the *affinis* group were identical in BI and ML analyses, with most nodes receiving strong support (Fig. 1). The sister relationship between *T. aureogularis* and *T. paucisquamis* was not strongly supported (PP = 0.58, UFboot = 93), and the sister relationship between *T. gonwouoi* and *T. affinis* was only strongly supported in the BI analysis (PP = 1, UFboot = 94). The Seychelles group is endemic to the Seychelles Archipelago and includes two species, *T. sechellensis* and *T. wrightii*, both of which are strongly supported as monophyletic. The *maculilabris* group includes nine species, of which, only two (*T. maculilabris* and *T. boulengeri*) occur on the African mainland, whereas three species (*T. atlantica*, *T. thomensis*, and *T. principensis*) are endemic to islands in the Atlantic Ocean, and four species (*T. albotaeniata*, *T. infralineata*, *T. comorensis*, and *T. casuarinae*) are endemic to islands in the Indian Ocean. Furthermore, *T. boulengeri* is rendered paraphyletic by *T. infralineata*, and *T. comorensis* is paraphyletic with respect to *T. casuarinae*. *Trachylepis maculilabris* is strongly supported as monophyletic in the BI analysis, but was recovered as paraphyletic in the ML analysis. In particular, populations of *T. maculilabris* from Gabon and Angola form a clade that is sister to *T. thomensis* (UFboot = 65), whereas populations of *T. maculilabris* from Malawi form a clade that is sister (UFboot = 80) to the clade containing *T. casuarinae*, *T. comorensis*, and *T. principensis*.

Clade C includes four strongly supported groups: the Malagasy group (endemic to Madagascar), the *depressa* group, the *varia* group, and the Oviparous, Bimodal, and Viviparous (OBV) group; the latter group contains most of the variation in reproductive mode relative to all other *Trachylepis*. The Malagasy group includes *T. gravenhorstii*, *T. madagascariensis*, *T. elegans*, *T. vezo*, *T. aureopunctata*, *T. vato*, *T. tavaratra*, *T. boettgeri*, and *T. tandrefana*. Both BI and ML analyses recovered *T. gravenhorstii* as paraphyletic with respect to a clade that includes *T. madagascariensis* + *T. elegans*. Additionally, the BI analysis recovered *T. tandrefana* and *T. tavaratra* as monophyletic, but without support (given low PPs: PP = 0.62 and PP = 0.77, respectively), whereas the ML analysis supports paraphyly for these two species. In particular, the ML analysis recovered a clade that includes all *T. tavaratra* + *T. tandrefana* individual ZSM 45.2006 (UFboot = 61), and a clade that includes *T. tandrefana* (except ZSM 45.2006) as the sister to *T. boettgeri* (UFboot = 60). Furthermore, the BI analysis recovered *T. vezo* as the sister group (PP = 0.29) to a clade that includes *T. aureopunctata* + *T. vato*; the ML analysis also supports *T. aureopunctata* as sister to *T. vato*, but *T. vezo* is recovered as the sister group (UFboot = 51) to the *T. boettgeri* + *T. tandrefana* (part) clade.

The *depressa* group includes four species and subspecies: *T. acutilabris*, *T. depressa*, *T. homalocephala homalocephala*, and *T. homalocephala peringueyi*, each of which is strongly supported as monophyletic by both the BI and ML analyses. Species-level relationships within the *depressa* group are all strongly supported (Fig. 1) and identical between between BI and ML analyses, such that *T. homalocephala peringueyi*, *T. depressa*, and *T. acutilabris* form sequential outgroups to *T. homalocephala homalocephala*. The *varia* group includes nine species or previously identified putative species that are each strongly supported as monophyletic in both BI and ML analyses. The species include *T. megalura*, *T. laevigata*, *T. albopunctata*, *T. damarana*, *T. varia*, *T.* cf. *varia* 1, *T.* cf. *varia* 2, *T.* cf. *varia* 3, and *T.* cf. *varia* 4. *Trachylepis albopunctata* and *Trachylepis* cf. *varia* 1–4 correspond to geographically coherent, species-level lineages, and correspond to *Trachylepis* cf. *varia* clades B, G, E, D, and C, respectively, that were previously identified by Weinell and Bauer (2018). The relationships among the *varia* group species are identical between BI and ML analyses, and the only relationship that did not receive strong support in the BI analysis is the sister relationship between *T. varia* and the clade containing *T. albopunctata* + *T.* cf. *varia* 3 + *T.* cf. *varia* 4 (PP = 0.92, UFboot = 98).

The OBV group includes three species: *T. planifrons*, *T. binotata*, *T. hoeschi*, plus four species subgroups: the *capensis*, *sulcata*, *variegata*, and *striata* subgroups, each of which is strongly supported as monophyletic in both BI and ML analyses. *Trachylepis planifrons* is strongly supported as sister to the remaining members of the OBV group. The *variegata* subgroup, *sulcata* subgroup, and *T. hoeschi* form sequential outgroups to the *striata* subgroup, which together are sister to the clade containing the *capensis* subgroup + *T. binotata*. The sister relationship between *T. binotata* and the *capensis* subgroup (*T. capensis* + *T. occidentalis*) is strongly supported only in the ML analysis (PP = 0.94, UFboot = 97). The *sulcata* subgroup includes three species or subspecies: *T. laevis* (previously placed in the genus *Oelofsia*), *T. sulcata ansorgi*, and *T. sulcata sulcata*, such that *T. laevis* is sister to *T. sulcata sulcata* + *T. sulcata ansorgi*. The *variegata* subgroup includes six species or subspecies: *T. bayonii bayonii*, *T. bayonii huilensis*, *T.* cf. *chimbana*, *T. bocagii*, *T. punctulata*, and *T. variegata*. *Trachylepis bayonii bayonii* and *T. bayonii huilensis* form a clade that is sister to the rest of the *variegata* subgroup. *Trachylepis variegata* renders *T. punctulata* paraphyletic (PP = 1, UFboot = 90), and the *T. variegata* + *T. punctulata* clade is sister to a clade containing *T.* cf. *chimbana* and *T. bocagii*.

The *striata* subgroup includes seven species: *T. brauni*, *T. spilogaster*, *T. wahlbergi*, *T. punctatissima*, *T. sparsa*, *T. striata*, and *T. mlanjensis*. Multilocus BI and ML analyses both strongly support *Trachylepis spilogaster* and *T. brauni* as sequential outgroups to the rest of the *striata* subgroup. The KIF24 ML tree also strongly supports *T. brauni* as a member of the *striata* subgroup, and as sister to the clade containing *T. whalbergi* and *T. striata*, excluding *T. spilogaster* (Fig. S4). In contrast to the multilocus BI and ML trees, or to the KIF24 ML tree, the 16S ML tree strongly supports *T. brauni* as a member of the *variegata* subgroup, within a clade that also contains *T. bocagii* and *T.* cf. *chimbana* (Fig. S8). In both BI and ML analyses, *T. mlanjensis* renders *T. striata* paraphyletic, such that Tanzanian and Ethiopian *T. striata* form sequential outgroups to *T. mlanjensis*. Additionally, both BI and ML recovered *T. wahlbergi* to be paraphyletic. In the BI analysis, Angolan populations of *T. wahlbergi* form the sister group to a clade that includes *T. striata* and *T. mlanjensis* (PP = 0.43), and Zambian *T. wahlbergi* form the sister group to a clade containing *T. punctatissima* and *T. sparsa* (PP = 0.56), whereas the ML analysis strongly supports Angolan *T. wahlbergi* as the sister group to *T. sparsa* (UFboot = 95), and Zambian *T. wahlbergi* as the sister group to the clade containing *T. punctatissima*, *T. sparsa*, and Angolan *T. wahlbergi*.

Multilocus BI and ML analyses both recovered the same strongly supported species groups, and identical relationships among these groups (Figs. 1 and S1). Within each species group, phylogenetic relationships were usually the same for BI and ML analyses, and cases of topological discordance between BI and ML analyses only occurred at nodes that lacked strong support in one or both analyses.

3.4. Reproductive mode evolution

Both MP and ML ancestral state reconstruction under the unconstrained set of evolution models support transitions from viviparity to oviparity and/or viviparity to bimodal parity. Additionally, MP and ML analyses support the hypotheses that (1) the most recent common ancestor (MRCA) of *Trachylepis* was oviparous, and that (2) the MRCA

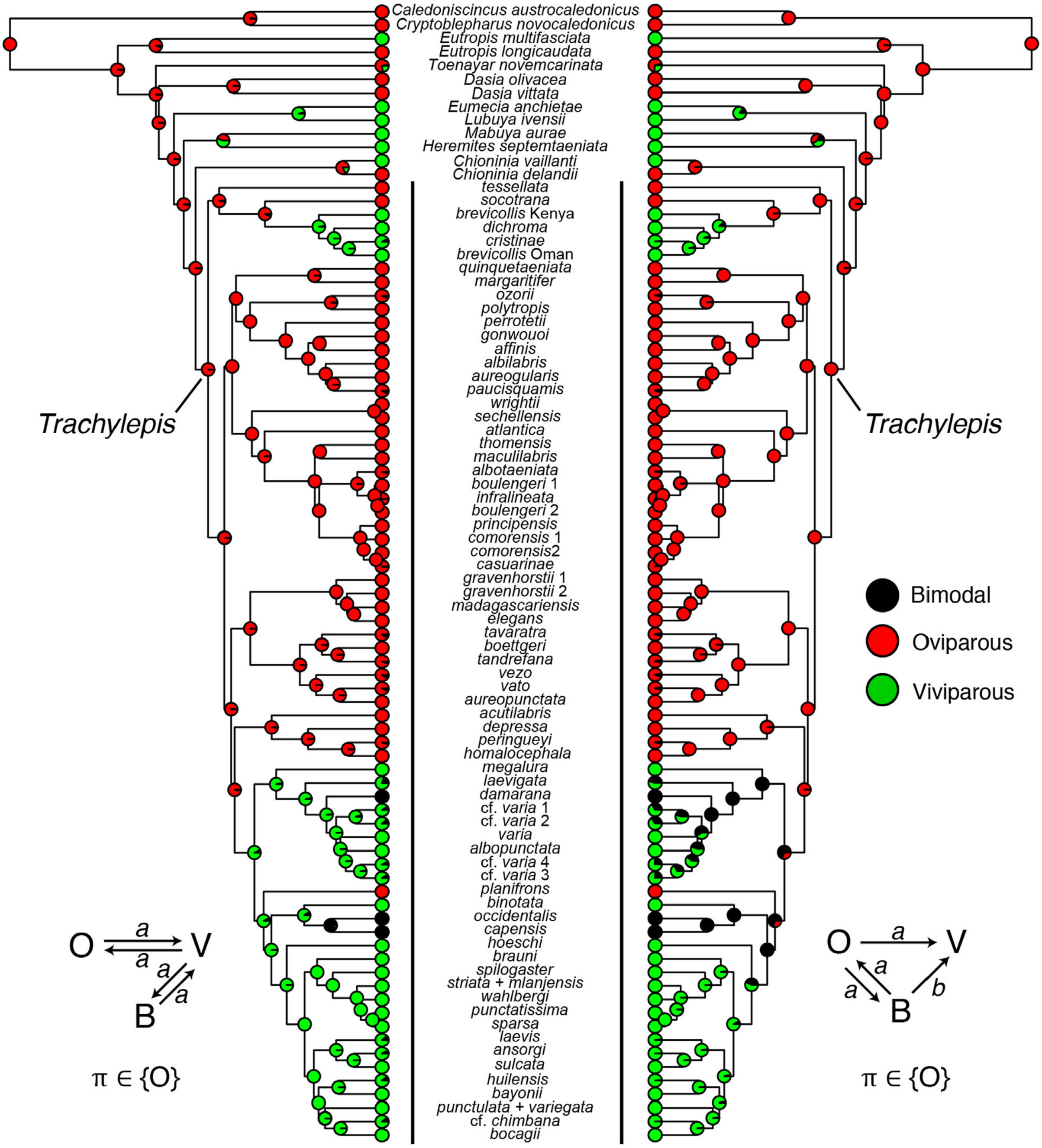

Fig. 2. Stochastic character mapping ancestral reconstruction of parity mode under alternative models of evolution. Left: reproductive mode evolution under the best-fit model among the full set of models; Right: reproductive mode evolution under the best-fit model among the subset of models that do not allow transitions from viviparity to oviparity or from viviparity to bimodal parity. Parity mode transition-rate models are indicated at the lower left and lower right of phylogenies: O = oviparous, V = viviparous, B = bimodal parity; transition-rate parameters are shown at arrows of transition-rate models.

of Mabuyinae was oviparous. Six MP reconstructions were equally parsimonious, each supporting nine parity mode transitions within Mabuyinae and five transitions within *Trachylepis* (Figs. S12–S18). Each of the six MP reconstructions support two transitions from viviparity to bimodal parity within *Trachylepis*. Additionally, half of the MP reconstructions support two transitions from oviparity to viviparity plus one transition from viviparity to oviparity, whereas the other MP reconstructions support three transitions from oviparity to viviparity and no viviparity to oviparity transitions (Figs. S12–S18).

Using maximum likelihood ancestral state reconstruction, we recovered identical ancestral state estimates when we included or omitted species for which parity mode was unknown, and, therefore, we only show our results for the analyses that included the missing-data species (Fig. 2). The best-fit model of parity mode evolution among all parity mode transition-rate models examined (n = 870 models; hereafter called the full set of models) is the same when $\pi \in \{O\}$ or $\pi \in \{O, V\}$, but differs slightly when $\pi \in \{O, V, B\}$ (Table 1; Fig. 2). When $\pi \in \{O\}$ or $\pi \in \{O, V\}$, the best-fit transition-rate model has a single transition-rate parameter, *a*, that defines the rate of forward and reverse transitions between oviparity and viviparity and forward and reverse transition rates between bimodal parity and viviparity; transition rates between oviparity and bimodal parity are zero. When $\pi \in \{O, V, B\}$, the best-fit transition rate model has a single transition-rate parameter, *a*, that defines the rate of forward and reverse transitions between

Table 1
Best-fit substitution models of the Full (n = 870 models) and Constrained (n = 47 models) sets of reproductive mode transition-rate models that we implemented in SIMMAP. The Constrained set of models is the subset of models from the Full set for which transitions from viviparity to bimodal parity or oviparity cannot occur. Oviparity (O), viviparity (V), bimodal parity (B); π = the set of reproductive states possible at the root of the phylogenetic tree.

Model set	π	Best-fit transition-rate model	AIC
Full	O, V, or B	Model 501: $O \leftrightarrow V = V \leftrightarrow B = B \rightarrow O > 0$; $O \rightarrow B = 0$	114.652
Full	O or V	Model 497: $O \leftrightarrow V = V \leftrightarrow B > 0$; $B \leftrightarrow O = 0$	113.893
Full	O	Model 497: $O \leftrightarrow V = V \leftrightarrow B > 0$; $B \leftrightarrow O = 0$	112.670
Constrained	O, V, or B	Model 55: $O \rightarrow V = O \leftrightarrow B \neq B \rightarrow V > 0$; $V \rightarrow O = V \rightarrow B = 0$	117.758
Constrained	O or V	Model 55: $O \rightarrow V = O \leftrightarrow B \neq B \rightarrow V > 0$; $V \rightarrow O = V \rightarrow B = 0$	116.954
Constrained	O	Model 55: $O \rightarrow V = O \leftrightarrow B \neq B \rightarrow V > 0$; $V \rightarrow O = V \rightarrow B = 0$	115.568

oviparity and viviparity, forward and reverse transitions between bimodal parity and viviparity, and forward (but not reverse) transitions from bimodal parity to oviparity. Regardless of the constraint imposed on π, the MRCA of all *Trachylepis* species is inferred to have been oviparous. Similarly, the MRCA of *Trachylepis* and each of the other genera is inferred to have been oviparous. Within *Trachylepis*, viviparity is estimated to have evolved from oviparity twice: once along the stem of the *brevicollis*, and additionally along the stem of the clade that includes all descendents of the MRCA of *T. megalura* and *T. bocagii*. Additionally, regardless of the prior on π, oviparity is estimated to have evolved from viviparity three times: (1) within *T. planifrons*, (2) within *T. damarana* (a bimodal parity species), and (3) within an ancestor of the clade containing *T. capensis* and *T. occidentalis* (bimodal parity species).

Among the subset of models that restrict transitions from viviparity to oviparity and from viviparity to bimodal parity (n = 47; hereafter called the constrained set of models), the best-fit model of parity mode evolution is the same regardless of whether $\pi \in \{O, V, B\}$, $\pi \in \{O, V\}$, or $\pi \in \{O\}$. The best-fit model among the constrained set of models has two transition-rate parameters: one parameter, *a*, that determines the rate of transitions from oviparity to viviparity, oviparity to bimodal parity, and bimodal parity to oviparity, and a second parameter, *b*, that determines the rate of transitions from bimodal parity to viviparity (Table 1; Fig. 2). The MRCA of *Trachylepis* is estimated to have been oviparous; similarly, the MRCA of *Trachylepis* and each of the other genera is inferred to have been oviparous. Transitions from oviparity to bimodal parity are estimated to have occurred once, along the stem of the clade that includes all descendents of the MRCA of *T. megalura* and *T. bocagii*. Furthermore, within *Trachylepis*, transitions from bimodal parity to viviparity are inferred to have occurred six times: (1) along the branch leading to *T. megalura*, (2) along the branch leading to *T. laevigata*, (3) along the branch leading to the clade that includes *T.* cf. *varia* 1 and 2, (4) along the branch leading to the clade containing all descendents of the common ancestor of *T. albopunctata* and *T. varia*, (5) along the branch leading to *T. binotata*, and (6) along the branch leading to the clade that includes all descendents of the common ancestor of *T. hoeschi* and *T. bocagii*. Transitions from oviparity to viviparity are inferred to have occurred within *Trachylepis* once, along the branch leading to the *brevicollis* group. Lastly, within *Trachylepis*, a single transition from bimodal parity to oviparity is predicted, along the branch leading to *T. planifrons*.

4. Discussion

4.1. Taxonomic implications

We estimated phylogenetic relationships among 67 *Trachylepis* species or species-level lineages, including 11 species that have not been included in earlier phylogenetic studies. For species that have been included in earlier phylogenetic studies, we recovered similar phylogenetic relationships (Fig. 1) (Allen et al., 2017; Castiglia et al., 2006; Ceríaco et al., 2016; Lima et al., 2013; Lima et al., 2014; Metallinou et al., 2016; Portik et al., 2010; Portik and Bauer, 2012; Rocha et al., 2010; Rocha et al., 2016; Sindaco et al., 2012; Weinell and Bauer, 2018; Whiting et al., 2006). However, we found some differences from previous phylogenetic studies that reflect our increased within-species sampling. Portik and Bauer (2012) recovered *T. punctulata* and *T. variegata* to each be monophyletic sister species, whereas our results strongly support *T. punctulata* to be paraphyletic with respect to *T. variegata*. Additionally, we recovered *T. principensis* to be the sister group to a clade containing *T. casuarinae* embedded within *T. comorensis*, which suggests that *T. principensis* recently colonized Príncipe Island from the Comoros (Fig. 1). In contrast, the position of *T. principensis* was unresolved in the study by Rocha et al. (2010), Ceríaco et al. (2016) did not include samples of *T. comorensis* for comparison with *T. principensis*. Furthermore, we included multiple *T. boulengeri* samples and recovered this species to be paraphyletic with respect to *T. infralineata*, whereas Rocha et al. (2010) included a single individual of *T. boulengeri* (as "*T. maculilabris* Mozambique") that was recovered as the sister lineage to *T. infralineata*. *Trachylepis infralineata* and *T. boulengeri* differ considerably in their color patterns (Spawls et al., 2018; Brygoo, 1981), and, therefore, we prefer to continue to recognize these species as valid until additional population-level sampling can be undertaken.

Species and subspecies that we included in our phylogenetic analyses that have not been included in previous studies include *Trachylepis sulcata ansorgi*, *T. aureogularis*, *T. bayonii bayonii*, *T. bayonii huilensis*, *T. bocagii*, *T. brauni*, *T.* cf. *chimbana*, *T. laevis*, *T. mlanjensis*, *T. planifrons*, and *T. sparsa*. We treat *T. paucisquamis* as a full species, rather than as a subspecies of *T. polytropis*, because we recovered *T. paucisquamis* to be more closely related to *T. albilabris* and *T. aureogularis*, than to *T. polytropis* (Fig. 1). Furthermore, *Trachylepis sulcata ansorgi*, *T. bayonii huilensis*, and *T. homalocephala peringueyi* may eventually be recognized as full species, considering that each is deeply genetically diverged from other *Trachylepis*, but we refrain from elevating these taxa to full species until range-wide genetic sampling is conducted. *Trachylepis aureogularis* is usually treated as a subspecies of *T. albilabris* (Uetz et al., 2018), but is considered to be a distinct species by Trape et al. (2012). Our analyses are ambiguous as to whether *T. aureogularis* is more closely related to the nominate (Central African) populations of *T. albilabris* or to *T. paucisquamis* (Fig. 1), but we support Trape et al.'s (2012) decision to recognize *T. aureogularis* as a full species considering that it is relatively deeply genetically divergent from *T. albilabris* and from *T. paucisquamis*, and because of its allopatric distribution and color pattern differences Trape et al. (2012).

We follow Marques et al. (2018) in using the name *Trachylepis albopunctata* for most Angolan and Zambian populations of what are usually called *Trachylepis varia*. Boulenger (1887) synonymized *Euprepes Olivierii* var. *albo-punctatus* Bocage, 1867 and *Euprepes angolensis* Bocage, 1872 with *T. varia* (Peters, 1867). However, Weinell and Bauer (2018) showed that Angolan and Zambian populations of the *T. varia* complex are united as a clade distinct from *T. varia sensu stricto*. The name *albopunctata* is older than *angolensis*, and, therefore, *T. albopunctata* is assignable to most Angolan and Zambian populations formerly treated as *T. varia*.

Broadley (1975) considered *T. chimbana* to be closely related to *T. punctulata* and to *T. variegata*, and that these three species along with with *T. lacertiformis* together form the *lacertiformis* group (here called the *variegata* group). Furthermore, based on the more lateral position of the nostril on the snout of *T. bocagii* compared to the species in Broadley's *lacertiformis* group, Broadley (1975) did not consider *T. bocagii* to be a member of the *lacertiformis* group, and noted that the general build of *T. bocagii* is more like that of *T. sulcata*. However, our results strongly support *T. bocagii* to be the sister species of *T.* cf.

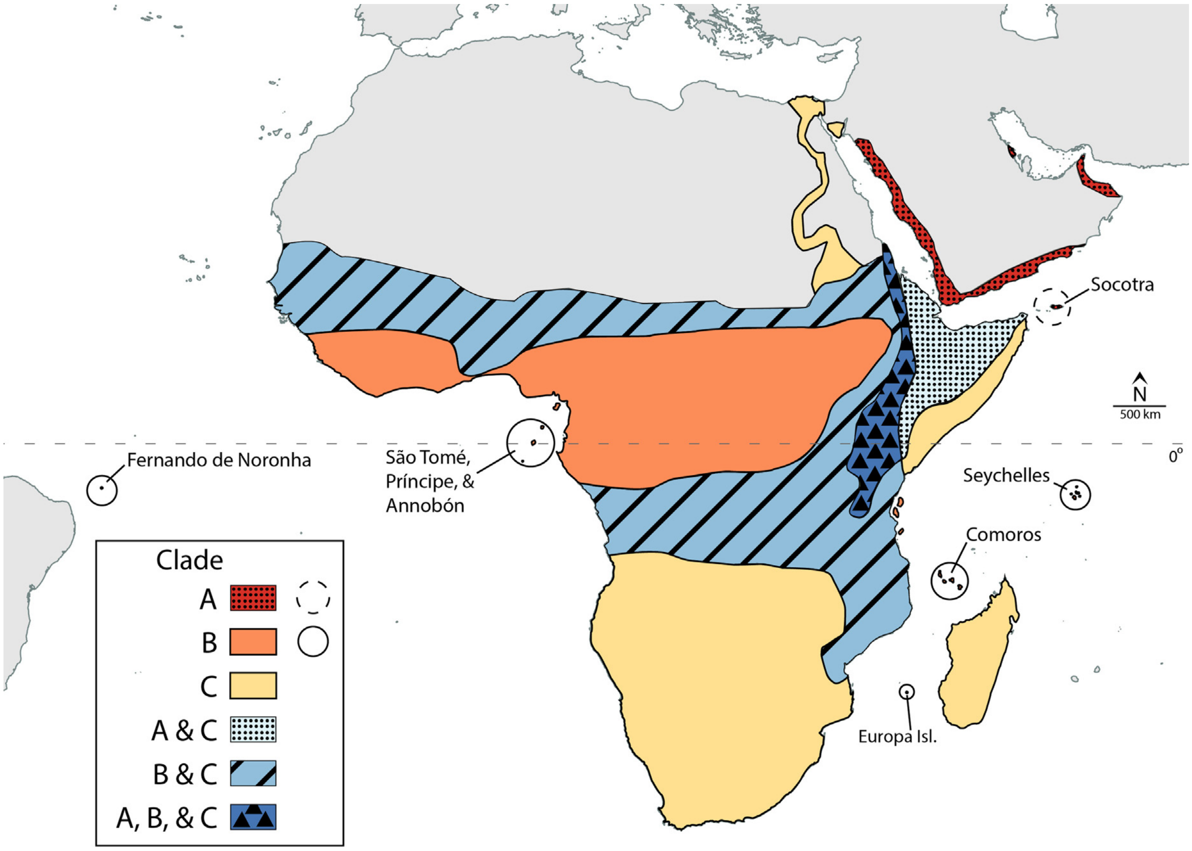

Fig. 3. Geographic distributions of the three major *Trachylepis* clades.

chimbana, and that both of these species form a clade sister to the *T. punctulata/variegata* clade (Fig. 1). Furthermore, we found strong support for the placement of *T. bayonii bayonii* + *T. bayonii huilensis* as the sister clade to *T. bocagii* + *T.* cf. *chimbana* + *T. punctulata/variegata*. The *variegata* group is supported by the shared, derived condition of having the nostrils placed anterior to the rostral-first labial scale suture (Broadley, 1975; pers. obs.).

Trachylepsi laevis is a crevice-dwelling species with a highly derived, dorsoventrally compressed body plan. Although Boulenger (1908) correctly recognized *T. laevis* as a member of what was then *Mabuya*, Steyn and Mitchell (1965) placed *T. laevis* in a new genus, *Oelofsia*. Subsequent authors recognized *T. laevis* as a member of the *Mabuya* group and have suggested that it is closely related to *T. sulcata* (Welch, 1982; Branch, 1998; Greer and Broadley, 2000; Greer et al., 2000), a species that exhibits a head and body that is intermediately dorsoventrally compressed between to *T. laevis* and other *Trachylepis* (Paluh and Bauer, 2017). Paluh and Bauer (2017) showed that both *T. laevis* and *T. sulcata* lack pterygoid teeth, which are present in other *Trachylepis* species osteologically examined thus far, and that *T. laevis* and *T. sulcata* also differ in many other aspects of their skull anatomy. Our results confirm the placement of *T. laevis* within *Trachylepis*, and the sister relationship between *T. laevis* and *T. sulcata*.

Trachylepis planifrons has been suggested to be closely related to *T. perrotetti*, based on its similar color pattern and scalation characters (Broadley and Cotterill, 2004). *Trachylepis perrotetti upembae* exhibits an intermediate body shape between *T. p. perrotetti*, which has a robust body and a short tail, and *T. planifrons*, which has a slender body and a long tail (Loveridge, 1956). However, our results do not support a close relationship between *T. planifrons* and *T. perrotetti*. *Trachylepis perrotetti* is a member of the *affinis* group, which occurs primarily in West and Central Africa, whereas *T. planifrons* is a member of the OBV group, which primarily occurs in eastern and southern areas of Africa (Fig. 1). Moreover, *T. planifrons* is arboreal (Spawls et al., 2018), whereas *T. perrotetti* is terrestrial (Trape et al., 2012).

Broadley (1977) proposed that *T. brauni*, *T. punctatissima*, *T. sparsa*, *T. striata*, *T. spilogaster*, and *T. wahlbergi* were all closely related to one another, and called this group the *striata* group, which our results strongly support as monophyletic. Furthermore, Broadley (1977) considered *T. mlanjensis* to be too morphologically similar to *T. punctatissima* to warrant its recognition as a distinct taxon, but we recovered *T. mlanjensis* to be embedded within *T. striata*, and *T. punctatissima* is sister to either *T. sparsa* (Fig. 1) or a clade containing *T. sparsa* + Angolan *T. wahlbergi* (ML analysis). Additionally, *T. wahlbergi* is often treated as a subspecies of *T. striata* (Uetz et al., 2018).

Trachylepis brauni has been associated with the *T. striata* subgroup, based on morphological and color pattern characters (Broadley, 1977; Broadley, 2000), and genetic data variably support or reject this hypothesis. The KIF24 (nuclear) gene tree supports *T. brauni* as a member of the *striata* subgroup, whereas the 16S (mitochondrial) gene tree supports *T. brauni* as a member of the *variegata* subgroup. Furthermore, the concatenated phylogenetic analyses agree with the KIF24 tree with respect to the position of *T. brauni*. Incongruence among gene trees can occur from historical or ongoing gene flow between different populations or species, or from incomplete lineage sorting during the process of diversification. We are unable to differentiate among these alternative scenarios with our current dataset, and broader sampling across the genome of members of the *T. striata* group is needed to identify alternative processes leading to gene tree discordance.

Our phylogenetic results support *T. wahlbergi* as paraphyletic (Fig. 1), despite its distinct color pattern and the geographic cohesiveness of its distribution. Based on specimens that appear intermediate between different *striata* group species, Broadley (1977) identified areas where hybridization between *striata* group species may occur. In particular, Broadley (1977) noted (1) a broad region of

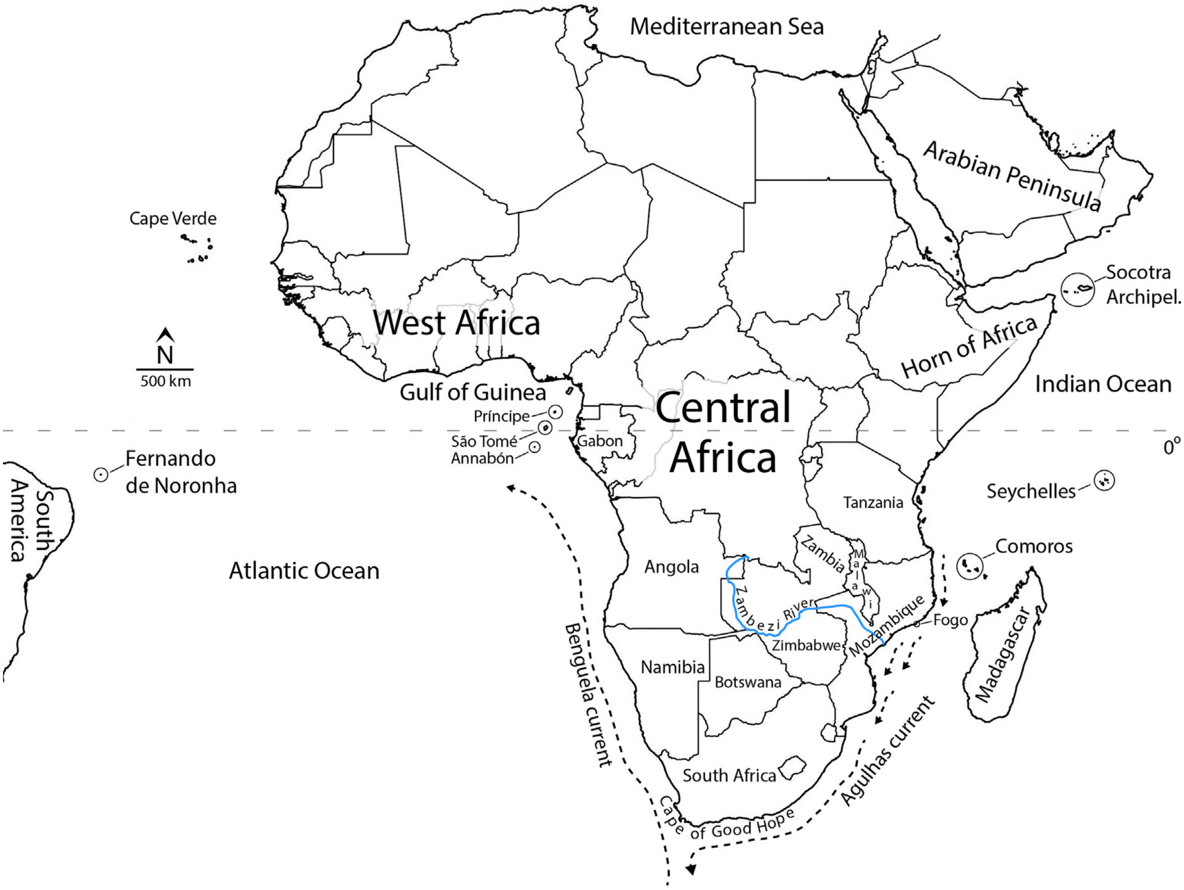

Fig. 4. Map of the study area, including all places mentioned by name in this article.

possible hybridization between *T. punctatissima* and *T. striata* in eastern Botswana; (2) potential hybridization between *T. striata* and *T. wahlbergi* along the Zambezi River in Mozambique, and in Malawi, and northern Zambia; and (3) potential hybridization between *T. sparsa* and *T. punctatissima* in southern Botswana. Our results do not provide insight into the extent or existence of gene flow between members of the *striata* group. Therefore, a phylogenetic study focused on the *striata* group that incorporates dense geographic sampling within each species is necessary to confidently determine species boundaries within this group.

4.2. Biogeography

Several large *Trachylepis* clades are geographically cohesive, although major clades B and C both contain one or more groups that are relatively wide-ranging, as well as several groups that have undergone regional diversification (Figs. 1, 3 and 4). Clade A is distributed from northern Tanzania across the Horn of Africa, the Arabian Peninsula, and the Socotra Archipelago (Fig. 3). Our results are consistent with earlier studies that suggest that this group has independently colonized the Socotra Archipelago at least twice (Sindaco et al., 2012), during the last 28 Ma (Figs. 1 and 3).

Clade B contains several wide-ranging groups, particularly the *quinquetaeniata* and *maculilabris* groups, whereas the Seychelles group is endemic to the Seychelles Archipelago, and the *affinis* group is confined to Central and West Africa, and has undergone substantial diversification (Figs. 1, 3 and 4). The estimated mean divergence time of 25 Ma (95% highest posterior density 21.4–28.7 Ma) between the Seychelles group and the *maculililabris* group suggests that *Trachylepis* colonized the Seychelles from Africa during the Oligocene or early Miocene, which is consistent with over-water dispersal rather than Gondwanan vicariance (Townsend et al., 2011). Similar to a previous study by Lima et al. (2013), we recovered the Malagasy group to be monophyletic, despite the fact that other groups (particularly the *maculilabris* group) have dispersed long distances over water numerous times, and presumably could have survived oceanic dispersal to Madagascar. The relatively early colonization of Madagascar by the Malagasy group (~22–32 Ma), compared to the relatively recent (< 15 Ma) bouts of Indian Ocean dispersal by the *maculilabris* group, suggests that historical competition between arriving *maculilabris* group species and well-established Malagasy group species might explain why the *maculilabris* group was unsuccessful at colonizing Madagascar, despite having undergone a species radiation on various Indian Ocean islands.

In addition to colonizing islands in the Indian Ocean, multiple lineages in clade B have colonized archipelagos in the Atlantic Ocean, including the Fernando de Noronha Archipelago and islands in the Gulf of Guinea. Divergence between *T. atlantica*, which is endemic to the island of Fernando de Noronha, Brazil, and the rest of the *maculilabris* group is estimated to have occurred 18.8–26.4 Ma, an age that is older than the oldest rocks (8–12 Ma) known from Fernando de Noronha (Lopes and Ulbrich, 2015). These results suggest that *T. atlantica* may have belonged to a larger (more diverse) clade that was sister to the rest of the *maculilabris* group, and that the mainland lineages in this larger clade went extinct following a relatively recent dispersal (< 12 Ma) of *T. atlantica* to Fernando de Noronha Island.

Our results are consistent with multiple dispersal events of the *affinis* and *maculilabris* groups (both within clade B) to islands in the Gulf of Guinea, during the last 2–15 Ma. In particular, our results suggest that *T. ozorii* dispersed from continental Africa to Annobón Island 4.7–15.6 Ma, and that *T. thomensis* dispersed from Africa to São Tomé Island 9.8–14.3 Ma. Additionally, our results support dispersal of *T. principensis* from either the Comoros Archipelago or Fogo Island (both in the southwestern Indian Ocean) to Príncipe Island 2–8.5 Ma, which would have required over-water dispersal around the Cape of Good Hope — a scenario that is plausible if paleocurrents were similar to the modern Mozambique, Agulhas, and Benguela Currents (Fig. 4). Alternatively, *T. principensis* may have dispersed from West or Central Africa, prior to extinction of the mainland lineage. Alternatively, if the ancestor of *T. principensis*,*T. comorensis*, and *T. casuarinae* was a widespread mainland species, *T. principensis* may have dispersed to Príncipe Island from West or Central Africa, rather than from the Comoros, with subsequent extinction of the mainland lineage leading to the inferred sister relationship between *T. principensis* and *T. comorensis* + *T. casuarinae*. Our estimates for the timing of colonization of *Trachylepis* on the Gulf of Guinea islands are consistent with age estimates for these islands, which have been dated to be as young as 15 Ma for São Tomé Island, to as old as 30 Ma for Príncipe Island (Déruelle et al., 2007).

Unlike clades A and B, which have each undergone multiple over-water dispersal events, our results, which agree with Lima et al. (2013), suggest that clade C only successfully colonized an oceanic island once: Madagascar, resulting in the Malagasy group. The *varia* group, *variegata* subgroup, and *striata* subgroup are each wide-ranging across southern and eastern Africa (Castiglia et al., 2006; Portik and Bauer, 2012; Weinell and Bauer, 2018), whereas *T. binotata* and *T. hoeschi*, the *depressa* group, and the *capensis* and *sulcata* subgroups are confined to southern and south-western Africa (Portik et al., 2010; Branch, 1998). The robustly sampled phylogeny presented herein provides a backbone for testing future hypotheses about biogeography and trait evolution within the larger context of Old World scincids.

4.3. Parity mode evolution

Trachylepis includes nearly half of all species in the *Mabuya* group — a circumtropical clade of skinks that is emerging as a model system for studying reproductive mode evolution. Consistent with the hypothesis that viviparity is an adaption to cold environments (Shine, 1985), viviparous *Trachylepis* species tend to occur in relatively cold environments compared to the oviparous species (Fig. 5). Blackburn and Vitt (1992) suggested that viviparity has evolved from oviparity four or more times in the *Mabuya* group. Earlier authors have studied the placenta of species with highly specialized forms of viviparity in the genera *Mabuya*, *Eumecia*, and *Lubuya* (Flemming and Branch, 2001; Flemming and Blackburn, 2003; Ramírez-Pinilla, 2006; Ramírez-Pinilla et al., 2011; Blackburn and Flemming, 2012; Wooding et al., 2010). Cornelis et al. (2017) identified an endogenous retroviral gene (*Mab-Env1*) that may have been acquired by an ancestor of *Mabuya*, *Trachylepis*, *Chioninia*, *Heremites*, *Eumecia*, and *Lubuya*, and the gene may play an important functional role for the placenta of *Mabuya*. However, *Trachylepis* species are not known to have highly specialized placentae, and future research should focus on whether *Mab-Env1* plays a role in viviparity in *Trachylepis*. In any case, parity mode transitions have occurred multiple times in *Trachylepis*, with oviparity, viviparity, and bimodal parity all represented, suggesting that this genus may be preadapted for parity mode changes. Our phylogeny of *Trachylepis* will enable research into the reproductive mode evolution of this group and complement research that has been conducted on other species in Mabuyinae.

Many authors consider transitions from viviparity to oviparity to be impossible, because specialization towards viviparity may be accompanied by losses of mechanisms needed to build an eggshell (Blackburn, 2015; Griffith et al., 2015). Nevertheless, transitions from viviparity to oviparity have been suggested for other squamate groups (e.g., *Lachesis* and *Eryx*), although such reversals have at best only received equivocal support (Lynch and Wagner, 2010; Fenwick et al., 2012). However, we found that for *Trachylepis*, the best-fit model of parity mode evolution allows transitions from viviparity back to oviparity, suggesting that transitions to viviparity may be reversible if additional specializations (such as a primarily placenta-dependent nutrient supply) have not also occurred. Unlike in *Eumecia*, *Lubuya*, and New World Mabuyinae, which have highly specialized forms of viviparity, viviparity in *Trachylepis* may be relatively unspecialized (Flemming and Branch, 2001; Flemming and Blackburn, 2003; Ramírez-Pinilla et al., 2011; Blackburn and Flemming, 2012). As a result of having a relatively unspecialized form of viviparity, reproductive mode can be difficult to distinguish in pregnant or gravid *Trachylepis*, which has resulted in many incorrect reports of parity mode in the literature (Visser, 1975; Blackburn, 1993). Therefore, we suspect that our best-fit model of parity mode evolution may be possible for *Trachylepis*, and that viviparity to oviparity mode transitions can be reversible if there has been little to no specialization towards more extreme forms of viviparity.

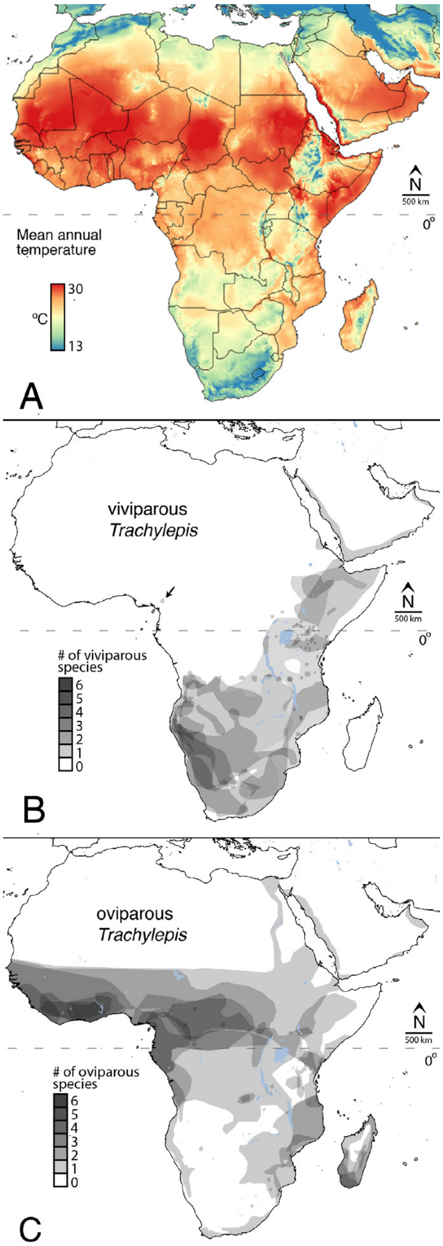

Fig. 5. Environmental temperature and parity mode distributions across Africa. Mean annual temperature (a); *Trachylepis* species richness of viviparous (b), oviparous (c), and bimodal parity species (d). Viviparous species tend to occur in colder areas compared to oviparous species.

We recovered a somewhat different pattern of reproductive mode evolution when we only considered constrained models that do not allow transitions from viviparity to oviparity (including viviparity to bimodal parity) (Fig. 2, right). The best-fit constrained model predicts more reproductive mode transitions compared to the overall best-fit model. Additionally, the best-fit constrained model suggests that viviparity and oviparity were able to persist together in at least several lineages for millions of generations (i.e., without fixation of either parity mode), despite the fact that bimodal parity appears to be relatively uncommon among modern species (Brown-Wessels, 1989) (Fig. 2). Southern Africa is climatically heterogeneous, and perhaps widely distributed species were able to maintain bimodal reproduction if selection favored oviparity in some populations and viviparity in other populations. One of the best understood cases of bimodal reproduction is in the lacertid species *Zootoca vivipara*, which has subspecies that are either viviparous or oviparous, and syntopic viviparous and oviparous populations are reproductively isolated (Guillaume et al., 1997; Cornetti et al., 2014; Cornetti et al., 2015). Therefore, bimodal reproduction in *Z. vivipara* is an artifact of the current species taxonomy. Reports of bimodal parity remain rare, and *Trachylepis* species currently classified as having bimodal parity await genetic confirmation of monophyly between oviparous and viviparous populations.

5. Conclusions

The monophyly of *Trachylepis* is supported, whereas the monophyly of some traditionally recognized species is rejected, including *T. brevicollis*, *T. comorensis*, *T. punctulata*, and *T. striata*. Three large clades were identified within *Trachylepis*, each of which have likely undergone long-distance dispersal to colonize oceanic islands. Clade A colonized the Socotra Archipelago (northern Indian Ocean) twice, clade B successfully dispersed to many islands in the Indian and Atlantic Oceans, and clade C colonized Madagascar. Our results support oviparity as the ancestral parity mode state of *Trachylepis*, and that viviparity evolved from oviparity twice within *Trachylepis*, including once within clade A and once within clade C. Our results also support a model of reproductive evolution that allows for reversibility from viviparity to oviparity, a process that is not generally accepted. If viviparity to oviparity transitions are not possible, bimodal reproduction may have persisted for millions of years within many lineages of the OBV group. Future studies are needed to determine if parity mode is polymorphic within populations of *Trachylepis* species that are currently considered to have bimodal parity, or if viviparous and oviparous clades exist within bimodal species.

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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.2019.04.002.

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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.)
Cytb	[9]CYTB-F.1	TGAGGACARATATCHTTYTGRGG	forward (PCR & Seq.)
Cytb	[9]CYTB-R.2	GGGTGRAAKGGRATTTTATC	reverse (PCR & 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.)
CMOS	[9]cmosG77.1	TGGCYTGGTGCWGCATTGACT	forward PCR & Seq.)
CMOS	[9]cmosG79	CCTTTAAGGAGTTCAGGAGCAC	reverse (PCR & Seq.)
CMOS	[9]cmosG73.1	GGCTRTAAARCARGTGAAGAAA	forward (PCR & Seq.)
CMOS	[9]cmosG74.1	GARCWTCCAAAGTCTCCAATC	reverse (PCR & Seq.)
BDNF	[8]BDNF-F1	ACCATCCTTTTCCTKACTATGG	forward (PCR & Seq.)
BDNF	[8]BDNF-R1	CTATCTTCCCCTTTTAATGGTC	reverse (PCR & Seq.)

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Table S2. Individuals sampled in this study. GenBank accession codes in bold indicate new sequences generated for this study. For chimeras, superscripts match GenBank and locality information to a particular individuals catalog or field number. Acronyms associated with tissues or specimens in this study include: ACZC (Angelica Crottini field numbers); ADL (Adam D. Leaché field numbers); AMB and MCZ A (Aaron M. Bauer field numbers); BE, JR, TJR, and TE (Sindaco et al. [2012] sample identification numbers); BM (Bryan Maritz field numbers); BMNH (The Natural History Museum, London [formerly British Museum of Natural History]); BRK (Benjamin R. Karin field numbers); AM R (Australian Museum, Sydney); BYU (Bean Museum, Brigham Young University, Utah); CAS (California Academy of Sciences); CDS (Cameron D. Siler field numbers); CT (Colin Tilbury field numbers); EBG or ELI (Eli Greenbaum field numbers); EBU (Evolutionary Biology Unit, South Australian Museum, Adelaide); FGZC (Frank Glaw field numbers); FMNH (Field Museum of Natural History, Chicago); HKV (Harold K. Voris field numbers); INBAC (Instituto Nacional da Biodiversidade e Áreas de Conservaçao, Angola); JBS (Joseph B. Slowinski field numbers); JVV (Jens V. Vindum field numbers); JM (Johan Marais field numbers); WRB, AG, ARG, JET, and KC (Bill Branch field numbers); KTH (Krystal Tolley field numbers); KU (University of Kansas Biodiversity Institute); KUZ (Kyoto University Museum); LJW (Luke J. Welton field numbers); LSUMZ (Louisiana Museum of Natural History); Mab and L (Allison Whiting tissue numbers); MB (Mike Bates field numbers); MBUR (Marius Burger field numbers); MCZ FSA, and MCZ Z (Museum of Comparative Zoology field numbers); MCZ R (Museum of Comparative Zoology, Harvard University, Cambridge); MGR (Michael Griffin field numbers); MH, GC, and PB (Rocha et al. [2010] sample identification numbers); MRT (Miguel T. Rodrigues field numbers); MUHNAC.MB (Museu Nacional de História Natural e da Ciência, Lisbon, Portugal); MVZ (Museum of Vertebrate Zoology, University of California at Berkeley); NCSM (North Carolina Museum of Natural Sciences); PEM R (Port Elizabeth Museum); PEM-FRN and CAR (Port Elizabeth Museum, field series); PGF (Phillip. G. Frank field numbers); PW (Philipp Wagner field numbers); RAX (Christopher Raxworthy field numbers); RAN (Ronald A. Nussbaum field numbers); RCB (Rayna C. Bell field numbers); RCD (Robert C. Drewes field numbers); RFI (Robert F. Inger field numbers); RUZM-ZB (Razi University Zoological Museum, Kermanshah, Iran [Zahed Bahmani collection]); SBH (S. Blair Hedges field numbers); TJC (Timothy J. Colston field numbers); UADBA (Department of Animal Biology, University of Antananarivo, Madagascar); UMMZ (Museum of Zoology, University of Michigan, Ann Arbor); USNM and USNM-FS (National Museum of Natural History, Washington, D.C.); UWBM (University of Washington Burke Museum); WC and WC-ANG (Werner Conradie field numbers); ZCMV (Miguel Vences field numbers); ZMKU (Zoological Museum at Kasetsart University, Bangkok); ZFMK (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn); ZSI (Zoological Survey of India); ZSM (Zoologisches Staatssammlung, München). Most samples in private collections are currently awaiting accessioning in CAS, MCZ, the National Museum of Namibia, or the National Museum of Ethiopia.

Species	**Catalog #**	**Other ID #**	**Locality**	**Lat., Lon.**	**16S**	**12S**	**Cytb**	**RAG1**	**CMOS**	**BDNF**	**KIF24**	**ND2**	**BRCA2**
Cryptoblepharus novocaledonicus	AM R163245	——	Île Aventure, New Caledonia	S22.683, E167.45	KX231460	——	——	KX231390	KX231489	KX231444	KX231531	KX231475	KX231543
Caledoniscincus austrocaledonicus chimera	^{1}AM R163262	^{2}EBU 3522	^{1}Île Koomo, New Caledonia; ^{2}New Caledonia	^{1}S22.616, E167.4; ^{2}unknown	^{1}KX231459	^{2}EU567931	^{2}EU567835	^{1}KX231389	^{1}KX231488	^{1}KX231443	^{1}KX231530	^{1}KX231474	^{1}KX231542
Eutropis longicaudata chimera	^{1}ZMKU R00704; ^{2}FMNH 255526	^{2}HKV 63167	^{1}Nong Bua Lamphu, Thailand; ^{2}Boualapha District, Laos	^{1,2}unknown	^{1}KX231449	^{2}DQ239220	^{2}DQ239139	^{1}KX231379	^{1}KX231479	^{1}KX231433	^{1}KX231523	^{1}KX231465	^{1}KX231536
Eutropis multifasciata chimera	^{1}FMNH 269170; ^{2}KU 302890; ^{3}FMNH 255530	^{1}RFI 52525; ^{2}CDS 145; ^{3}HKV 63475	^{1}Penyilam, Bintulu Division, Sarawak, Malaysia; ^{2}Barangay Duyong, Pandan, Antique Province, Philippines; ^{3}Mounlapamok District, Laos	^{1}N2.90, E113.383; ^{2}N11.76, E122.04	^{1}KX231451	^{2}JF497861	^{3}DQ239138	^{1}KX231381	^{1}KX231481	^{1}KX231435	^{1}KX231524	^{1}KX231467	^{1}KX231538
Lubuya ivensii	——	PW87	Hillwood Farm, Nahila Reserve, Mwinilunga, Zambia	——	KX231456	——	——	KX231386	KX231485	KX231440	KX231529	KX231471	——
Heremites septemtaeniata chimera	^{1}ZFMK 84085; ^{2}RUZM-ZB 5714	——	^{1}Kuh-e-Sahand, Iran; ^{2}Al-Jubaila, Iraq	^{2}N30.533, E47.80	^{1}KX364964	——	^{2}MF590412	^{1}KX365050	——	^{1}KX364972	^{1}GU931477	^{1}GU931546	——
Toenayar novemcarinata chimera	^{1}CAS 216022; ^{2}CAS 215714	^{1}JBS 5538; ^{2}JBS 4978	^{1}Na Htoe Gyi Township, Minsontaung Wildlife Sanctuary, Htan Taw Village, Mandalay Division, Myanmar; ^{2}Gon Nyin Bin Camp, Alaung Daw Kathapa National Park, Sagging Division, Myanmar	^{1}N21.422, E95.83; ^{2}N22.24, E94.605	^{1}KX364956	^{2}KT633603	——	^{1}KX365043	^{1}KX364990	^{1}KX364967	^{1}KX365009	^{1}KX365035	^{1}KX364983
Mabuya aurae chimera	^{1}CAS 231775	^{1}PGF 356; ^{2}SBH 268935	^{1}Manzanilla Beach, Trinidad Island, Trinidad and Tobago; ^{2}Union Island, Saint Vincent and the Grenadines	^{1}N10.454, W61.038	^{1}KX364959	^{2}JN227576	^{2}JN227555	^{1}KX365046	^{1}KX364993	——	——	——	^{1}KX364986
Eumecia anchietae	PEM R16779	——	Klein’s Camp, Loliondo Game Controlled Area, Mara, Tanzania	S1.845, E35.253	KX231448	——	——	KX231378	KX231478	KX231432	KX231522	——	KX231535
Dasia vittata chimera	^{2}KUZ 27168	^{1}BRK 391	^{1}Nanga Benin Longhouse, Kapit Division, Sarawak, Malaysia; ^{2}Matang, Borneo	^{1}N2.165, E113.08	^{1}KX231446	^{2}AB028771	——	^{1}KX231376	^{1}KX231477	^{1}KX231430	^{1}KX231520	^{1}KX231464	——
Dasia olivacea chimera	^{2}ZSI 10642	^{1}BRK 392	^{1}Nanga Benin Longhouse, Kapit Division, Sarawak, Malaysia	^{1}N2.165, E113.08	^{1}KX231445	^{2}JN990818	——	^{1}KX231375	^{1}KX231476	^{1}KX231429	——	^{1}KX231463	^{1}KX231533
Chioninia delalandii chimera	^{1}BMNH 2000.18	^{1}M45-45de4F; ^{2}Uma-R52	^{1}Cha das caldeiras, Fogo Island, Cape Verde Islands; ^{2}Fogo Island, Cape Verde Islands	——	^{1}AY151482	^{1}AF280185	^{1}AF280317	^{1}KX231373	^{2}AF335081	^{1}KX231427	^{1}KX231519	^{1}KX231461	^{1}KX231532
Chioninia vaillanti chimera	^{1}BMNH 2000.10	^{1}M50; ^{1}50Mva2St; ^{2}Uma-49Mva6F	^{1}Santa Cruz, Santiago Island, Cape Verde Islands; ^{2}Feijoal, Fogo Island, Cape Verde Islands	——	^{2}AY151483	^{2}AF280198	^{2}AF280330	^{1}KX231374	^{2}AF335088	^{1}KX231428	——	^{1}KX231462	——
Trachylepis acutilabris	——	AMB 6935; Mab126	Puros Rd, 80.9km W of Sesfontein, Kunene, Namibia	S18.831, E13.153	MK791990	MK791920	MK792137	MK791899	——	MK791760	——	——	——
Trachylepis acutilabris	PEM R24047	AG45	Namibe, Angola	S13.690, E12.912	MK792067	——	——	——	——	——	——	MK791976	——
Trachylepis acutilabris	CAS 223990	AMB 6901; Mab131	Torrabaai Rd, 63.4 Km W Of Kamanjab, Khorixas, Kunene, Namibia	S19.683, E14.319	MK791991	MK791919	MK792076	MK791898	——	MK791759	MK792138	MK791974	——
Trachylepis acutilabris	CAS 214651	AMB 6413; L090	Torra Bay Rd, 48 Km W Of Kamanjab, Khorixas, Kunene, Namibia	S19.654, E14.351	DQ238940	DQ239262	DQ239181	——	DQ239020	MK791761	——	——	——
Trachylepis affinis	BYU 62095	LJW 0088	Buea City and surrounding areas, Mt. Cameroon, Southwest, Cameroon	N04.198, E09.333	MK791992	——	——	MK791896	——	——	MK792139	MK791971	——
Trachylepis affinis	NCSM 88359	RCB 0079	Luba-Malabo Road, Bioko Sur, Bioko Island, Equatorial Guinea	N03.533, E08.6	MK791993	——	——	MK791913	——	——	MK792140	MK791972	——
Trachylepis affinis	PEM R5425	Mab02	Loango National Park, Ogooué-Maritime, Gabon	S02.345, E09.591	MK791995	MK791921	MK792078	MK791859	MK791824	MK791762	——	——	——

Table S2 (continued).

Species	Catalog #	Other ID #	Locality	Lat., Lon.	16S	12S	Cytb	RAG1	CMOS	BDNF	KIF24	ND2	BRCA2
Trachylepis affinis	PEM R5340	PEM-FNR# 174; MB 5629; Mab04	Rabi, Gabon	S01.797, E09.893	MK791994	MK791922	MK792077	MK791860	MK791825	MK791763	——	——	——
Trachylepis albilabris	PEM R5384	Mab07	"Rabi, Shell Gabon" [= Rabi Kounga oil field], Ogoué-Maritime, Gabon	S01.937, E09.881	MK791996	MK791923	MK792126	MK791861	MK791826	MK791764	——	——	——
Trachylepis albilabris	PEM R5422	Mab08	Loango National Park, Ogooué-Maritime, Gabon	S02.340, E09.595	MK791997	MK791924	MK792079	MK791862	MK791827	MK791765	——	——	——
Trachylepis albopunctata	PEM R21739	WC 1809; JET13; ARG183	13km N of Quilengues on road to Benguela, Huila, Angola	S13.972, E14.047	MG605608	——	——	MG605366	——	——	——	MG605224	MG605496
Trachylepis albopunctata	PEM R21738	WC 1832; JET26; ARG198	SE foothills of Mt Moko, on dirt track between Cuma and the Lobito-Huambo tar road, Huambo Province, Angola	S12.503, E15.225	MG605609	——	——	MG605367	——	——	MG605435	MG605225	MG605497
Trachylepis albotaeniata	——	PB27	Ngezi, Pemba Island, Tanzania	——	——	——	HM192727	——	——	——	——	——	——
Trachylepis albotaeniata	——	PB29	airport, Pemba Island, Tanzania	——	——	——	HM192726	——	——	——	——	——	——
Trachylepis atlantica	——	MRT 4427	Fernando de Noronha Island, Pernambuco, Brazil	——	DQ238913	DQ239235	DQ239154	——	DQ238993	——	——	——	——
Trachylepis atlantica	——	MRT 4428	Fernando de Noronha Island, Pernambuco, Brazil	——	DQ238914	DQ239236	DQ239155	——	DQ238994	——	——	——	——
Trachylepis atlantica	——	MRT 4429; L021	Fernando de Noronha Island, Pernambuco, Brazil	——	DQ238912	DQ239234	DQ239153	——	DQ238992	MK791766	——	——	——
Trachylepis aureogularis	MVZ 252612	#3344	Cocoa plantation, Ajenjua Bepo Forest Reserve, Eastern Region, Ghana	N06.362, W01.035	MK791998	——	——	MK791918	——	——	MK792141	MK791973	——
Trachylepis aureopunctata	UADBA#	RAN 54509	Ambalarano, Tsingy de Bemaraha Strict Nature Reserve, Antsalova, Madagascar	——	DQ238880	DQ239201	DQ239121	——	DQ238961	MK791767	——	——	——
Trachylepis aureopunctata	——	PEM-FNR# 437; Mab09	Toliara, Madagascar	——	KX364962	MK791925	MK792080	KX365049	KX364994	KX364970	KX365012	——	KX364987
Trachylepis aureopunctata	UMMZ 222169	RAN 56250; L116	Amoasary, Vohidava Mountain, Toliara Province, Madagascar	——	DQ238878	DQ239200	DQ239119	——	DQ238959	MK791768	——	——	——
Trachylepis bayonii bayonii	INBAC#	JVV 9273	Cangandala National Park, Malanje, Angola	S09.827, E16.650	MK791999	——	——	MK791911	——	——	MK792142	MK791978	MK791753
Trachylepis bayonii huilensis	——	AG201	3km NE of Tundavala, Huila, Angola	S14.806, E13.407	MK792071	——	——	——	——	——	——	MK791988	——
Trachylepis binotata	ZFMK 66426	——	Ruacana waterfall, Omusati, Namibia	——	KC345405	KC345345	——	——	KC345292	KC345182	——	——	——
Trachylepis binotata	MCZ R185902	MCZ A-38943	101km N of Opuwo, near Okangwati, Kunene, Namibia	S17.464, E13.328	MK792000	——	MK792131	MK791908	——	——	MK792143	——	——
Trachylepis bocagii	——	MCZ A-36458	Quiçama National Park, KAWA camp headquarters, Luanda, Bengo, Angola	S09.184, E13.371	MK792060	——	——	——	——	——	——	MK791979	——
Trachylepis bocagii	——	MCZ A-36456	Quiçama National Park, KAWA camp headquarters, Luanda, Bengo, Angola	S09.184, E13.371	MK792066	——	——	——	——	——	——	MK791980	——
Trachylepis bocagii	PEM R21735	WC 1823; ARG166; JET20	riverine forest on S bank of Kwanze River, Bengo Province, Angola	S09.772, E14.521	MK792001	——	——	MK791910	——	——	MK792171	——	——
Trachylepis boettgeri	UMMZ 208917	RAN 43033; L117	Ambatolampy, Vakinankaratra, Antananarivo, Madagascar	——	DQ238879	DQ239201	DQ239120	——	DQ238960	MK791769	——	——	——

Table S2 (continued).

Species	Catalog #	Other ID #	Locality	Lat., Lon.	16S	12S	Cytb	RAG1	CMOS	BDNF	KIF24	ND2	BRCA2
Trachylepis cf. *boettgeri*	ZSM 362.200	——	Ambatolampy, Madagascar	——	AY070355	AY070337	——	——	——	——	——	——	——
Trachylepis boulengeri	PEM R5533	Mab011	Nampula, Mozambique	S15.118, E39.268	KX231454	MK791926	MK792081	KX231384	KX231483	KX231438	KX231527	KX231470	KX231540
Trachylepis boulengeri	PEM R16179	Mab013	Mekula Mt. Camp, Niassa Game Reserve, Niassa, Mozambique	S12.049, E37.642	MK792003	MK791928	MK792083	MK791864	MK791828	MK791771	——	——	——
Trachylepis boulengeri	PEM R15451	Mab012	Malinga Pansi, Zambezi Delta, Mozambique	S18.677, E36.105	MK792002	MK791927	MK792082	MK791863	MK791846	MK791770	——	——	——
Trachylepis brauni	PEM R20128	CT578	Kitulo Plateau, Iringa, Tanzania	S09.073, E33.981	MK792004	——	——	——	——	——	MK792144	——	——
Trachylepis brevicollis	CAS 198871	JVV 3324; Mab14	Elangata Wuas Ecosystem Management Program, 36.8km bearing 287 (true North) from Kajiado, Kajiado, Rift Valley, Kenya	S01.761, E36.480	AY907714	AY907712	AY907716	MK791895	MK791829	MK791772	——	——	——
Trachylepis brevicollis	——	BE100361	Salalah, Dhofar, Oman	——	JQ598783	JQ598770	——	——	——	——	——	——	——
Trachylepis capensis	LSUMZ 57253	AMB 4765; L087	19.4km on Akkedis Drive (plains Beyond Brown's Pass), Richtersveld National Park, Northern Cape, South Africa	S28.184, E17.037	DQ238937	DQ239259	DQ239178	——	DQ239017	MK791773	——	——	——
Trachylepis capensis	CAS 234152	MCZ F-38750	Farm Brenhilda, Limpopo, South Africa	S22.681, E29.487	MK792005	——	MK792132	——	——	——	MK792168	——	——
Trachylepis casuarinae	PEM R13442	Field#3719; Mab18	Fogo Island [=Ilha do Fogo], Premieras Islands, Zambezia, Mozambique	S17.234, E38.879	MK792006	——	MK792084	——	——	——	——	——	——
Trachylepis casuarinae	——	71Mcaguri	Fogo Island, [=Ilha do Fogo], Premieras Islands, Zambezia, Mozambique	——	AY151474	——	AF280270	——	——	——	——	——	——
Trachylepis cf. *chimbana*	PEM R21727	WC 1791; JET1; ARG181	15km W of bottom of Leba Pass, Namibe, Angola	S15.055, E13.074	MK792061	——	——	——	——	——	MK792145	——	——
Trachylepis cf. *chimbana*	PEM R24097	AG82	campsite 17km W of Chicambi Village, Namibe, Angola	S13.917, E12.681	MK792062	——	——	——	——	——	——	MK791989	——
Trachylepis comorensis	ZFMK 62192	——	Nosy Tanikely, Madagascar	——	AF153565	AF153565	——	——	——	——	——	——	——
Trachylepis comorensis	——	MH23	Ouhoni, Moheli, Comoros	——	HM192757	KC345355	HM192706	——	KC345299	KC345192	——	——	——
Trachylepis comorensis	——	GC16	N of Moroni airport, Grand Comoro, Comoros	——	——	KC345356	HM192713	——	——	KC345193	——	——	——
Trachylepis cristinae	——	JR15	Abd Al Kuri Island, Socotra Archipelago, Yemen	——	JQ598784	JQ598771	——	——	——	——	——	——	——
Trachylepis damarana	MCZ R193241	MCZ A-28788	Farm Ohange, near hill along B1 fence line, Otjozondjudpa, Namibia	S19.496, 17.559	MG605622	——	——	MG605368	——	——	MG605438	MG605250	MG605501
Trachylepis damarana	PEM R20514	WC ANG-389	pan 18 km East of Jamba, Cuando Cubango, Angola	S17.463, E22.866	MG605629	——	——	MG605370	——	——	MG605439	MG605259	MG605503
Trachylepis depressa	PEM R17745	JM 1215	Osabeni, KwaZulu-Natal, South Africa	S27.647, E32.647	KX231455	——	——	KX231385	KX231484	KX231439	KX231528	——	——
Trachylepis depressa	PEM R15573	Mab19	3km NE of Chibuto, Gaza, Mozambique	S24.665, E33.558	MK792007	MK791929	MK792086	MK791865	MK791847	MK791774	——	——	——
Trachylepis dichroma	probably ZMB#	Mab187	pet trade; probably from Dodoma, Tanzania	——	MK792008	MK791930	MK792087	——	——	MK791775	——	——	——

Table S2 (continued).

Species	Catalog #	Other ID #	Locality	Lat., Lon.	16S	12S	Cytb	RAG1	CMOS	BDNF	KIF24	ND2	BRCA2
Trachylepis dichroma	probably ZMB#	Mab189	pet trade; probably from Dodoma, Tanzania	——	MK792009	MK791931	MK792088	——	——	MK791776	——	——	——
Trachylepis elegans	——	PEM-FNR# 438; Mab21	Basibass, Madagascar	——	MK792010	MK791932	MK792089	MK791866	——	MK791777	——	——	——
Trachylepis elegans	UADBA#	RAN 56248; L119	Amoasary, Vohidava Mountain, Toliara Province, Madagascar	——	DQ238881	DQ239203	DQ239122	MK791867	DQ238962	MK791778	——	——	——
Trachylepis gonwouoi	CAS 261092	LJW 0147	oil palm plantation; Buea City and surrounding areas; Fako, Sud-ouest, Cameroon	N04.194, E09.004	MK792070	——	——	MK791917	——	——	MK792146	KY696691	——
Trachylepis gonwouoi	USNM 584340	USNM-FS-246551	Impongui, Likouala, Congo	N01.088, E17.307	MK496158	——	——	——	——	——	MK542299	MK583041	——
Trachylepis gonwouoi	PEM R20428	CAR161; Mab66	Mabea Bay, Park National de Dzanga-Ndoki, Sangha-Mbaere, Central African Republic	N03.034, E16.409	MK792011	MK791933	MK792125	MK791868	MK791830	MK791779	——	——	——
Trachylepis gravenhorstii	UADBA#	RAX 00265; L120	Namoroka Reserve, Madagascar	——	DQ238882	DQ239204	DQ239123	——	DQ238963	MK791780	——	——	——
Trachylepis gravenhorstii	——	Mab182; M40	Ranobe Village, Ifaty, Tulear, Madagascar	S23.011, E43.609	MK792012	MK791934	MK792090	——	——	MK791781	——	——	——
Trachylepis hoeschi	PEM R24143	AG154	Farm Mucongo, Namibe, Angola	S14.795, E12.495	MK792068	——	——	——	——	——	——	MK791977	——
Trachylepis hoeschi	MCZ R184257	AMB 8483, Mab134	Gai-As, Kunene Region, Namibia	S20.779, E14.075	MG605668	MK791935	MK792091	MG605401	MK791831	MK791782	MG605462	MG605305	MK791754
Trachylepis homalocephala homalocephala	PEM R23918	MBUR 01374	Koeberg Nature Reserve, Western Cape, South Africa	S33.666, E18.436	MK792014	——	——	GU931616	——	——	GU931479	GU931548	——
Trachylepis homalocephala homalocephala	——	AMB 7072; L109	ca. 4.6km N of Grootbaai, Bloubergstrand on Melkbos Road, Western Cape, South Africa	S33.751, E18.443	DQ238875	DQ239197	DQ239116	——	DQ238956	MK791783	——	——	——
Trachylepis homalocephala homalocephala	PEM R23917	MBUR 01363	Koeberg Nature Reserve, Western Cape, South Africa	S33.666, E18.436	——	——	MK792133	GU931615	——	——	GU931478	——	——
Trachylepis homalocephala peringueyi	PEM R17458	BM 186	Farm Noup, Northern Cape, South Africa	S30.139, E17.208	MK792074	——	MK792128	GU931619	——	——	GU931481	——	——
Trachylepis homalocephala peringueyi	PEM R17459	BM 198	Farm Noup, Northern Cape, South Africa	S30.142, E17.208	MK792013	——	MK792127	GU931618	——	——	GU931482	——	——
Trachylepis infralineata	——	Mab4EUR	Île Europa	S22.38, E40.37	——	——	HM192728	——	——	——	——	——	——
Trachylepis laevigata	MCZ R184536	AMB 8412	33.1km S Kgama, on gravel road to Modimolle, Papstraat, Limpopo, South Africa	S24.333, E28.385	MG605594	——	——	MG605357	——	——	MG605430	MG605210	MG605489
Trachylepis laevis	——	MGR 300	Otjitambi Guest Farm, Kunene, Namibia	S19.809, E15.183	MK792015	——	MK792135	MK791869	——	MK791784	——	——	——
Trachylepis laevis	——	MGR 301	Otjitambi Guest Farm, Kunene, Namibia	S19.809, E15.183	MK792016	——	MK792136	MK791897	——	MK791785	——	——	——
Trachylepis maculilabris	PEM R9737	Mab90	Sayama Tea Estate, [southern slopes of] Mt. Mulanje, Malawi	S16.064, E35.544	MK792019	MK791937	MK792093	MK791871	——	MK791787	——	——	——
Trachylepis maculilabris	PEM R16325	Mab94	Sayama Tea Estate, [southern slopes of] Mt. Mulanje, Malawi	S16.064, E35.544	MK792020	MK791938	MK792094	MK791872	——	——	——	——	——

Table S2 (continued).

Species	Catalog #	Other ID #	Locality	Lat., Lon.	16S	12S	Cytb	RAG1	CMOS	BDNF	KIF24	ND2	BRCA2
Trachylepis maculilabris	——	AMB 9883	abandoned coffee plantation, Cada Amboim, Cuanza Sul, Angola	S10.867, E14.324	MK792017	——	——	MK791916	——	——	——	——	MK791755
Trachylepis maculilabris	PEM R5844	MB 20301; PEM-FNR#492; Mab23	At DFC camp, 32km before Doussala, Nyanga, Gabon	S02.558, E10.734	MK792018	MK791936	MK792092	MK791870	MK791848	MK791786	MK792148	——	——
Trachylepis maculilabris	PEM R19463	WC 0970; ANG0003	Lunda Norte, Angola	S08.445, E20.720	MK792072	——	——	——	——	——	——	MK791975	——
Trachylepis madagascariensis	UMMZ 209103	RAN 43077; L121	Ambatolampy, Vakinankaratra, Antananarivo, Madagascar	——	DQ238883	DQ239205	DQ239124	——	DQ238964	MK791788	——	——	——
Trachylepis margaritifer	PEM R5539	Mab27	base of western Inselberg, Mbatamila Camp, Niassa Game Reserve, Niassa, Mozambique	S12.183, E37.546	MK792023	MK791939	MK792095	MK791873	MK791849	MK791789	——	——	——
Trachylepis margaritifer	PEM R9745	Mab77	Likabula Forest Station, Mt. Mulanje, Mulanje, Malawi	S15.939, W35.504	MK792024	MK791940	MK792096	MK791874	——	MK791790	——	——	——
Trachylepis margaritifer	CAS 234165	MCZ F-38818	Farm Brenhilda, Limpopo, South Africa	S22.907, 29.618	MK792021	——	MK792130	——	MK791855	——	MK792149	——	——
Trachylepis margaritifer	CAS 234173	MCZ F-38839	Mogalakwena (Farm Canterbury), Limpopo, South Africa	S22.755, E28.777	MK792022	——	MK792134	——	——	——	MK792150	——	——
Trachylepis raymondlaurenti (formerly *T. megalura*)	CAS 258401	JVV 9219	Cangandala National Park, Malanje, Angola	S09.846, E16.722	MG605669	——	——	MG605400	——	——	MG605461	MG605304	MG605522
Trachylepis megalura	PEM R16775	KC 18; Mab192	Klein's Camp lodge, Loliondo Game Controlled Area, Mara, Tanzania	S01.835, E35.247	MK792025	MK791941	MK792097	——	——	MK791791	——	——	——
Trachylepis mlanjensis	PEM R17482	Mab85	Chilemba Peak, Mt. Mulanje, Malawi	S15.962, E35.533	MK792027	MK791944	MK792099	MK791877	MK791834	MK791794	——	——	——
Trachylepis mlanjensis	PEM R17484	Mab79	Chilemba Peak, Mt. Mulanje, Malawi	S15.963, E35.538	MK792028	MK791942	MK792100	MK791875	MK791832	MK791792	——	——	——
Trachylepis mlanjensis	PEM R17480	Mab84	Chilemba Peak, Mt. Mulanje, Malawi	S15.962, E35.533	MK792026	MK791943	MK792098	MK791876	MK791833	MK791793	——	——	——
Trachylepis occidentalis	CAS 214511	AMB 6253; L091	Farm Avondsehijn, Kalahari Guest Farm, Northern Cape, South Africa	S26.863, E21.107	DQ238941	DQ239263	DQ239182	——	DQ239021	——	——	——	——
Trachylepis occidentalis	MCZ R184266	MCZ Z-37823; Mab161	Gai-as, Namibia	S20.779, E14.075	MK792029	MK791945	MK792101	——	——	——	MK792151	——	——
Trachylepis ozorii	——	Voucher625	Annobón Island, Equatorial Guinea	——	——	——	HM192747	——	——	——	——	——	——
Trachylepis paucisquamis	UWBM 6041	ADL 3864	Atewa Hills, Eastern Region, Ghana	N06.231, W00.558	KX364963	——	——	——	——	——	KX365006	KX365040	——
Trachylepis paucisquamis	PEM R4436	Mab29	Cavally Classified Forest Reserve, Moyen-Cavally, Ivory Coast	N06.154, W07.805	MK792030	MK791946	MK792102	MK791878	MK791835	MK791795	MK792152	——	——
Trachylepis paucisquamis	PEM R4438	Mab30	Cavally Classified Forest Reserve, Moyen-Cavally, Ivory Coast	N06.154, W07.805	MK792031	MK791947	MK792103	MK791879	KX364995	KX364971	MK792153	——	——
Trachylepis perrotetii	MVZ 245351	#1795	ca. 34km NE of Accra, Greater Accra, Ghana	N05.841, E00.116	MK496083	——	——	HM161160	——	——	MK792154	MK583080	——
Trachylepis perrotetii	FMNH 262231	L160	Ghana	——	DQ238901	DQ239223	DQ239142	——	DQ238982	MK791796	——	——	——
Trachylepis perrotetii	FMNH 262230	L161	Ghana	——	DQ238902	DQ239224	DQ239143	——	DQ238983	MK791797	——	——	——

Table S2 (continued).

Species	**Catalog #**	**Other ID #**	**Locality**	**Lat., Lon.**	**16S**	**12S**	**Cytb**	**RAG1**	**CMOS**	**BDNF**	**KIF24**	**ND2**	**BRCA2**
Trachylepis planifrons	——	TJC 1478	Dollo Mena, Borena, Oromia, Ethiopia	N06.268, E39.807	MK792075	——	——	MK791915	——	——	——	MK791981	MK791756
Trachylepis polytropis	PEM R5443	Mab31	Loango National Park, Ogooué-Maritime, Gabon	S02.341, E09.597	MK792032	MK791948	MK792104	MK791880	——	MK791798	MK792155	——	——
Trachylepis polytropis	PEM R5377	Mab32	"Rabi, Shell Gabon" [= Rabi Kounga oil field], Ogooué-Maritime, Gabon	S01.937, E09.881	MK792033	MK791949	MK792105	MK791881	——	MK791799	MK792156	——	——
Trachylepis principensis	MUHNAC MB03-000979	——	Príncipe Island, São Tomé and Príncipe	——	KU954503	——	——	——	——	——	——	——	——
Trachylepis principensis	CAS 238898	RCD 14674	Bom Bom Resort, Príncipe Island, São Tomé and Príncipe	N01.698, E07.403	KU954511	——	——	——	——	——	——	——	——
Trachylepis principensis	MUHNAC MB03-000956	——	Príncipe Island, São Tomé and Príncipe	——	KU954501	——	——	——	——	——	——	——	——
Trachylepis punctatissima	PEM R16655	JM 856; Mab180	Long Tom Pass, Lydenburg, Mpumalanga Province, South Africa	S25.141, E30.608	MK792034	MK791950	MK792106	MK791882	MK791836	MK791800	——	——	——
Trachylepis punctulata	——	MCZ Z-37900; Mab165	Kunene, Namibia	S19.717, E14.312	MK792040	MK791951	MK792108	JX568124	MK791856	MK791801	MK792170	——	——
Trachylepis punctulata	MCZ R183759	AMB 7608; Mab48	98.2km S Khorixas, Erongo, Namibia	S20.991, E14.927	MK792039	MK791952	MK792107	JX568117	MK791850	MK791802	——	——	——
Trachylepis punctulata	PEM R24137	AG148	Farm Mucongo, Namibe, Angola	S14.787, E12.496	MK792069	——	——	——	——	——	——	MK791982	——
Trachylepis punctulata	PEM R17998	KTH-09-114; MBUR 2176	9km S of Camp at the Red Canyon, Namibe, Angola	——	MK792037	——	——	MK791901	——	——	MK792147	——	——
Trachylepis punctulata	PEM R18001	KTH-09-274	road from Lake Arco to Espinheira, Namibe, Angola	——	MK792038	——	——	MK791900	——	——	MK792169	——	——
Trachylepis punctulata	CAS 254769	JVV 8713	ca. 124 km SSW (by air) of Namibe, coastal dunes, Namibe, Angola	S16.272, E11.832	MK792035	——	——	MK791903	——	——	——	——	——
Trachylepis punctulata	CAS 254770	JVV 8715	ca. 124 km SSW (by air) of Namibe, coastal dunes, Namibe, Angola	S16.272, E11.832	MK792036	——	——	MK791904	——	——	MK792157	——	——
Trachylepis quinquetaeniata	——	TJC 1372	Lodge Falls, Awash National Park, Afar, Ethiopia	N08.840, E40.015	MK792041	——	——	MK791909	——	——	——	——	MK791757
Trachylepis quinquetaeniata	FMNH 262232	L159	Ghana	——	DQ238899	DQ239221	DQ239140	MK791883	DQ238980	MK791803	——	——	——
Trachylepis quinquetaeniata	MVZ 249790	#2825	Mole Motel, Mole National Park, Northern Region, Ghana	N09.259, W01.855	MK496149	——	——	MK542207	——	——	MK542092	MK583095	——
Trachylepis sechellensis	——	TRASEY1	Silhoutte Island, Seychelles	——	MK792042	MK791953	MK792129	MK791884	MK791857	MK791804	MK792158	——	——
Trachylepis socotrana	——	M73	Socotra Island, Yemen	——	AY151476	AF280140	AF280272	——	——	——	——	——	——
Trachylepis socotrana	——	M74	Socotra Island, Yemen	——	AY151477	AF280141	AF280273	——	——	——	——	——	——
Trachylepis sparsa	CAS 214458	AMB 6200; Mab37	Farm Avonschijn, Northern Cape, South Africa	S26.900, E21.117	MK792043	MK791956	MK792109	MK791887	MK791851	MK791807	——	——	——
Trachylepis sparsa	——	MCZ A-38356; Mab146	Karas, Namibia	S27.385, E18.465	MK792044	MK791954	MK792110	MK791885	MK791858	MK791805	——	——	——
Trachylepis sparsa	MCZ R184370	MCZ FSA-38349; Mab147	Karas, Namibia	S27.385, E18.465	MK792045	MK791955	MK792111	MK791886	MK791837	MK791806	——	——	——

Table S2 (continued).

Species	Catalog #	Other ID #	Locality	Lat., Lon.	16S	12S	Cytb	RAG1	CMOS	BDNF	KIF24	ND2	BRCA2
Trachylepis spilogaster	——	MCZ A-38261; Mab136	6.8km S of Helminghause on road to Aus, Karas, Namibia	S25.933, E16.817	MK792048	MK791957	MK792114	——	MK791838	MK791808	MK792160	——	——
Trachylepis spilogaster	——	MCZ A-38295, Mab140	Karas, Namibia	S26.749, E17.221	MK792049	MK791958	MK792115	MK791888	MK791839	MK791809	——	——	——
Trachylepis spilogaster	——	MCZ Z-37947; Mab172	Marienflus, Kunene, Namibia	S17.471, E12.515	MK792050	MK791961	MK792116	MK791902	——	MK791812	MK792167	——	——
Trachylepis spilogaster	——	AMB 7614; Mab50	62.5km S of Kamanjab, Kunene, Namibia	S20.064, E15.042	MK792046	MK791960	MK792112	MK791892	MK791854	MK791811	——	——	——
Trachylepis spilogaster	PEM R21842	WC 3538	Cuando Cubango, Angola	S14.663, E17.665	MK792073	——	——	——	——	——	MK792172	——	——
Trachylepis spilogaster	MCZ R183768	AMB 7636; Mab49	7.1km NE of Warmquelle on D3704 To Opuwo, Kunene, Namibia	S19.083, 13.748	MK792047	MK791959	MK792113	MK791891	MK791853	MK791810	——	——	——
Trachylepis striata	——	TJC 1373	Awash National Park, Afar, Ethiopia	N08.847, E40.011	MK792053	——	——	MK791912	——	——	——	MK791983	MK791758
Trachylepis striata	PEM R16772	WRB 0036; KC 27; Mab191	Klein's Camp lodge, Loliondo Game Controlled Area, Mara Region, Tanzania	S01.835, E35.247	MK792052	MK791962	MK792117	MK791907	MK791840	MK791813	MK792161	——	——
Trachylepis sulcata ansorgi	PEM R21737	WC 1836; JET35; ARG199	13km N of Quilengues on road to Benguela in miombo woodland with a low granite outcrop and small forest stream, Huila District, Angola	S13.972, E14.047	MK792055	——	——	MK791914	——	——	——	——	——
Trachylepis sulcata sulcata	CAS 223979	AMB 6987; Mab129	4.2km E of Sesfontein Road junction on Kaoko Otavi-Opuwo Road, Kunene, Namibia	S18.213, E13.800	MK792054	MK791963	MK792118	MK791889	GU931629	MK791814	GU931492	——	——
Trachylepis tandrefana	ZSM 45.2006	FGZC 766	Antranopasasy, Tsingy de Bemaraha, Madagascar	——	——	——	——	——	KC345272	KC345156	——	——	——
Trachylepis tandrefana	No Voucher	——	Kirindy, Madagascar	——	AF153566	AF153555	AF153588	——	——	——	——	——	——
Trachylepis tandrefana	ZSM 24.2006	FGZC 716	Antranopasasy, Tsingy de Bemaraha, Madagascar	——	——	KC345320	——	——	——	——	——	——	——
Trachylepis tandrefana	ZSM 76.2006	FGZC 827	Bendrao Forest, Tsingy de Bemaraha, Madagascar	——	——	KC345321	——	——	KC345273	KC345157	——	——	——
Trachylepis tavaratra	ZSM 1550.2008	FGZC 1820	Montagne des Français, Madagascar	——	——	KC345376	——	——	KC345317	KC345205	——	——	——
Trachylepis tavaratra	ZSM 1551.2008	FGZC 3134	Forêt d'Ambre, Madagascar	S12.466, E49.230	——	KC345377	——	——	KC345318	KC345206	——	——	——
Trachylepis tessellata	——	TJR 38	Wadi Haql, Oman	——	JQ598789	JQ598777	——	——	——	——	——	——	——
Trachylepis tessellata	——	TE100363	Mughsayl, Oman	——	JQ598788	JQ598776	——	——	——	——	——	——	——
Trachylepis thomensis	CAS 218722	RCD 13630; Mab26	Rio Paga Fogo, ca. 25m upstream of coast road, São Tomé Island, São Tomé and Príncipe	N00.284, E06.484	MK792056	MK791964	MK792119	MK791890	MK791841	MK791815	——	——	——
Trachylepis thomensis	CAS 218821	RCD 13746	Mouth Of Agua Anambo, São Tomé, São Tomé and Príncipe	N00.326, E06.508	KU954510	——	——	——	——	——	——	——	——
Trachylepis thomensis	MUHNAC MB03-000963	——	São Tomé, São Tomé and Príncipe	——	KU954507	——	——	——	——	——	——	——	——
Trachylepis varia	PEM R5413	Mab43	Mtentu Gorge, Transkei, Eastern Cape, South Africa	S31.194, E29.945	MG605541	MK791965	MK792120	MG605320	MK791852	MK791816	——	MG605166	MG605470
Trachylepis varia	PEM R5542	Mab44	Mbatamila camp, Niassa Game Reserve, Niassa, Mozambique	S12.184, E37.551	MG605540	MK791966	MK792121	MG605319	MK791842	MK791817	MG605405	MG605165	MG605469

Table S2 (continued).

Species	Catalog #	Other ID #	Locality	Lat., Lon.	16S	12S	Cytb	RAG1	CMOS	BDNF	KIF24	ND2	BRCA2
Trachylepis cf. *varia* clade 1	——	TJC 1409	Dolo Ado-Negele Borena Road, Filtu, Somali, Ethiopia	N05.169, E40.503	MG605650	——	——	MG605375	——	——	MG605444	MG605278	——
Trachylepis cf. *varia* clade 2	PEM R16768	KC 25; Mab190	Klein's Camp, Loliondo Game Controlled Area, Mara, Tanzania	S01.845, E35.253	MG605525	MK791967	MK792085	MG605308	——	MK791818	MG605403	——	——
Trachylepis cf. *varia* clade 2	PEM R16789	KC05	Woodbury Crossing, Gnimeti River, Klein's Camp, Loliondo Game Controlled Area, Mara, Tanzania	S01.836, E35.259	MG605548	——	——	MG605323	——	——	——	——	——
Trachylepis cf. *varia* clade 3	——	TJC 1335	Robe-Sof Omar Road, Bale, Oromia, Ethiopia	N07.076, E40.151	MG605647	——	——	MG605373	——	——	MG605442	MG605275	MG605519
Trachylepis cf. *varia* clade 3	——	TJC 1336	Robe-Sof Omar Road, Bale, Oromia, Ethiopia	N07.076, E40.151	MG605648	——	——	MG605374	——	——	——	MG605276	MG605520
Trachylepis cf. *varia* clade 4	——	EBG 2256	near Kilwemapante, Katanga Province, Democratic Republic of the Congo	S05.034, E28.585	MG605661	——	——	——	——	——	——	——	——
Trachylepis cf. *varia* clade 4	——	ELI 713	Lwemba, South Kivu, Democratic Republic of the Congo	S03.696, E28.719	MG605666	——	——	——	——	——	——	——	——
Trachylepis variegata	MCZ R185110	MCZ A-38696	Farm Oas, Karas, Namibia	S27.494, E19.222	——	——	——	JX568152	——	——	MK792165	JX568100	——
Trachylepis variegata	CAS 200019	AMB 4505; L089	Richtersveld National Park, Lookout Point Off Of Nicodaemus Road, Northern Cape Prov., South Africa	S28.342, E16.977	DQ238938	DQ239260	DQ239179	MK791905	DQ239018	MK791819	MK792163	——	——
Trachylepis variegata	MCZ R184365	MCZ A-38304; Mab152	Savanna Guest Farm, Karas, Namibia	S27.390, E18.492	MK792057	MK791968	MK792122	MK791906	MK791843	MK791820	MK792164	——	——
Trachylepis vato	UMMZ 222377	RAN 56249	Toliara, Madagascar	——	DQ238884	DQ239205	DQ239125	——	DQ238965	MK791821	——	——	——
Trachylepis vato	——	ZCMV 5538	Isalo, Madagascar	——	——	KC345328	——	——	——	KC345164	——	——	——
Trachylepis vato	ZSM 398.2000	——	Madagascar	——	AY159097	——	——	——	——	——	——	——	——
Trachylepis vezo	——	ZCMV 13051; ACZC 1915 (=ACZC 1992)	Lavenombato, Madagascar	——	——	KC345374	——	——	——	——	——	——	——
Trachylepis vezo	ZSM 787.2009	ZCMV 13024; ACZC 1993	Lavenombato, Madagascar	——	——	KC345375	——	——	——	——	——	——	——
Trachylepis wahlbergi	CAS 258400	JVV 9459	Cangandala National Park, vicinity of park headquarters, Malanje, Angola	S09.819, E16.655	MK792051	——	——	——	——	——	MK792162	MK791986	——
Trachylepis wahlbergi	PEM R21818	——	Village above Lunda Falls, Bie Province, Angola	——	MK792063	——	——	——	——	——	MK792159	MK791984	——
Trachylepis wahlbergi	PEM R21819	——	Village above Lunda Falls, Bie Province, Angola	——	MK792064	——	——	——	——	——	——	MK791985	——
Trachylepis wahlbergi	——	MB 20393; Mab60	SW Zambia	——	MK792059	MK791970	MK792124	MK791894	MK791845	MK791823	——	——	——
Trachylepis wahlbergi	MCZ R193549	AMB 9279	Copperbelt University, Kitwe, Copperbelt, Zambia	S12.808, E28.244	MK792065	——	——	——	——	——	MK792166	MK791987	——
Trachylepis wahlbergi	——	MB 20380; Mab59	SW Zambia	——	MK792058	MK791969	MK792123	MK791893	MK791844	MK791822	——	——	——
Trachylepis wrightii	——	Mawr1	Fregate Island, Seychelles	——	AY151472	AF280124	AF280135	——	AY818788	——	——	——	——

Table S3. Reproductive mode information for species sampled in this study.

Species	Reproductive mode	Source
Caledoniscincus austrocaledonicus	oviparous	Bauer and Sadlier, 2000
Cryptoblepharus novocaledonicus	oviparous	Bauer and Sadlier, 2000
Eutropis multifasciata	viviparous	Horton 1983; Shine, 1985
Eutropis longicaudata	oviparous	Huang 2006; Horton 1983; Shine 1985
Toenayar novemcarinata	unknown	——
Dasia olivacea	oviparous	Allen Greer (pers. comm.)
Dasia vittata	oviparous	Mori et al., 1995
Eumecia anchietae	viviparous	Blackburn, 2015c
Lubuya ivensii	viviparous	Flemming and Branch, 2001
Mabuya aurae	viviparous	Hedges and Conn, 2012 (Fig. 25e: photo of embryo)
Heremites septemtaeniata	viviparous	Arakekyan et al., 2011
Chioninia delalandii	oviparous	Rösler and Wranik, 2008
Chioninia vaillanti	viviparous	Schleich, 1987; Hauschild and Gassner, 1995
Trachylepis acutilabris	oviparous	Cooper and Whiting, 2000
Trachylepis affinis	oviparous	Hoogmoed, 1974; Burger et al., 2004; Allen Greer (pers. comm.)
Trachylepis albilabris	oviparous	Burger et al., 2004 [Gabon]
Trachylepis albopunctata	viviparous	pers. obs. [Kafue N.P., Zambia]
Trachylepis albotaeniata	unknown	——
Trachylepis atlantica	oviparous	Allen Greer (pers. comm.)
Trachylepis aureogularis	oviparous	Hoogmoed, 1974 (as *Mabuya albilabris*) [Ghana]
Trachylepis aureopunctata	oviparous	Horton, 1983
Trachylepis bayonii bayonii	viviparous	Manaças, 1963; Horton, 1983; Shine, 1985; Allen Greer (pers. comm.); pers. obs.
Trachylepis bayonii huilensis	unknown	——
Trachylepis binotata	viviparous	Scharf et al., 2015; Slavens and Slavens, 1999
Trachylepis bocagii	viviparous	Loveridge, 1953
Trachylepis boettgeri	oviparous	Andreone and Greer, 2002
Trachylepis cf. *boettgeri*	unknown	——
Trachylepis boulengeri	oviparous	Broadley, 2000; Loveridge, 1955
Trachylepis brauni	viviparous	Broadley, 2000
Trachylepis brevicollis Kenya	viviparous	Goldberg, 2009 [Kenya]
Trachylepis brevicollis Oman	viviparous	Arnold, 1980 [Oman]
Trachylepis capensis	bimodal	Broadley, 2000; Jacobsen, 1989; Brown-Wessels, 1989
Trachylepis casuarinae	unknown	——
Trachylepis cf. *chimbana*	unknown	——
Trachylepis comorensis	oviparous	Barbour and Loveridge, 1928
Trachylepis cristinae	unknown	——
Trachylepis damarana	bimodal	pers. obs.; Jacobsen, 1989
Trachylepis depressa	oviparous	Branch, 1998; Bruton and Haacke, 1980
Trachylepis dichroma	viviparous	Günther et al., 2005
Trachylepis elegans	oviparous	UMMZ 217756: "unhatched egg and hatchling"
Trachylepis gravenhorsti	oviparous	Andreone and Greer, 2002
Trachylepis gonwouoi	oviparous	Walter Tapondjou, Katie Allen (pers. comm.)
Trachylepis hoeschi	viviparous	Scharf et al., 2015

Table S3 (continued).

Species	**Reproductive mode**	**Source**
Trachylepis homalocephala homalocephala	oviparous	Visser, 1975
Trachylepis homalocephala peringueyi	unknown	——
Trachylepis infralineata	unknown	——
Trachylepis laevigata	unknown	——
Trachylepis laevis	unknown	——
Trachylepis maculilabris	oviparous	Loveridge, 1936,1942; Robertson et al., 1962
Trachylepis madagascariensis	oviparous	Glaw and Vences, 2007; Blanc and Blanc, 1967
Trachylepis margaritifer	oviparous	Broadley, 2000; Allen Greer (pers. comm.)
Trachylepis megalura	viviparous	Loveridge, 1936, 1942; Horton, 1983; Broadley, 2000
Trachylepis mlanjensis	viviparous	Patterson, 1992; Broadley, 2000
Trachylepis occidentalis	bimodal	Branch, 1998; Broadley, 2000
Trachylepis ozorii	unknown	——
Trachylepis paucisquamis	unknown	——
Trachylepis perrotetii	oviparous	Horton, 1983; Shine, 1985; Branch and Bauer, 1995; Parker, 1927
Trachylepis planifrons	oviparous	Goldberg, 2010a
Trachylepis polytropis	oviparous	Burger et al., 2004 [Gabon]; Allen Greer (pers. comm.)
Trachylepis principensis	oviparous	CAS 234518: "Gravid, 3 eggs and 1 undeveloped egg"
Trachylepis punctatissima	viviparous	Jacobsen, 1989; Meiri et al., 2013; Huey and Pianka, 2007
Trachylepis punctulata	viviparous	Jacobsen, 1989; Broadley, 2000
Trachylepis quinquetaeniata	oviparous	Schmidt and Inger, 1957; Loveridge, 1936; Horton, 1983; Allen Greer (pers. comm.)
Trachylepis raymondlaurenti	viviparous	Marques et al., 2019
Trachylepis sechellensis	oviparous	Cheke, 1984; Crawford and Thorpe, 1979; Brooke and Houston, 1983; Bourquin and Hitchins, 1998; Bringsøe, 2008
Trachylepis socotrana	oviparous	Allen Greer (pers. comm.), *fide* H. Rösler (pers. comm.)
Trachylepis sparsa	viviparous	Huey and Pianka, 1977, 2007; Broadley, 2000
Trachylepis spilogaster	viviparous	Pianka, 1986; Huey and Pianka, 1977
Trachylepis striata	viviparous	Shine, 1985; Jacobsen, 1989
Trachylepis sulcata ansorgi	unknown	——
Trachylepis sulcata sulcata	viviparous	FitzSimons, 1943; Branch and Bauer, 1995; Goldberg, 2010b
Trachylepis tandrefana	unknown	——
Trachylepis tavaratra	unknown	——
Trachylepis tessellata	oviparous	Arnold and Gallagher, 1977
Trachylepis thomensis	oviparous	CAS 218768: "Egg found under roofing tiles in grassy field. Egg length 20.5mm, width 16.0mm, SVL 30.4mm"
Trachylepis varia	viviparous	Bates, 1992 [Orange Free State, South Africa]
Trachylepis cf. *varia* clade 1	unknown	——
Trachylepis cf. *varia* clade 2	unknown	——
Trachylepis cf. *varia* clade 3	unknown	——
Trachylepis cf. *varia* clade 4	unknown	——
Trachylepis variegata	viviparous	Huey and Pianka, 1977, 2007; Pianka, 1986; Broadley, 2000
Trachylepis vato	unknown	——
Trachylepis vezo	unknown	——
Trachylepis wahlbergi	viviparous	Loveridge, 1953
Trachylepis wrightii	oviparous	Brooke and Houston, 1983; Hauschild and Gassner, 1995; Bourquin and Hitchins, 1998

Table S3 (continued).

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Supplementary Figure Legends

Fig. S1. Maximum likelihood tree of concatenated mitochondrial and nuclear loci (16S, 12S, CYTB, ND2, CMOS, KIF24, BRCA2, BDNF, and RAG1) of Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S2. Maximum likelihood tree of concatenated mitochondrial loci (16S, 12S, CYTB, and ND2) of Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S3. Maximum likelihood tree of the nuclear gene CMOS, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S4. Maximum likelihood tree of the nuclear gene KIF24, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S5. Maximum likelihood tree of the nuclear gene BRCA2, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S6. Maximum likelihood tree of the nuclear gene BDNF, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S7. Maximum likelihood tree of the nuclear gene RAG1, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S8. Maximum likelihood tree of the mitochondrial gene 16S, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S9. Maximum likelihood tree of the mitochondrial gene 12S, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S10. Maximum likelihood tree of the mitochondrial gene CYTB, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S11. Maximum likelihood tree of the mitochondrial gene ND2, for Mabuyinae, estimated using IQTREE. Values at internal nodes indicate ultra-fast bootstrap (UFBoot) support, and UFBoot ≥ 95 is considered to be strong support for a clade. Branch lengths are in substitutions/site.

Fig. S12. Unordered parsimony ancestral state reconstruction of parity mode within *Trachylepis*. Consensus mapping of the six maximum parsimony reconstructions.

Fig. S13. Maximum parsimony reconstruction #1 (of 6) of parity mode within *Trachylepis*.

Fig. S14. Maximum parsimony reconstruction #2 (of 6) of parity mode within *Trachylepis*.

Fig. S15. Maximum parsimony reconstruction #3 (of 6) of parity mode within *Trachylepis*.

Fig. S16. Maximum parsimony reconstruction #4 (of 6) of parity mode within *Trachylepis*.

Fig. S17. Maximum parsimony reconstruction #5 (of 6) of parity mode within *Trachylepis*.

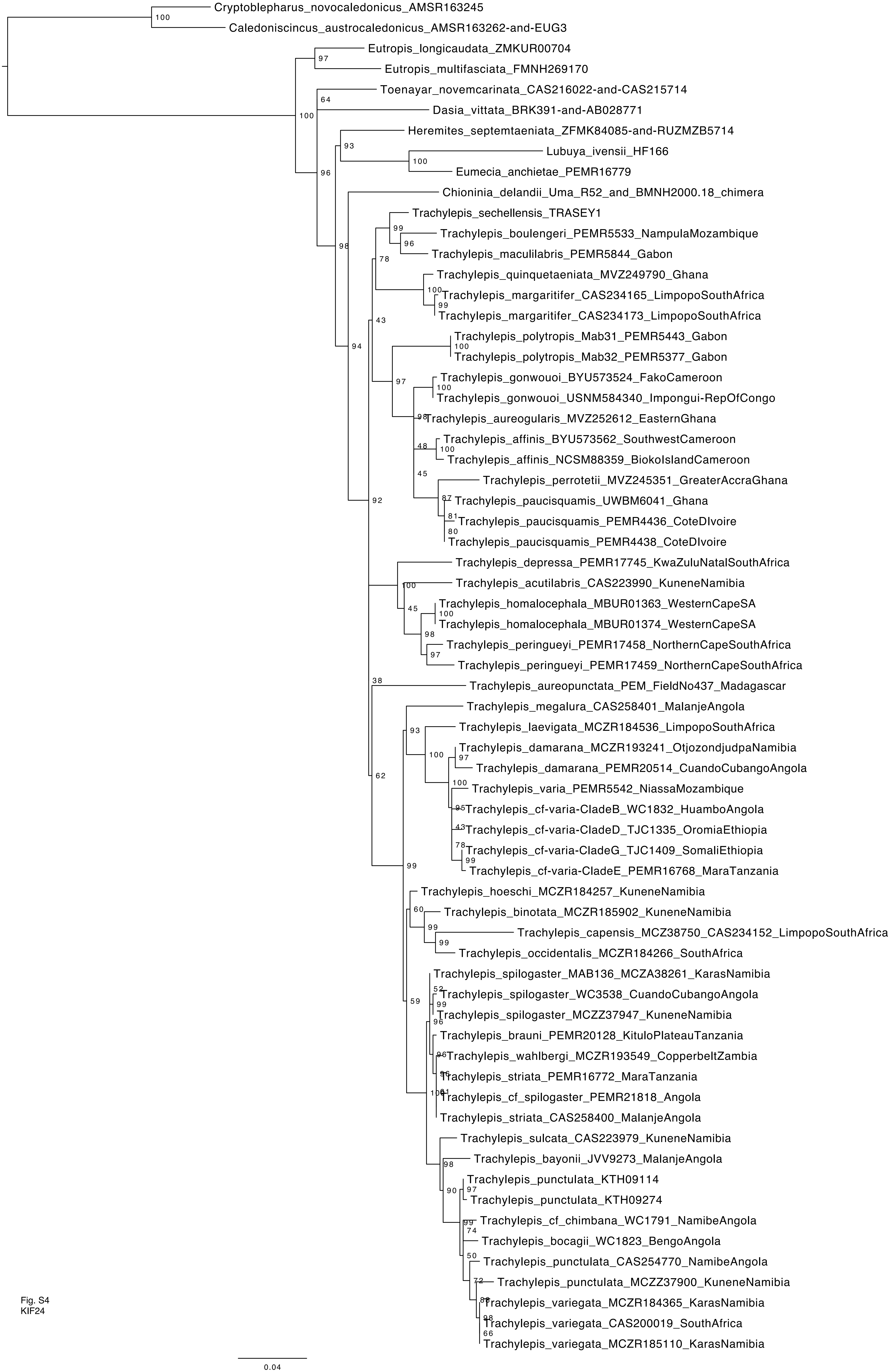
Fig. S18. Maximum parsimony reconstruction #6 (of 6) of parity mode within *Trachylepis*.

Fig. S1
All loci concatenated

Fig. S2
Mitochondrial loci concatenated


Cryptoblepharus_novocaledonicus_AMSR163245
99
Caledoniscincus_austrocaledonicus_AMSR163262-and-EUG3
Copeoglossum_aurae_SBH268935-and-CAS231775
Dasia_vittata_BRK391-and-AB028771
90
Dasia_olivacea_BRK392-and-ZSI10642
61
Toenayar_novemcarinata_CAS216022-and-CAS215714
99
Eutropis_longicaudata_ZMKUR00704
55
74
Eutropis_multifasciata_FMNH269170
69
Heremites_septemtaeniata_ZFMK84085-and-RUZMZB5714
58
Chioninia_delandii_Uma_R52_and_BMNH2000.18_chimera
100
Chioninia_vaillanti_Uma_49Mva6F_and_BMNH2000.10_chimera
Lubuya_ivensii_HF166
99
34
Eumecia_anchietae_PEMR16779
Trachylepis_brevicollis_CAS198871_KajiadoKenya
49
Trachylepis_madagascariensis_UMMZ209103_Madagascar
98
Trachylepis_elegans_L119_RAN56248_Madagascar
61
Trachylepis_gravenhorstii_L120_RAX00265_Madagascar
83
Trachylepis_sechellensis_TRASEY1
95
Trachylepis_wrightii_Mawr1_Seychelles
92
Trachylepis_quinquetaeniata_L159_FMNH262232_Ghana
64
Trachylepis_margaritifer_PEMR5539_NiassaMozambique
64
Trachylepis_margaritifer_CAS234165_LimpopoSouthAfrica
85
Trachylepis_perrotetii_L160_FMNH262231_Ghana
98
Trachylepis_perrotetii_L161_FMNH262230_Ghana
Trachylepis_paucisquamis_PEMR4436_CoteDIvoire
97
100
Trachylepis_paucisquamis_PEMR4438_CoteDIvoire
46
Trachylepis_affinis_PEMR5425_Gabon
90
100
Trachylepis_affinis_PEMFNR174_RabiGabon
57
Trachylepis_gonwouoi_PEMR20428_CentAfRep
94
Trachylepis_albilabris_PEMR5384_RabiGabon
96
Trachylepis_albilabris_PEMR5422_OgoooueMaritimeGabon
Trachylepis_acutilabris_CAS214651_KuneneNamibia
86
Trachylepis_homalocephala_AMB7072_WesternCapeSA
32
Trachylepis_depressa_PEMR17745_KwaZuluNatalSouthAfrica
90
35
Trachylepis_depressa_PEMR15573_GazaMozambique
Trachylepis_boettgeri_UMMZ208917_Madagascar
Trachylepis_vato_UMMZ222377_Madagascar
Trachylepis_aureopunctata_L118_RAN54509_AmbalaranoMadagascar
Trachylepis_aureopunctata_PEM_FieldNo437_Madagascar
Trachylepis_aureopunctata_UMMZ222169_Madagascar
77
Trachylepis_tavaratra_FGZC3134_Madagascar
Trachylepis_tandrefana_ZSM76.2006_Madagascar
77
Trachylepis_tandrefana_ZSM45.2006_Madagascar
13
Trachylepis_tavaratra_FGZC1820_Madagascar
Trachylepis_maculilabris_PEMR5844_Gabon
Trachylepis_comorensis_MH23_MoheliComoros
80
Trachylepis_boulengeri_PEMR15451_SofalaMozambique
35
96
Trachylepis_boulengeri_PEMR5533_NampulaMozambique
99
Trachylepis_boulengeri_PEMR16179_NiassaMozambique
64
Trachylepis_thomensis_CAS218722_SaoTome
43
Trachylepis_atlantica_MRT4428_FernandoDeNoronha
55
97
Trachylepis_atlantica_MRT4427_FernandoDeNoronha
71
Trachylepis_atlantica_MRT4429_FernandoDeNoronha
Trachylepis_varia_PEMR5413_EasternCapeSouthAfrica
100
Trachylepis_varia_PEMR5542_NiassaMozambique
Trachylepis_binotata_ZFMK66426_OmusatiNamibia
94
Trachylepis_capensis_L087_LSUMZ57253_NorthernCapeSouthAfrica
70
97
Trachylepis_occidentalis_CAS214511_SouthAfrica
Trachylepis_sulcata_CAS223979_KuneneNamibia
90
Trachylepis_punctulata_MCZZ37900_KuneneNamibia
78
32
Trachylepis_punctulata_MCZR183759_ErongoNamibia
98
Trachylepis_variegata_CAS200019_SouthAfrica
22
20
Trachylepis_variegata_MCZR184365_KarasNamibia
Trachylepis_hoeschi_MCZR184257_KuneneNamibia
Trachylepis_spilogaster_MAB136_MCZA38261_KarasNamibia
30
58
Trachylepis_spilogaster_MAB140_MCZA38295_KarasNamibia
97
Trachylepis_spilogaster_AMB7636_MCZR183768_Namibia
83
Trachylepis_spilogaster_AMB7614_Namibia
Trachylepis_sparsa_CAS214458_NorthernCapeSouthAfrica
25
Trachylepis_wahlbergi_MB20380_Zambia
Trachylepis_mlanjensis_PEMR17480_MtMulanjeMalawi
Trachylepis_mlanjensis_PEMR17482_MtMulanjeMalawi
15
Trachylepis_sparsa_Mab146_MCZA38356_KarasNamibia
Trachylepis_wahlbergi_MB20393_Zambia
3
Trachylepis_punctatissima_PEMR16655_MpumalangaSouthAfrica
Trachylepis_sparsa_MCZR184370_KarasNamibia
Trachylepis_mlanjensis_PEMR17484_MtMulanjeMalawi
Trachylepis_striata_PEMR16772_MaraTanzania
0.02

Fig. S3
CMOS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64
Dasia_vittata_BRK391-and-AB028771
100
Heremites_septemtaeniata_ZFMK84085-and-RUZMZB5714
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Lubuya_ivensii_HF166
100
Eumecia_anchietae_PEMR16779
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Trachylepis_polytropis_Mab31_PEMR5443_Gabon
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Trachylepis_perrotetii_MVZ245351_GreaterAccraGhana
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Trachylepis_paucisquamis_PEMR4438_CoteDIvoire
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Trachylepis_bocagii_WC1823_BengoAngola
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Trachylepis_punctulata_MCZZ37900_KuneneNamibia
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Trachylepis_variegata_MCZR184365_KarasNamibia
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Trachylepis_variegata_CAS200019_SouthAfrica
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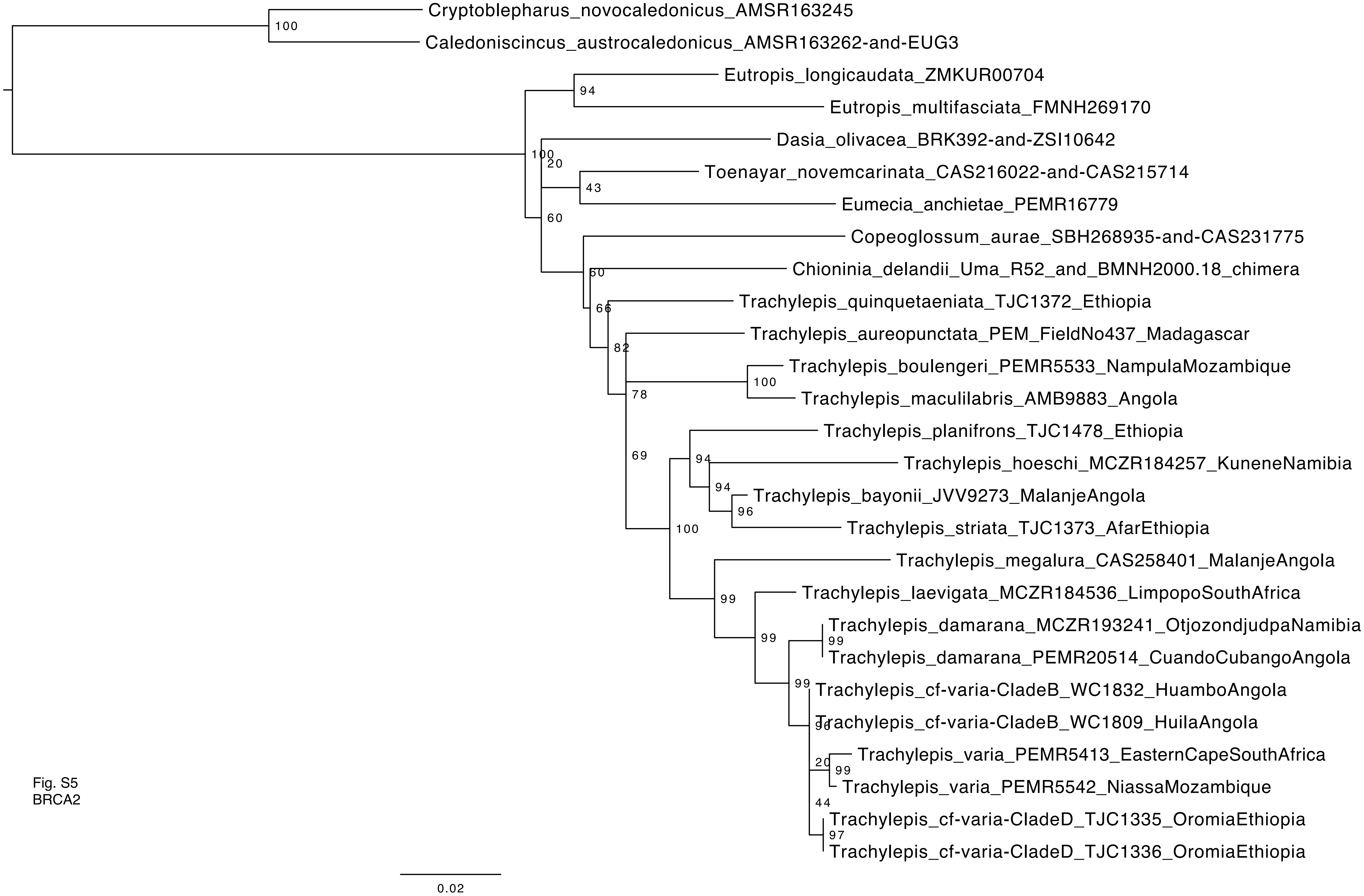
Fig. S4
KIF24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Eutropis_multifasciata_FMNH269170
Dasia_olivacea_BRK392-and-ZSI10642
100
20
Toenayar_novemcarinata_CAS216022-and-CAS215714
43
Eumecia_anchietae_PEMR16779
60
Copeoglossum_aurae_SBH268935-and-CAS231775
Chioninia_delandii_Uma_R52_and_BMNH2000.18_chimera
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66
Trachylepis_aureopunctata_PEM_FieldNo437_Madagascar
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Trachylepis_boulengeri_PEMR5533_NampulaMozambique
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78
Trachylepis_maculilabris_AMB9883_Angola
Trachylepis_planifrons_TJC1478_Ethiopia
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94
Trachylepis_hoeschi_MCZR184257_KuneneNamibia
94
Trachylepis_bayonii_JVV9273_MalanjeAngola
96
100
Trachylepis_striata_TJC1373_AfarEthiopia
Trachylepis_megalura_CAS258401_MalanjeAngola
Trachylepis_laevigata_MCZR184536_LimpopoSouthAfrica
99
Trachylepis_damarana_MCZR193241_OtjozondjudpaNamibia
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99
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Trachylepis_varia_PEMR5413_EasternCapeSouthAfrica
20
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Trachylepis_varia_PEMR5542_NiassaMozambique
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Trachylepis_cf-varia-CladeD_TJC1335_OromiaEthiopia
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Trachylepis_cf-varia-CladeD_TJC1336_OromiaEthiopia
0.02

Fig. S5
BRCA2


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Dasia_vittata_BRK391-and-AB028771
53
Eutropis_multifasciata_FMNH269170
Toenayar_novemcarinata_CAS216022-and-CAS215714
53
Heremites_septemtaeniata_ZFMK84085-and-RUZMZB5714
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Lubuya_ivensii_HF166
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Eumecia_anchietae_PEMR16779
15
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Trachylepis_dichroma_MAB189
Trachylepis_acutilabris_CAS223990_KuneneNamibia
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Trachylepis_acutilabris_AMB6935_Namibia
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Trachylepis_depressa_PEMR15573_GazaMozambique
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Trachylepis_sechellensis_TRASEY1
Trachylepis_capensis_L087_LSUMZ57253_NorthernCapeSouthAfrica
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Trachylepis_spilogaster_MAB136_MCZA38261_KarasNamibia
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Trachylepis_variegata_CAS200019_SouthAfrica
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Trachylepis_punctulata_MCZZ37900_KuneneNamibia
Trachylepis_sulcata_CAS223979_KuneneNamibia
Trachylepis_spilogaster_AMB7614_Namibia
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Trachylepis_laevis_MGR300_KuneneNamibia
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Trachylepis_laevis_MGR301_KuneneNamibia
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Trachylepis_sparsa_MCZR184370_KarasNamibia
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Trachylepis_striata_PEMR16772_MaraTanzania
Trachylepis_punctatissima_PEMR16655_MpumalangaSouthAfrica
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Trachylepis_spilogaster_MAB140_MCZA38295_KarasNamibia
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Trachylepis_sparsa_CAS214458_NorthernCapeSouthAfrica
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Trachylepis_tandrefana_ZSM76.2006_Madagascar
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Fig. S6
BDNF


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Eutropis_multifasciata_FMNH269170
46
Lubuya_ivensii_HF166
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Eumecia_anchietae_PEMR16779
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Heremites_septemtaeniata_ZFMK84085-and-RUZMZB5714
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Chioninia_delandii_Uma_R52_and_BMNH2000.18_chimera
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Chioninia_vaillanti_Uma_49Mva6F_and_BMNH2000.10_chimera
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Trachylepis_boulengeri_PEMR15451_SofalaMozambique
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62
Trachylepis_bocagii_WC1823_BengoAngola
68
86
Trachylepis_laevis_MGR300_KuneneNamibia
100
Trachylepis_laevis_MGR301_KuneneNamibia
85
Trachylepis_sulcata_CAS223979_KuneneNamibia
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99
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Trachylepis_variegata_MCZR185110_KarasNamibia
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Trachylepis_variegata_CAS200019_SouthAfrica
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Trachylepis_variegata_MCZR184365_KarasNamibia
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Trachylepis_spilogaster_MCZZ37947_KuneneNamibia
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Trachylepis_spilogaster_MAB140_MCZA38295_KarasNamibia
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0.02

Fig. S7
RAG1


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Heremites_septemtaeniata_ZFMK84085-and-RUZMZB5714
Copeoglossum_aurae_SBH268935-and-CAS231775
Lubuya_ivensii_HF166
Eutropis_longicaudata_ZMKUR00704
Eutropis_multifasciata_FMNH269170
Eumecia_anchietae_PEMR16779
Dasia_vittata_BRK391-and-AB028771
Dasia_olivacea_BRK392-and-ZSI10642
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Trachylepis_wrightii_Mawr1_Seychelles
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Trachylepis_atlantica_MRT4428_FernandoDeNoronha
Trachylepis_thomensis_CAS218722_SaoTome
Trachylepis_thomensis_CAS218821_SaoTome
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Trachylepis_maculilabris_PEMR9737_MtMulanjeMalawi
Trachylepis_maculilabris_PEMR16325_MtMulanjeMalawi
Trachylepis_maculilabris_AMB9883_Angola
Trachylepis_maculilabris_PEMR5844_Gabon
Trachylepis_maculilabris_ANG0003_LundaNorteAngola
Trachylepis_boulengeri_PEMR5533_NampulaMozambique
Trachylepis_boulengeri_PEMR16179_NiassaMozambique
Trachylepis_boulengeri_PEMR15451_SofalaMozambique
Trachylepis_casuarinae_PEMR13442_FogoIsdMozambique
Trachylepis_comorensis_ZFMK62192_Madagascar
Trachylepis_comorensis_MH23_MoheliComoros
Trachylepis_casuarinae_71Mcaguri_FogoIsdMozambique
Trachylepis_principensis_MUHNAC.MB03.000956
Trachylepis_principensis_CAS238898_PrincipeIsld
Trachylepis_principensis_MUHNAC.MB03.000979
Trachylepis_polytropis_Mab31_PEMR5443_Gabon
Trachylepis_polytropis_Mab32_PEMR5377_Gabon
Trachylepis_perrotetii_MVZ245351_GreaterAccraGhana
Trachylepis_perrotetii_L160_FMNH262231_Ghana
Trachylepis_perrotetii_L161_FMNH262230_Ghana
Trachylepis_tandrefana_Mausf2000_KirindyMadagascar
Trachylepis_boettgeri_UMMZ208917_Madagascar
Trachylepis_cf-boettgeri_ZSM362.200_Madagascar
Trachylepis_aureopunctata_L118_RAN54509_AmbalaranoMadagascar
Trachylepis_aureopunctata_PEM_FieldNo437_Madagascar
Trachylepis_aureopunctata_UMMZ222169_Madagascar
Trachylepis_vato_UMMZ222377_Madagascar
Trachylepis_vato_ZSM398.2000_Madagascar
Trachylepis_brevicollis_CAS198871_KajiadoKenya
Trachylepis_brevicollis_BE100361_DhofarOman
Trachylepis_cristinae_JR15_Socotra
Trachylepis_dichroma_MAB187
Trachylepis_dichroma_MAB189
Trachylepis_gravenhorstii_Mab182_Madagascar
Trachylepis_elegans_Mab21_PEM_FieldNo438_Madagascar
Trachylepis_madagascariensis_UMMZ209103_Madagascar
Trachylepis_elegans_L119_RAN56248_Madagascar
Trachylepis_gravenhorstii_L120_RAX00265_Madagascar
Trachylepis_quinquetaeniata_TJC1372_Ethiopia
Trachylepis_quinquetaeniata_L159_FMNH262232_Ghana
Trachylepis_quinquetaeniata_MVZ249790_Ghana
Trachylepis_margaritifer_PEMR5539_NiassaMozambique
Trachylepis_margaritifer_PEMR9745_MulanjeMalawi
Trachylepis_margaritifer_CAS234165_LimpopoSouthAfrica
Trachylepis_margaritifer_CAS234173_LimpopoSouthAfrica
Trachylepis_aureogularis_MVZ252612_EasternGhana
Trachylepis_albilabris_PEMR5384_RabiGabon
Trachylepis_albilabris_PEMR5422_OgoooueMaritimeGabon
Trachylepis_paucisquamis_UWBM6041_Ghana
Trachylepis_paucisquamis_PEMR4436_CoteDIvoire
Trachylepis_paucisquamis_PEMR4438_CoteDIvoire
Trachylepis_gonwouoi_USNM584340_Impongui-RepOfCongo
Trachylepis_gonwouoi_PEMR20428_CentAfRep
Trachylepis_affinis_PEMR5425_Gabon
Trachylepis_affinis_PEMFNR174_RabiGabon
Trachylepis_affinis_BYU573562_SouthwestCameroon
Trachylepis_affinis_NCSM88359_BiokoIslandCameroon
Trachylepis_gonwouoi_BYU573524_FakoCameroon
Trachylepis_homalocephala_AMB7072_WesternCapeSA
Trachylepis_homalocephala_MBUR01374_WesternCapeSA
Trachylepis_peringueyi_PEMR17458_NorthernCapeSouthAfrica
Trachylepis_peringueyi_PEMR17459_NorthernCapeSouthAfrica
Trachylepis_depressa_PEMR17745_KwaZuluNatalSouthAfrica
Trachylepis_depressa_PEMR15573_GazaMozambique
Trachylepis_acutilabris_AG45_NamibeAngola
Trachylepis_acutilabris_AMB6935_Namibia
Trachylepis_acutilabris_CAS223990_KuneneNamibia
Trachylepis_acutilabris_CAS214651_KuneneNamibia
Trachylepis_laevigata_MCZR184536_LimpopoSouthAfrica
Trachylepis_cf-varia-CladeE_PEMR16768_MaraTanzania
Trachylepis_cf-varia-CladeE_PEMR16789_MaraTanzania
Trachylepis_damarana_MCZR193241_OtjozondjudpaNamibia
Trachylepis_damarana_PEMR20514_CuandoCubangoAngola
Trachylepis_cf-varia-CladeG_TJC1409_SomaliEthiopia
Trachylepis_cf-varia-CladeB_WC1809_HuilaAngola
Trachylepis_cf-varia-CladeB_WC1832_HuamboAngola
Trachylepis_varia_PEMR5413_EasternCapeSouthAfrica
Trachylepis_varia_PEMR5542_NiassaMozambique
Trachylepis_cf-varia-CladeD_TJC1335_OromiaEthiopia
Trachylepis_cf-varia-CladeD_TJC1336_OromiaEthiopia
Trachylepis_cf-varia-CladeC_EBG2256_KatangaDRC
Trachylepis_cf-varia-CladeC_ELI713_SouthKivuDRC
Chioninia_delandii_Uma_R52_and_BMNH2000.18_chimera
Chioninia_vaillanti_Uma_49Mva6F_and_BMNH2000.10_chimera
Trachylepis_planifrons_TJC1478_Ethiopia
Trachylepis_megalura_PEMR16775_MaraTanzania
Trachylepis_megalura_CAS258401_MalanjeAngola
Trachylepis_capensis_L087_LSUMZ57253_NorthernCapeSouthAfrica
Trachylepis_capensis_MCZ38750_CAS234152_LimpopoSouthAfrica
Trachylepis_occidentalis_CAS214511_SouthAfrica
Trachylepis_occidentalis_MCZR184266_SouthAfrica
Trachylepis_binotata_ZFMK66426_OmusatiNamibia
Trachylepis_binotata_MCZR185902_KuneneNamibia
Trachylepis_hoeschi_AG154_NamibeAngola
Trachylepis_hoeschi_MCZR184257_KuneneNamibia
Trachylepis_laevis_MGR300_KuneneNamibia
Trachylepis_laevis_MGR301_KuneneNamibia
Trachylepis_punctulata_AG148_NamibeAngola
Trachylepis_punctulata_KTH09114
Trachylepis_punctulata_KTH09274
Trachylepis_punctulata_MCZZ37900_KuneneNamibia
Trachylepis_punctulata_MCZR183759_ErongoNamibia
Trachylepis_punctulata_CAS254769_NamibeAngola
Trachylepis_punctulata_CAS254770_NamibeAngola
Trachylepis_variegata_CAS200019_SouthAfrica
Trachylepis_variegata_MCZR184365_KarasNamibia
Trachylepis_bayonii_JVV9273_MalanjeAngola
Trachylepis_bayonii_AG201_HuilaAngola
Trachylepis_cf_chimbana_WC1791_NamibeAngola
Trachylepis_cf_chimbana_AG82_NamibeAngola
Trachylepis_brauni_PEMR20128_KituloPlateauTanzania
Trachylepis_bocagii_WC1823_BengoAngola
Trachylepis_bocagii_MCZA36458_BengoAngola
Trachylepis_bocagii_MCZA36456_BengoAngola
Trachylepis_sulcata_CAS223979_KuneneNamibia
Trachylepis_sulcata_WC1836_HuilaAngola
Trachylepis_spilogaster_WC3538_CuandoCubangoAngola
Trachylepis_spilogaster_AMB7636_MCZR183768_Namibia
Trachylepis_spilogaster_MAB136_MCZA38261_KarasNamibia
Trachylepis_spilogaster_MAB140_MCZA38295_KarasNamibia
Trachylepis_punctatissima_PEMR16655_MpumalangaSouthAfrica
Trachylepis_wahlbergi_MB20393_Zambia
Trachylepis_striata_TJC1373_AfarEthiopia
Trachylepis_mlanjensis_PEMR17484_MtMulanjeMalawi
Trachylepis_mlanjensis_PEMR17480_MtMulanjeMalawi
Trachylepis_mlanjensis_PEMR17482_MtMulanjeMalawi
Trachylepis_striata_PEMR16772_MaraTanzania
Trachylepis_wahlbergi_MCZR193549_CopperbeltZambia
Trachylepis_wahlbergi_MB20380_Zambia
Trachylepis_cf_spilogaster_PEMR21818_Angola
Trachylepis_cf_spilogaster_PEMR21819_Angola
Trachylepis_striata_CAS258400_MalanjeAngola
Trachylepis_spilogaster_AMB7614_Namibia
Trachylepis_spilogaster_MCZZ37947_KuneneNamibia
Trachylepis_sparsa_CAS214458_NorthernCapeSouthAfrica
Trachylepis_sparsa_Mab146_MCZA38356_KarasNamibia
Trachylepis_sparsa_MCZR184370_KarasNamibia
0.2

Fig. S8
16S


Caledoniscincus_austrocaledonicus_AMSR163262-and-EUG3
Eutropis_multifasciata_FMNH269170
Eutropis_longicaudata_ZMKUR00704
Dasia_vittata_BRK391-and-AB028771
92
Toenayar_novemcarinata_CAS216022-and-CAS215714
75
Dasia_olivacea_BRK392-and-ZSI10642
97
Chioninia_delandii_Uma_R52_and_BMNH2000.18_chimera
100
Chioninia_vaillanti_Uma_49Mva6F_and_BMNH2000.10_chimera
61
Copeoglossum_aurae_SBH268935-and-CAS231775
64
Trachylepis_tessellata_TJR38
100
100
Trachylepis_tessellata_TE100363
Trachylepis_socotrana_M73
100
Trachylepis_socotrana_M74
100
Trachylepis_brevicollis_BE100361_DhofarOman
97
Trachylepis_cristinae_JR15_Socotra
92
87
Trachylepis_brevicollis_CAS198871_KajiadoKenya
87
Trachylepis_dichroma_MAB187
100
Trachylepis_dichroma_MAB189
Trachylepis_polytropis_Mab31_PEMR5443_Gabon
100
Trachylepis_polytropis_Mab32_PEMR5377_Gabon
Trachylepis_gravenhorstii_L120_RAX00265_Madagascar
100
Trachylepis_madagascariensis_UMMZ209103_Madagascar
65
72
Trachylepis_elegans_L119_RAN56248_Madagascar
45
Trachylepis_elegans_Mab21_PEM_FieldNo438_Madagascar
47
Trachylepis_gravenhorstii_Mab182_Madagascar
70
Trachylepis_tavaratra_FGZC1820_Madagascar
100
Trachylepis_tavaratra_FGZC3134_Madagascar
Trachylepis_vato_ZCMV5538_IsoloMadagascar
35
Trachylepis_vato_UMMZ222377_Madagascar
99
95
Trachylepis_aureopunctata_UMMZ222169_Madagascar
99
84
Trachylepis_aureopunctata_PEM_FieldNo437_Madagascar
99
Trachylepis_aureopunctata_L118_RAN54509_AmbalaranoMadagascar
96
Trachylepis_vezo_ACZC1915_Madagascar
100
Trachylepis_vezo_ACZC1993_Madagascar
94
Trachylepis_boettgeri_UMMZ208917_Madagascar
100
Trachylepis_tandrefana_Mausf2000_KirindyMadagascar
100
Trachylepis_tandrefana_ZSM24.2006_Madagascar
100
Trachylepis_tandrefana_ZSM76.2006_Madagascar
Trachylepis_megalura_PEMR16775_MaraTanzania
Trachylepis_cf-varia-CladeE_PEMR16768_MaraTanzania
100
Trachylepis_varia_PEMR5413_EasternCapeSouthAfrica
49
100
Trachylepis_varia_PEMR5542_NiassaMozambique
71
Trachylepis_capensis_L087_LSUMZ57253_NorthernCapeSouthAfrica
90
100
Trachylepis_occidentalis_CAS214511_SouthAfrica
100
Trachylepis_occidentalis_MCZR184266_SouthAfrica
Trachylepis_binotata_ZFMK66426_OmusatiNamibia
89
99
Trachylepis_hoeschi_MCZR184257_KuneneNamibia
Trachylepis_sulcata_CAS223979_KuneneNamibia
87
Trachylepis_punctulata_MCZZ37900_KuneneNamibia
100
100
Trachylepis_punctulata_MCZR183759_ErongoNamibia
100
Trachylepis_variegata_CAS200019_SouthAfrica
100
Trachylepis_variegata_MCZR184365_KarasNamibia
Trachylepis_spilogaster_MCZZ37947_KuneneNamibia
89
100
Trachylepis_spilogaster_AMB7636_MCZR183768_Namibia
100
Trachylepis_spilogaster_AMB7614_Namibia
97
Trachylepis_spilogaster_MAB136_MCZA38261_KarasNamibia
100
Trachylepis_spilogaster_MAB140_MCZA38295_KarasNamibia
100
Trachylepis_striata_PEMR16772_MaraTanzania
95
Trachylepis_mlanjensis_PEMR17482_MtMulanjeMalawi
14
100
Trachylepis_mlanjensis_PEMR17484_MtMulanjeMalawi
59
Trachylepis_mlanjensis_PEMR17480_MtMulanjeMalawi
100
Trachylepis_wahlbergi_MB20380_Zambia
100
Trachylepis_wahlbergi_MB20393_Zambia
100
Trachylepis_punctatissima_PEMR16655_MpumalangaSouthAfrica
98
Trachylepis_sparsa_CAS214458_NorthernCapeSouthAfrica
92
Trachylepis_sparsa_Mab146_MCZA38356_KarasNamibia
100
Trachylepis_sparsa_MCZR184370_KarasNamibia
Trachylepis_atlantica_MRT4428_FernandoDeNoronha
100
Trachylepis_atlantica_MRT4427_FernandoDeNoronha
49
Trachylepis_atlantica_MRT4429_FernandoDeNoronha
63
Trachylepis_depressa_PEMR15573_GazaMozambique
100
Trachylepis_homalocephala_AMB7072_WesternCapeSA
97
Trachylepis_acutilabris_CAS214651_KuneneNamibia
100
Trachylepis_acutilabris_CAS223990_KuneneNamibia
100
Trachylepis_acutilabris_AMB6935_Namibia
Trachylepis_boulengeri_PEMR5533_NampulaMozambique
100
Trachylepis_boulengeri_PEMR15451_SofalaMozambique
45
97
Trachylepis_boulengeri_PEMR16179_NiassaMozambique
100
Trachylepis_thomensis_CAS218722_SaoTome
Trachylepis_comorensis_GC16_GrandComoro
98
84
Trachylepis_comorensis_ZFMK62192_Madagascar
89
Trachylepis_comorensis_MH23_MoheliComoros
70
Trachylepis_maculilabris_PEMR5844_Gabon
78
92
Trachylepis_maculilabris_PEMR9737_MtMulanjeMalawi
100
Trachylepis_maculilabris_PEMR16325_MtMulanjeMalawi
Trachylepis_quinquetaeniata_L159_FMNH262232_Ghana
100
Trachylepis_margaritifer_PEMR5539_NiassaMozambique
100
Trachylepis_margaritifer_PEMR9745_MulanjeMalawi
79
Trachylepis_sechellensis_TRASEY1
100
Trachylepis_wrightii_Mawr1_Seychelles
Trachylepis_perrotetii_L160_FMNH262231_Ghana
49
100
Trachylepis_perrotetii_L161_FMNH262230_Ghana
Trachylepis_affinis_PEMR5425_Gabon
100
100
Trachylepis_affinis_PEMFNR174_RabiGabon
96
Trachylepis_gonwouoi_PEMR20428_CentAfRep
Trachylepis_albilabris_PEMR5384_RabiGabon
63
100
Trachylepis_albilabris_PEMR5422_OgooueMaritimeGabon
59
Trachylepis_paucisquamis_PEMR4436_CoteDIvoire
100
Trachylepis_paucisquamis_PEMR4438_CoteDIvoire
0.06

Fig. S9
12S


Caledoniscincus_austrocaledonicus_AMSR163262-and-EUG3
Trachylepis_atlantica_MRT4429_FernandoDeNoronha
100
Trachylepis_atlantica_MRT4427_FernandoDeNoronha
59
Trachylepis_atlantica_MRT4428_FernandoDeNoronha
53
Trachylepis_maculilabris_PEMR5844_Gabon
93
Trachylepis_albotaeniata_PB27_PembaIslandTZ
99
Trachylepis_albotaeniata_PB29_PembaIslandTZ
100
Trachylepis_boulengeri_PEMR5533_NampulaMozambique
99
Trachylepis_boulengeri_PEMR16179_NiassaMozambique
100
Trachylepis_boulengeri_PEMR15451_SofalaMozambique
100
Trachylepis_infralineata_Mab4EUR_EuropaIsl
99
Trachylepis_thomensis_CAS218722_SaoTome
41
Trachylepis_maculilabris_PEMR9737_MtMulanjeMalawi
100
Trachylepis_maculilabris_PEMR16325_MtMulanjeMalawi
30
Trachylepis_comorensis_GC16_GrandComoro
100
Trachylepis_casuarinae_PEMR13442_FogoIsdMozambique
100
Trachylepis_casuarinae_71Mcaguri_FogoIsdMozambique
99
Trachylepis_comorensis_MH23_MoheliComoros
Trachylepis_ozorii_Voucher625_HM192747
100
Trachylepis_polytropis_Mab31_PEMR5443_Gabon
100
Trachylepis_polytropis_Mab32_PEMR5377_Gabon
Eutropis_multifasciata_FMNH269170
36
Chioninia_delandii_Uma_R52_and_BMNH2000.18_chimera
100
Chioninia_vaillanti_Uma_49Mva6F_and_BMNH2000.10_chimera
33
Eutropis_longicaudata_ZMKUR00704
90
Copeoglossum_aurae_SBH268935-and-CAS231775
44
Trachylepis_sechellensis_TRASEY1
100
Trachylepis_wrightii_Mawr1_Seychelles
33
Trachylepis_acutilabris_AMB6935_Namibia
100
Trachylepis_acutilabris_CAS223990_KuneneNamibia
100
Trachylepis_acutilabris_CAS214651_KuneneNamibia
65
Trachylepis_depressa_PEMR15573_GazaMozambique
100
Trachylepis_homalocephala_AMB7072_WesternCapeSA
98
Trachylepis_homalocephala_MBUR01363_WesternCapeSA
100
Trachylepis_peringueyi_PEMR17458_NorthernCapeSouthAfrica
100
Trachylepis_peringueyi_PEMR17459_NorthernCapeSouthAfrica
44
18
Trachylepis_gonwouoi_PEMR20428_CentAfRep
Trachylepis_affinis_PEMR5425_Gabon
100
Trachylepis_affinis_PEMFNR174_RabiGabon
100
46
Trachylepis_perrotetii_L160_FMNH262231_Ghana
100
Trachylepis_perrotetii_L161_FMNH262230_Ghana
45
Trachylepis_albilabris_PEMR5384_RabiGabon
100
Trachylepis_albilabris_PEMR5422_OgooueMaritimeGabon
98
Trachylepis_paucisquamis_PEMR4436_CoteDIvoire
100
Trachylepis_paucisquamis_PEMR4438_CoteDIvoire
Trachylepis_socotrana_M73
100
Trachylepis_socotrana_M74
80
Trachylepis_brevicollis_CAS198871_KajiadoKenya
100
Trachylepis_dichroma_MAB187
100
Trachylepis_dichroma_MAB189
28
76
Heremites_septemtaeniata_ZFMK84085-and-RUZMZB5714
59
Trachylepis_quinquetaeniata_L159_FMNH262232_Ghana
99
Trachylepis_margaritifer_PEMR5539_NiassaMozambique
100
Trachylepis_margaritifer_PEMR9745_MulanjeMalawi
100
Trachylepis_margaritifer_CAS234165_LimpopoSouthAfrica
100
Trachylepis_margaritifer_CAS234173_LimpopoSouthAfrica
58
Trachylepis_elegans_Mab21_PEM_FieldNo438_Madagascar
100
Trachylepis_elegans_L119_RAN56248_Madagascar
65
Trachylepis_madagascariensis_UMMZ209103_Madagascar
65
Trachylepis_gravenhorstii_L120_RAX00265_Madagascar
67
Trachylepis_gravenhorstii_Mab182_Madagascar
79
Trachylepis_boettgeri_UMMZ208917_Madagascar
100
Trachylepis_tandrefana_Mausf2000_KirindyMadagascar
100
Trachylepis_vato_UMMZ222377_Madagascar
100
Trachylepis_aureopunctata_UMMZ222169_Madagascar
100
Trachylepis_aureopunctata_PEM_FieldNo437_Madagascar
96
Trachylepis_aureopunctata_L118_RAN54509_AmbalaranoMadagascar
30
Trachylepis_megalura_PEMR16775_MaraTanzania
87
Trachylepis_cf-varia-CladeE_PEMR16768_MaraTanzania
100
Trachylepis_varia_PEMR5413_EasternCapeSouthAfrica
100
Trachylepis_varia_PEMR5542_NiassaMozambique
Trachylepis_occidentalis_CAS214511_SouthAfrica
100
Trachylepis_occidentalis_MCZR184266_SouthAfrica
87
99
Trachylepis_binotata_MCZR185902_KuneneNamibia
99
Trachylepis_capensis_L087_LSUMZ57253_NorthernCapeSouthAfrica
100
Trachylepis_capensis_MCZ38750_CAS234152_LimpopoSouthAfrica
Trachylepis_hoeschi_MCZR184257_KuneneNamibia
89
68
Trachylepis_punctulata_MCZZ37900_KuneneNamibia
100
Trachylepis_punctulata_MCZR183759_ErongoNamibia
100
Trachylepis_variegata_CAS200019_SouthAfrica
100
Trachylepis_variegata_MCZR184365_KarasNamibia
88
Trachylepis_sulcata_CAS223979_KuneneNamibia
100
Trachylepis_laevis_MGR300_KuneneNamibia
100
Trachylepis_laevis_MGR301_KuneneNamibia
Trachylepis_spilogaster_MCZZ37947_KuneneNamibia
100
Trachylepis_spilogaster_AMB7636_MCZR183768_Namibia
92
100
Trachylepis_spilogaster_AMB7614_Namibia
99
Trachylepis_spilogaster_MAB136_MCZA38261_KarasNamibia
99
Trachylepis_spilogaster_MAB140_MCZA38295_KarasNamibia
99
Trachylepis_mlanjensis_PEMR17480_MtMulanjeMalawi
100
Trachylepis_mlanjensis_PEMR17484_MtMulanjeMalawi
Trachylepis_mlanjensis_PEMR17482_MtMulanjeMalawi
100
Trachylepis_striata_PEMR16772_MaraTanzania
98
Trachylepis_wahlbergi_MB20380_Zambia
100
Trachylepis_wahlbergi_MB20393_Zambia
99
Trachylepis_punctatissima_PEMR16655_MpumalangaSouthAfrica
100
Trachylepis_sparsa_CAS214458_NorthernCapeSouthAfrica
99
Trachylepis_sparsa_Mab146_MCZA38356_KarasNamibia
100
Trachylepis_sparsa_MCZR184370_KarasNamibia
0.06

Fig. S10
CYT-B


Cryptoblepharus_novocaledonicus_AMSR163245
100
Caledoniscincus_austrocaledonicus_AMSR163262-and-EUG3
Eutropis_multifasciata_FMNH269170
100
Dasia_vittata_BRK391-and-AB028771
100
Dasia_olivacea_BRK392-and-ZSI10642
97
Eutropis_longicaudata_ZMKUR00704
51
Toenayar_novemcarinata_CAS216022-and-CAS215714
50
Lubuya_ivensii_HF166
Heremites_septemtaeniata_ZFMK84085-and-RUZMZB5714
70
Chioninia_delandii_Uma_R52_and_BMNH2000.18_chimera
100
Chioninia_vaillanti_Uma_49Mva6F_and_BMNH2000.10_chimera
93
Trachylepis_quinquetaeniata_MVZ249790_Ghana
Trachylepis_homalocephala_MBUR01374_WesternCapeSA
100
Trachylepis_acutilabris_CAS223990_KuneneNamibia
100
Trachylepis_acutilabris_AG45_NamibeAngola
90
45
Trachylepis_boulengeri_PEMR5533_NampulaMozambique
100
Trachylepis_maculilabris_ANG0003_LundaNorteAngola
96
60
Trachylepis_perrotetii_MVZ245351_GreaterAccraGhana
99
Trachylepis_gonwouoi_BYU573524_FakoCameroon
100
Trachylepis_gonwouoi_USNM584340_Impongui-RepOfCongo
89
Trachylepis_affinis_BYU573562_SouthwestCameroon
100
Trachylepis_affinis_NCSM88359_BiokoIslandCameroon
84
Trachylepis_aureogularis_MVZ252612_EasternGhana
97
Trachylepis_paucisquamis_UWBM6041_Ghana
89
Trachylepis_megalura_CAS258401_MalanjeAngola
98
Trachylepis_laevigata_MCZR184536_LimpopoSouthAfrica
Trachylepis_damarana_MCZR193241_OtjozondjudpaNamibia
100
100
Trachylepis_damarana_PEMR20514_CuandoCubangoAngola
Trachylepis_cf-varia-CladeG_TJC1409_SomaliEthiopia
97
95
Trachylepis_cf-varia-CladeB_WC1809_HuilaAngola
100
Trachylepis_cf-varia-CladeB_WC1832_HuamboAngola
98
Trachylepis_varia_PEMR5413_EasternCapeSouthAfrica
97
100
Trachylepis_varia_PEMR5542_NiassaMozambique
75
Trachylepis_cf-varia-CladeD_TJC1335_OromiaEthiopia
100
Trachylepis_cf-varia-CladeD_TJC1336_OromiaEthiopia
Trachylepis_planifrons_TJC1478_Ethiopia
Trachylepis_hoeschi_AG154_NamibeAngola
100
69
Trachylepis_hoeschi_MCZR184257_KuneneNamibia
Trachylepis_wahlbergi_MCZR193549_CopperbeltZambia
100
Trachylepis_striata_TJC1373_AfarEthiopia
100
85
Trachylepis_striata_CAS258400_MalanjeAngola
100
Trachylepis_cf_spilogaster_PEMR21818_Angola
100
Trachylepis_cf_spilogaster_PEMR21819_Angola
99
Trachylepis_punctulata_AG148_NamibeAngola
99
Trachylepis_variegata_MCZR185110_KarasNamibia
95
Trachylepis_bayonii_JVV9273_MalanjeAngola
99
Trachylepis_bayonii_AG201_HuilaAngola
91
Trachylepis_cf_chimbana_AG82_NamibeAngola
96
Trachylepis_bocagii_MCZA36458_BengoAngola
100
Trachylepis_bocagii_MCZA36456_BengoAngola
0.1

Fig. S11
ND2

Fig. S12

Edited, based on Imported tree 1

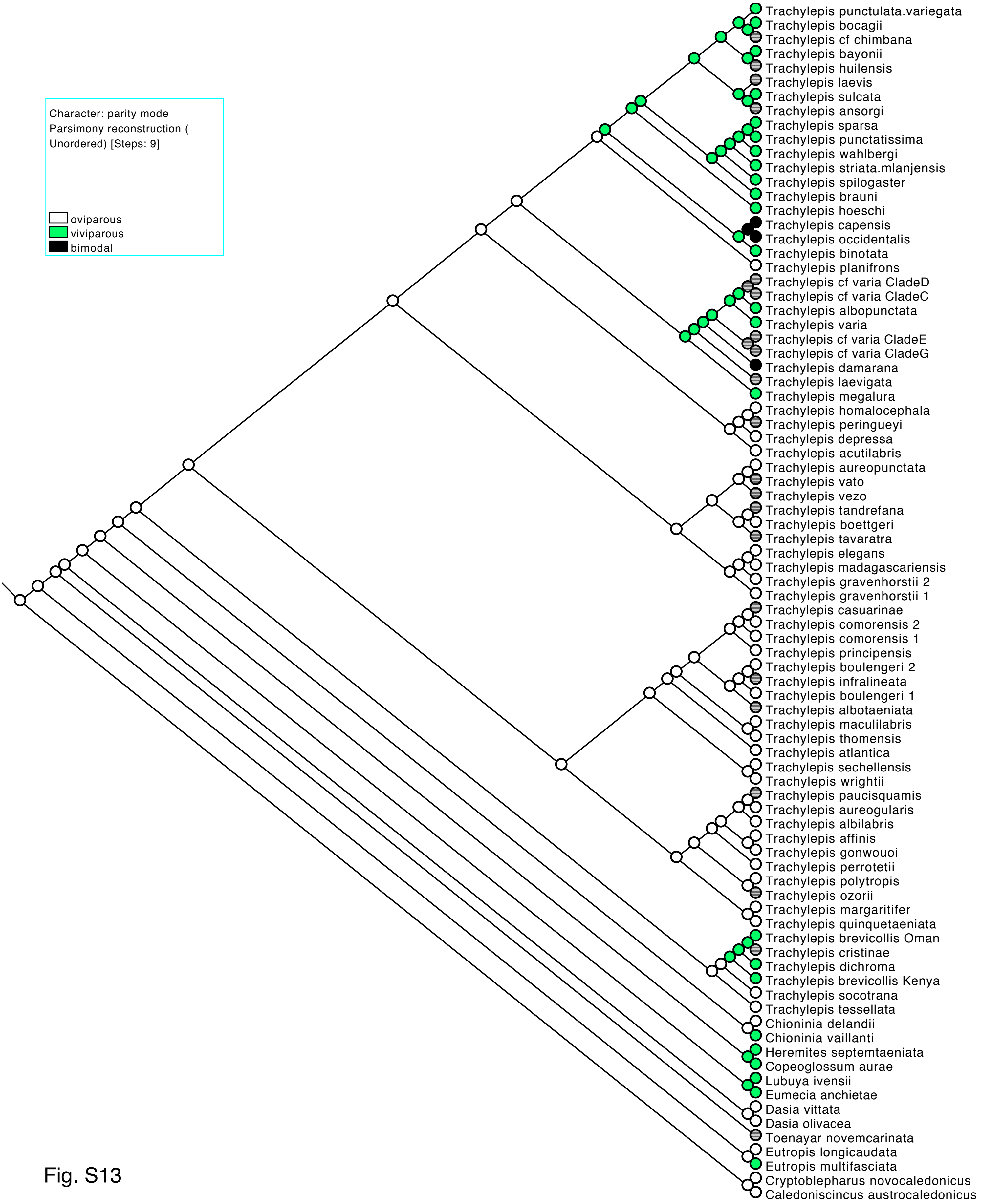

Fig. S13

Edited, based on Imported tree 1

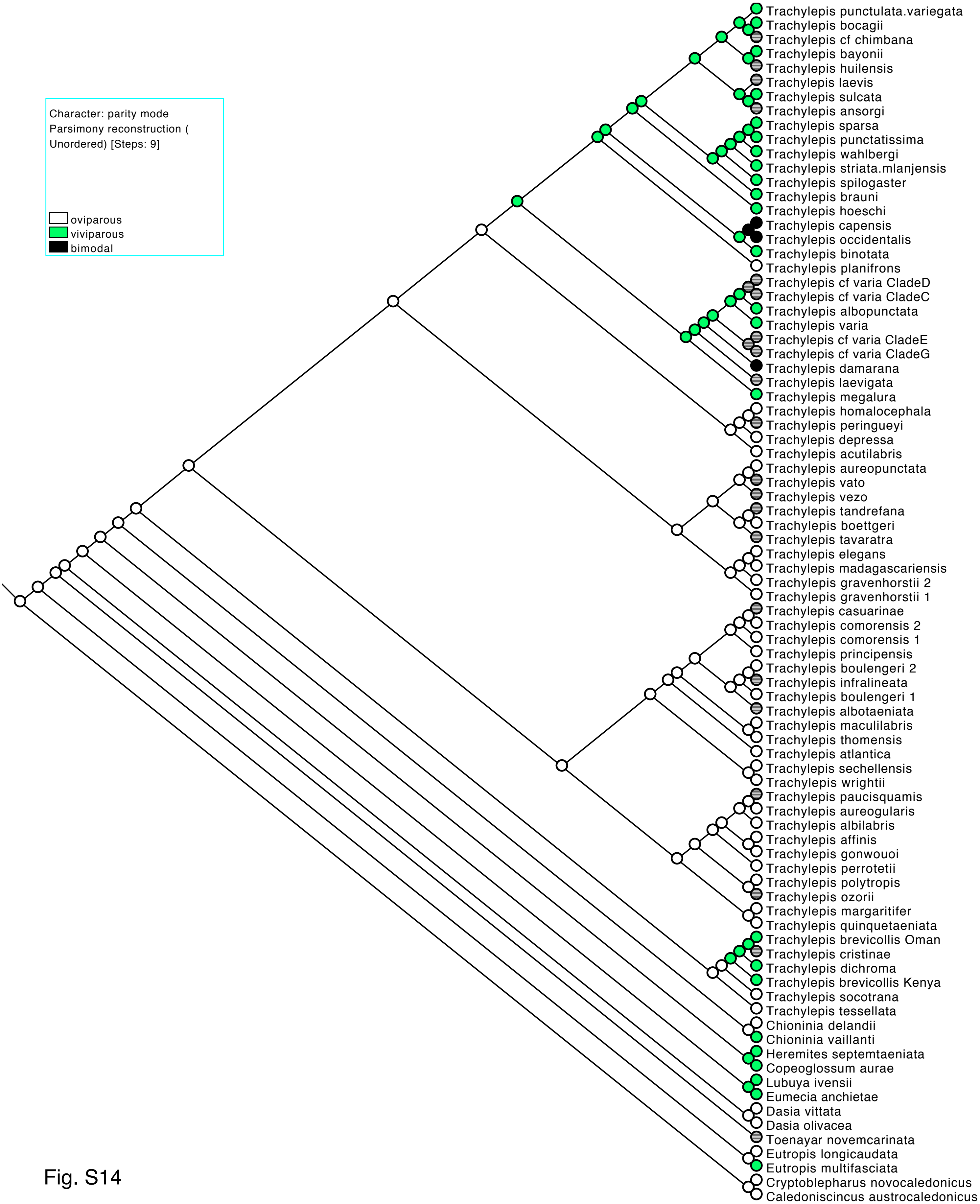

Fig. S14

Edited, based on Imported tree 1

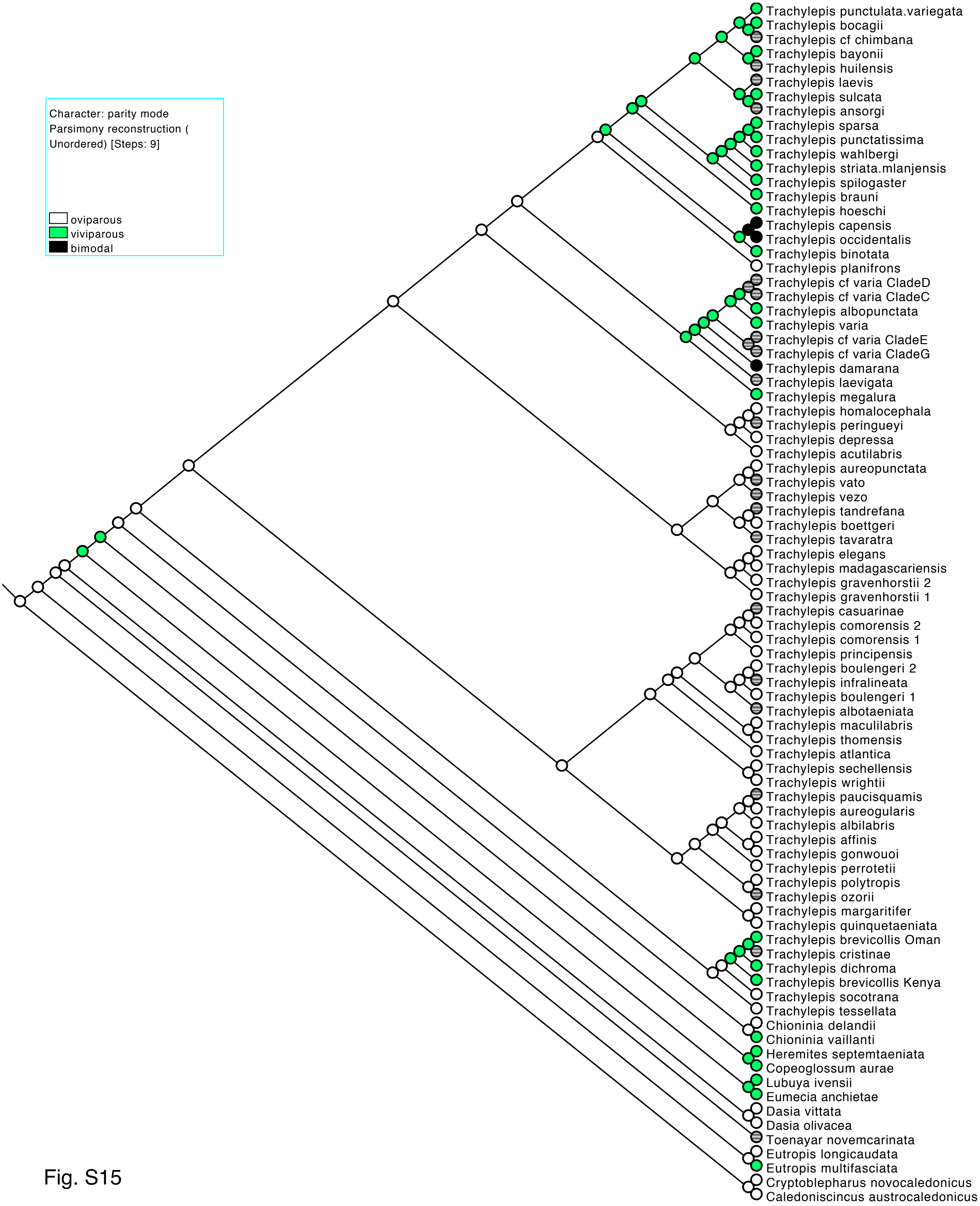

Fig. S15

Edited, based on Imported tree 1

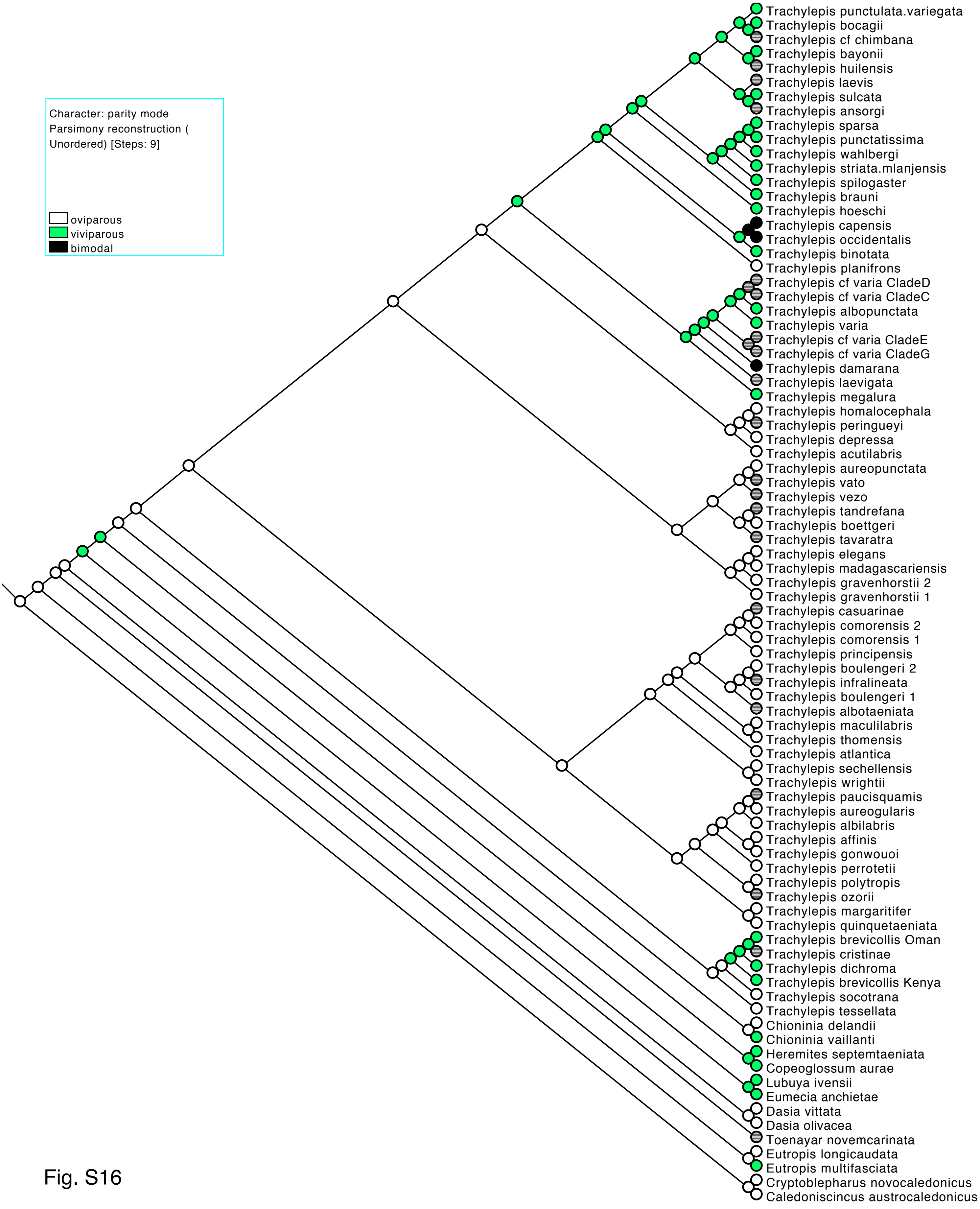

Fig. S16

Edited, based on Imported tree 1

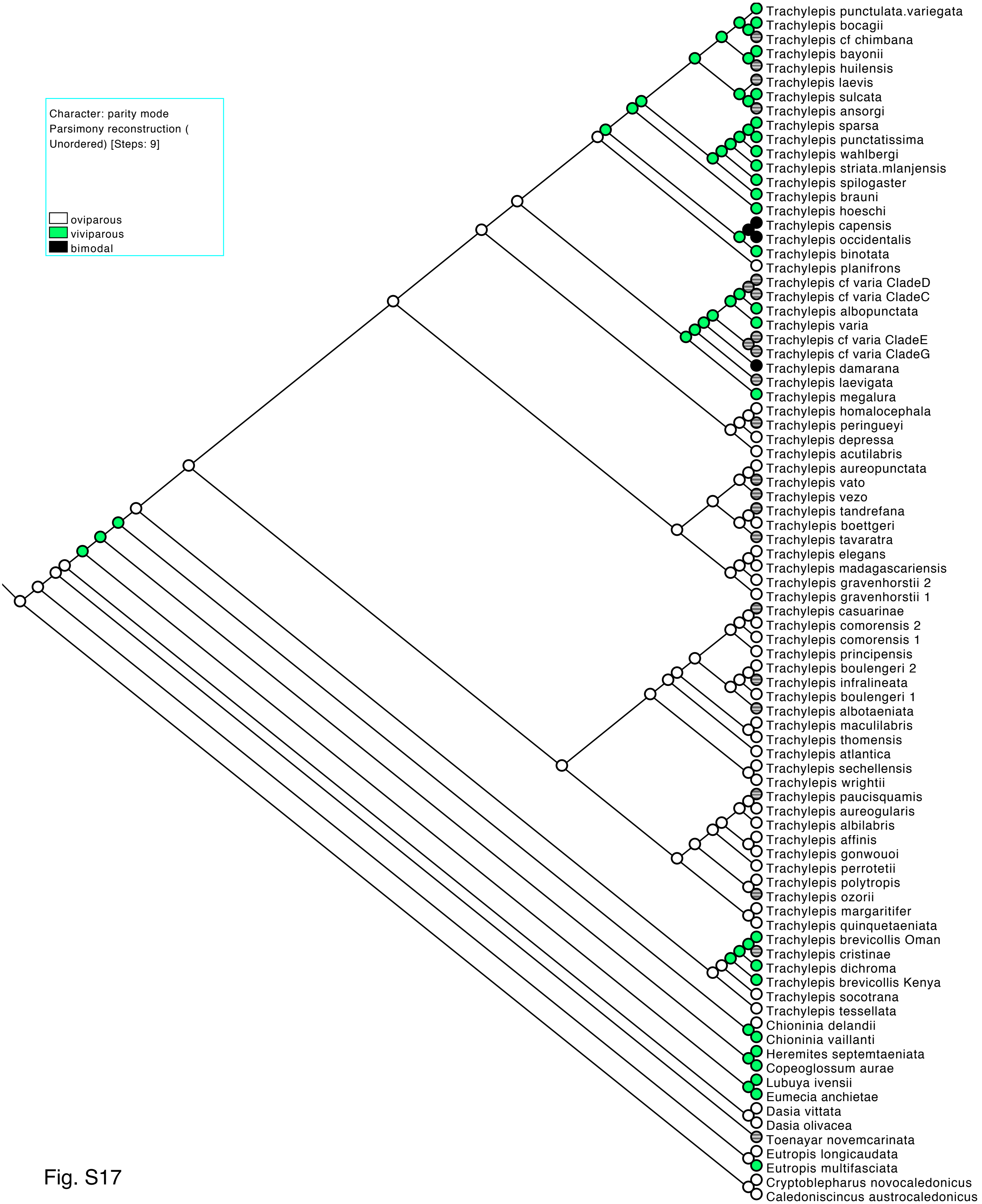

Fig. S17

Edited, based on Imported tree 1

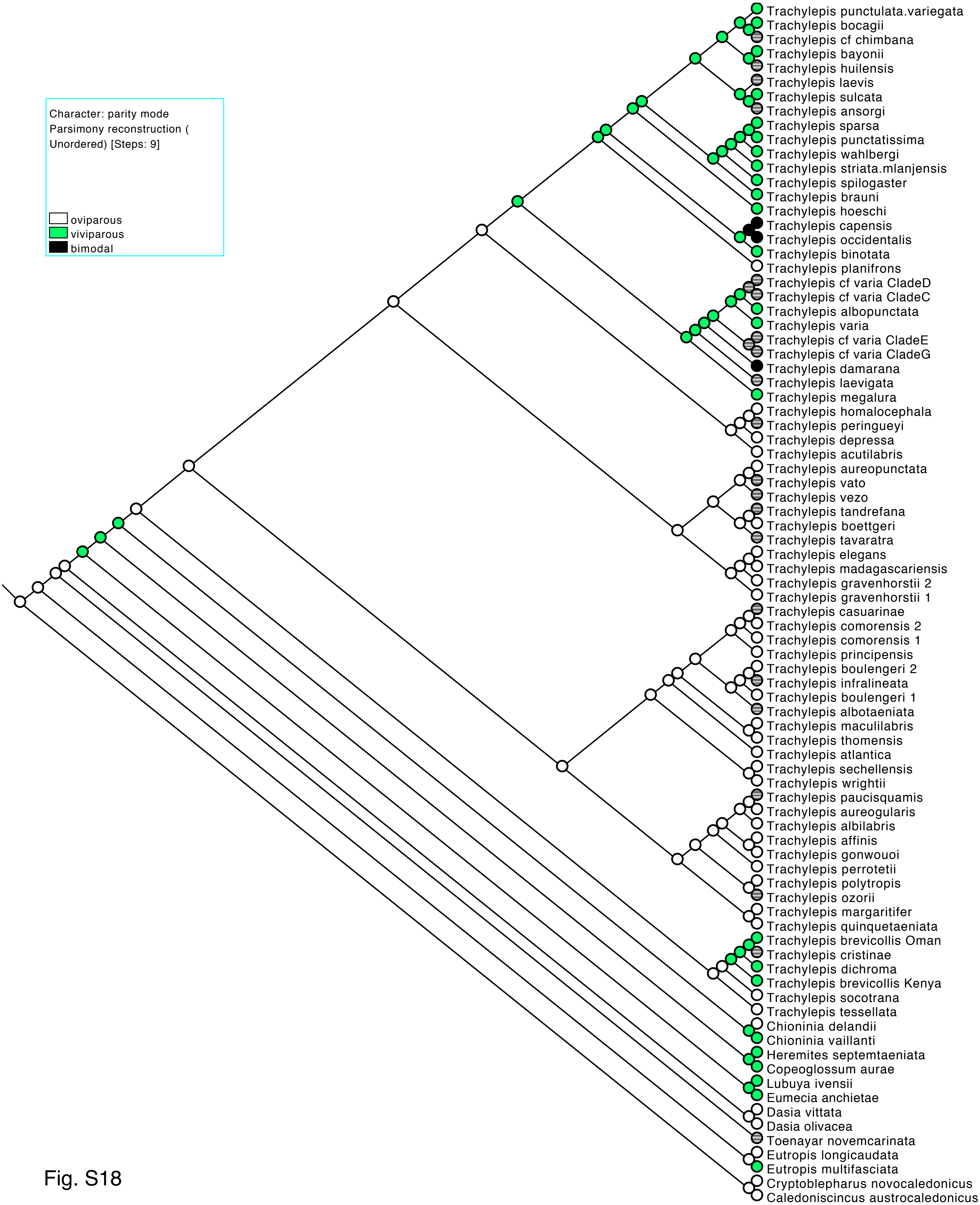

Fig. S18

Edited, based on Imported tree 1