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Methodological congruence in phylogenomic analyses with morphological support for teiid lizards (Sauria: Teiidae)

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ABSTRACT

A well-known issue in phylogenetics is discordance among gene trees, species trees, morphology, and other data types. Gene-tree discordance is often caused by incomplete lineage sorting, lateral gene transfer, and gene duplication. Multispecies-coalescent methods can account for incomplete lineage sorting and are believed by many to be more accurate than concatenation. However, simulation studies and empirical data have demonstrated that concatenation and species tree methods often recover similar topologies. We use three popular methods of phylogenetic reconstruction (one concatenation, two species tree) to evaluate relationships within Teiidae. These lizards are distributed across the United States to Argentina and the West Indies, and their classification has been controversial due to incomplete sampling and the discordance among various character types (chromosomes, DNA, musculature, osteology, etc.) used to reconstruct phylogenetic relationships. Recent morphological and molecular analyses of the group resurrected three genera and created five new genera to resolve non-monophyly in three historically ill-defined genera: *Ameiva*, *Cnemidophorus*, and *Tupinambis*. Here, we assess the phylogenetic relationships of the Teiidae using "next-generation" anchored-phylogenomics sequencing. Our final alignment includes 316 loci (488,656 bp DNA) for 244 individuals (56 species of teiids, representing all currently recognized genera) and all three methods (ExaML, MP-EST, and ASTRAL-II) recovered essentially identical topologies. Our results are basically in agreement with recent results from morphology and smaller molecular datasets, showing support for monophyly of the eight new genera. Interestingly, even with hundreds of loci, the relationships among some genera in Tupinambinae remain ambiguous (i.e. low nodal support for the position of *Salvator* and *Dracaena*).

1. Introduction

Discordant phylogenetic signal in different data partitions (such as morphological and molecular datasets) has long been both a nuisance and a subject of great interest to systematists (Wiens, 1998). In particular, phylogeneticists have long recognized the potential for discordance between a gene tree and its species tree (Goodman et al., 1979; Pamilo and Nei, 1988). Factors that may contribute to this phenomenon include incomplete lineage sorting (ILS), lateral gene transfer, and gene duplication and extinction (Edwards, 2009; Maddison, 1997). Traditional approaches to using molecular data for phylogenetic estimation involve the use of concatenation, where multiple loci are linked together in a supermatrix. More recently, researchers have favored methods that attempt to account for some of the known sources of gene tree/species tree discordance.

Specifically, modeling the multispecies coalescent can account for the effects of ILS and a summary for many of these algorithms was provided by Tonini et al. (2015). The superiority of newer methods which account for potential error caused by ILS has been demonstrated theoretically, however, specific conditions under which concatenation would result is a less accurate topology are unclear. Some simulation studies show that concatenation often

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performs as well or better than methods that attempt to control for ILS (Tonini et al., 2015), particularly when gene trees have poor phylogenetic signal or the level of ILS is low (Mirarab et al., 2014). In addition, many empirical studies show strong congruence between these methods (Berv and Prum, 2014; Pyron et al., 2014; Thompson et al., 2014). The use of multiple approaches to phylogenetic reconstruction is especially important for groups in need of taxonomic realignment.

The lizard family Teiidae consists of 151 species spread across 18 genera, with species richness as follows: *Ameiva* (13), *Ameivula* (10), *Aspidoscelis* (41), *Aurivela* (2), *Callopistes* (2), *Cnemidophorus* (19), *Contomastix* (5), *Crocodilurus* (1), *Dicrodon* (3), *Dracaena* (2), *Glaucomastix* (4), *Holcosus* (10), *Kentropyx* (9), *Medopheos* (1), *Pholidoscelis* (19), *Salvator* (3), *Teius* (3), and *Tupinambis* (4) (Uetz and Hosek, 2016). These lizards are widely distributed across the Americas and West Indies and ecologically characterized as diurnal, terrestrial, or semi-aquatic, and active foragers (Presch, 1970; Vitt and Pianka, 2004). Some of the earliest work on teiid systematics gathered genera previously scattered across 27 families, and organized them into four groups within Teiidae (Boulenger, 1885). Three of the groups consisted of various genera of "microteiids" (currently Gymnophthalmidae), while the "macroteiids" that comprised the remaining group were distinct based on the condition of nasal scales (anterior nasals not separated medially by a frontonasal), well-developed limbs, and a moderate to large body size. Later morphological work recognized the macroteiids as a distinct subfamily within Teiidae consisting of two tribes: Teiini and Tupinambini (Presch, 1970, 1974). Eventually, Presch (1983) reduced Teiidae to the macroteiids, and placed the microteiids in Gymnophthalmidae.

Though recent molecular and morphological studies consistently resolve Teiidae and Gymnophthalmidae as separate, monophyletic groups (Conrad, 2008; Pellegrino et al., 2001; Pyron, 2010; Reeder et al., 2015; Wiens et al., 2012), earlier works had questioned this division due to a lack of synapomorphic characters (Harris, 1985; Myers and Donnelly, 2001). Separate analyses of chromosomal (Gorman, 1970), integumental (Vanzolini and Valencia, 1965), myological (Rieppel, 1980), neurological (Northcutt, 1978), osteological (Presch, 1974; Veronese and Krause, 1997), and mitochondrial DNA (Giugliano et al., 2007), consistently resolve two subfamilies: Tupinambinae (large tegus) and Teiinae (smaller whiptails and racerunners) (Table 1). Other studies did not find support for these groups (Moro and Abdala, 2000), and have recommended transferring *Callopistes* to Teiinae (Teixeira, 2003), or recognizing a subfamily Callopistinae (Harvey et al., 2012).

Table 1
Taxonomic authorities for teiid subfamilies (Costa et al., 2016) and genera (Harvey et al., 2012).

Taxon	Taxonomic Authority
Teiidae	Gray (1827)
Teiinae	Gray (1827)
Ameiva	Meyer (1795)
Ameivula	Harvey et al. (2012)
Aspidoscelis	Fitzinger (1843)
Aurivela	Harvey et al. (2012)
Cnemidophorus	Wagler (1830)
Contomastix	Harvey et al. (2012)
Dicrodon	Duméril and Bibron (1839)
Holcosus	Cope (1862)
Glaucomastix	Fitzinger (1843)
Kentropyx	Spix (1825)
Medopheos	Harvey et al. (2012)
Pholidoscelis	Fitzinger (1843)
Teius	Merrem (1820)
Tupinambinae	Bonaparte (1831)
Callopistes	Gravenhorst (1837)
Crocodilurus	Spix (1825)
Dracaena	Daudin (1801)
Salvator	Duméril and Bibron (1839)
Tupinambis	Daudin (1802)

Hypotheses of the phylogenetic relationships among genera within these subfamilies have also been discordant. For Tupinambinae, studies based on chromosomes (Gorman, 1970), external morphology (Vanzolini and Valencia, 1965), and trigeminal muscles (Rieppel, 1980), support a sister relationship between *Tupinambis* and *Dracaena*, whereas osteological data recover a close relationship between *Tupinambis* and *Crocodilurus* (Presch, 1974). Recent studies, however, were unable to resolve relationships among these genera with high nodal support (Giugliano et al., 2007; Harvey et al., 2012).

Within Teiinae, Reeder et al. (2002) coined the term "cnemidophorines," referring to a clade comprising *Ameiva*, *Aspidoscelis*, *Cnemidophorus*, and *Kentropyx* (*Ameivula*, *Aurivela*, *Contomastix*, *Glaucomastix*, *Holcosus*, *Medopheos*, and *Pholidoscelis* were described later but also belong in this group), and the monophyly of this group has been supported in other studies as well (Giugliano et al., 2007; Presch, 1974), but see Harvey et al. (2012). Generic relationships among cnemidophorine genera and others within Teiinae (*Teius* and *Dicrodon*) are unclear. Much of the confusion stems from repeated findings of paraphyly within the subfamily, most notably among members nested in *Cnemidophorus* and *Ameiva* (Giugliano et al., 2006; Gorman, 1970; Harvey et al., 2012; Reeder et al., 2002).

Recent analyses of morphology restricted the genus *Ameiva* to cis-Andean (east of Andes Mountains) South America and the West Indies, while 11 species from trans-Andean South America and Central America were placed in the resurrected genus *Holcosus* and the new genus *Medopheos* (Harvey et al., 2012). That study scored 742 specimens (101 species and subspecies) of teiids for 137 morphological characters. Additional taxonomic changes proposed by Harvey et al. (2012) and a molecular study by Goicoechea et al. (2016) include four new genera (*Ameivula*, *Aurivela*, *Contomastix*, and *Glaucomastix*) to resolve non-monophyly within *Cnemidophorus*, and one resurrected genus (*Salvator*) to accommodate a "southern" clade of *Tupinambis*. Unfortunately, many of these recommendations have little or no nodal support (BS < 70), particularly in the morphological analysis (Harvey et al., 2012). The results of Harvey et al. (2012)'s morphological analysis were mostly corroborated by a large-scale molecular analysis of Squamata (Pyron et al., 2013). However, that study only used the available data generated in the other studies cited above, and was thus limited in taxonomic sampling and resolving power for many nodes.

The first combined analysis of multiple datasets (mtDNA, morphology, and allozymes) recovered one species of Central American "*Ameiva*" (*Holcosus quadrilineatus*) to form a clade with South American *Ameiva* (bootstrap support [BS] = 91), while another species from Central America (*Holcosus undulatus*) was recovered as the sister group to a large South American clade (*Cnemidophorus* + *Kentropyx*), but with no support (BS < 50; Reeder et al., 2002). These authors also found that the two West Indian taxa were recovered as part of a clade with mostly North American *Aspidoscelis*, but with weak support (BS = 73). A more extensive phylogenetic study of West Indian *Ameiva* found that this island radiation was more closely related to Central American *Holcosus* than to South American *Ameiva ameiva*, though this finding was not well supported (BS = 50; Hower and Hedges, 2003). Goicoechea et al. (2016) also recovered a non-monophyletic *Ameiva* in their molecular study of Gymnophthalmoidea and resurrected the genus *Pholidoscelis* for the Caribbean species. However, their matrix had a high proportion of missing data, and results differed substantially among concatenated analyses, including

maximum likelihood and dynamically-optimized maximum parsimony. Thus, the relationships and taxonomy of Teiidae have yet to be rigorously evaluated using a large multi-locus molecular dataset and dense taxonomic sampling.

The purpose of this study is to assess the phylogenetic relationships within Teiidae using a "next-generation" sequencing (NGS) anchored phylogenomics approach. This will provide an independent test of the findings and taxonomy proposed by Harvey et al. (2012) and Goicoechea et al. (2016). Our study recovers some well-supported differences in the higher-level phylogeny of Teiidae, but we also recover much of the phylogenetic structure proposed by Harvey et al. (2012).

2. Materials and methods

2.1. Anchored phylogenomics probe design

The original 512 anchored hybrid-enrichment loci developed by Lemmon et al. (2012) for vertebrate-wide sampling have been further refined to a set of 394 loci ideal for Amniote phylogenomics. Probe sets specific to birds (Prum et al., 2015) and snakes (Ruane et al., 2015) have subsequently been designed. In order to improve the capture efficiency for Teiidae, we developed a lizard-specific probe set as follows. First, lizard-specific sequences were obtained from the *Anolis carolinensis* genome (UCSC genome browser) using the anoCar2 probe coordinates of Ruane et al. (2015). DNA extracted from the black and white tegu lizard, *Salvator merianae* (voucher CHUNB00503), was prepared for sequencing following Lemmon et al. (2012) and sequenced on one Illumina PE100 bp lane (~15× coverage) at Hudson Alpha Institute for Biotechnology (http://hudsonalpha.org). Reads passing the CASAVA quality filter were used to obtain sequences homologous to the *Anolis* probe region sequences. After aligning the *Anolis* and *Salvator* sequences using MAFFT (Katoh and Toh, 2008), alignments were trimmed to produce the final probe region alignments, and probes were tiled at 1.5× tiling density per species. Probe alignments and sequences are available in Dryad repository doi:http://dx.doi.org/10.5061/dryad.d4d5d.

2.2. Data collection and assembly

Phylogenomic data were generated by the Center for Anchored Phylogenetics (www.anchoredphylogeny.com) using the anchored hybrid enrichment methodology described by Lemmon et al. (2012). This approach uses probes that bind to highly conserved anchor regions of vertebrate genomes with the goal of sequencing the less conserved flanking regions. Targeting these variable regions can produce hundreds of unlinked loci from across the genome that are useful at a diversity of phylogenetic timescales. DNA extracts were sheared to a fragment size of 150–300 bp using a Covaris E220 Focused-ultrasonicator. Indexed libraries were then prepared on a Beckman-Coulter Biomek FXp liquid-handling robot following a protocol adapted from Meyer and Kircher (2010); with SPRIselect size-selection after blunt-end repair using a 0.9× ratio of bead to sample volume. Libraries were then pooled in groups of 16 samples for hybrid enrichment using an Agilent Custom SureSelect kit (Agilent Technologies) that contained the probes described above. The enriched library pools were then sequenced on six PE150 Illumina HiSeq2000 lanes by the Translational Science Laboratory in the College of Medicine at Florida State University.

Paired reads were merged following Rokyta et al. (2012), and assembled following Ruane et al. (2015). After filtering out consensus sequences generated from fewer than 100 reads, sets of orthologous sequences were obtained based on pairwise sequence distances as described by Ruane et al. (2015). Orthologous sets containing fewer than 155 sequences were removed from further analysis. Sequences were then aligned using MAFFT (Katoh and Standley, 2013; – genafpair – maxiterate 1000) and trimmed following Ruane et al. (2015), with good sites identified as those containing >30% identity, and fewer than 25 missing/masked characters required for an alignment site to be retained.

2.3. Phylogenetic analyses

All phylogenetic analyses (except ASTRAL-II; see below) were performed using resources from the Fulton Supercomputing Lab at Brigham Young University. A maximum likelihood tree was estimated with a Gamma model of rate heterogeneity (median was used for the discrete approximation) from the concatenated dataset of all loci with ExaML v3.0.15 (Kozlov et al., 2015). The k means option (Frandsen et al., 2015) in PartitionFinder2 was used to partition the data based on similarity in models of molecular evolution (Lanfear et al., 2012). Parsimony and random starting trees (N = 40) were generated in RaxML v8.2.8 (Stamatakis, 2014) and performance examined using Robinson-Foulds (RF) distances. Because ExaML does not compute bootstrap values, we generated one hundred bootstrap replicate files and Parsimony starting trees in RaxML using a General Time Reversible Gamma model of rate heterogeneity (GTRGAMMA). Replicate files and starting trees were used to produce 100 bootstrapped trees in ExaML, which were subsequently used to estimate nodal support on our best ExaML tree (see above) using the −z function and GTRGAMMA model in RaxML. The ExaML analysis was completed in 5 h and 46 min using 20 cores and 1 GB of memory per core on an Intel Haswell CPU.

Species tree analyses were reconstructed in MP-EST v1.5 (Liu et al., 2010) and ASTRAL-II v4.7.9 (Mirarab and Warnow, 2015). For the MP-EST analysis, 100 nonparametric bootstrapped gene trees per locus were generated in RaxML v7.7.8 (Stamatakis, 2006). Species trees were then estimated from the gene trees by maximizing a pseudo-likelihood function in MP-EST. Results were summarized by constructing a maximum clade credibility tree in the DendroPy package SumTrees (Sukumaran and Holder, 2010), with nodal support being calculated as the frequency at which each node was supported across the gene trees. The 100 species tree analyses in MP-EST ran for ~5 h using 10 cores and 250 MB of memory per core on an Intel Haswell CPU.

The gene trees with the highest likelihoods from the RaxML analyses on each locus were combined and used as the input for analysis in ASTRAL-II. This method finds the tree that maximizes the number of induced quartet trees in the set of gene trees that are shared by the species tree and has shown to be accurate, even in the presence of incomplete lineage sorting and horizontal gene transfer (Chou et al., 2015; Davidson et al., 2015). We used the heuristic search and multi-locus bootstrapping functions for phylogenetic reconstruction. Nonparametric bootstrap gene trees generated in RaxML for the MP-EST analysis were used to estimate nodal support for the ASTRAL-II analysis. Computations in ASTRAL-II were complete in less than one hour on a MacBook Pro with a 2.4 GHz Intel Core i5 processor and 4 GB of memory.

In both MP-EST and ASTRAL-II, a species allele or mapping file was used to accommodate analysis of multiple individuals per species. Due to apparent paraphyly in both *Ameivula* and *Kentropyx* in the ExaML analysis, we made adjustments to not force the monophyly of some species within these genera (Appendix A). *Ameivula jalapensis*, *A. mumbuca*, and *A. ocellifera* were combined in the "*A. ocellifera* complex" and we designated small species group within *Kentropyx*. Several non-teiid and gymnophthalmid taxa were included as outgroups and rooted with *Sphenodon punctatus* in all analyses. All of these analyses recovered a monophyletic Teiidae with strong support, but for clarity, outgroups have been removed

and trees rooted with gymnophthalmids *Cercosaura ocellata* and *Potamites ecpleopus* (all outgroups can be seen in Appendix B).

3. Results

3.1. Anchored phylogenomics data collection

An average of 1.04 billion bases were obtained for each individual. Between 6% and 64% of reads mapped to the target loci (average = 21%). Recovery of the anchor loci was consistently high, with >95% of loci being recovered for >99% of the samples. A detailed summary of the assembly results is given in the supplemental file (Appendix C). Of the 386 orthologous clusters identified, 316 were retained after alignment, trimming and masking. The final trimmed alignments containing 244 taxa, 488,656 sites (256,660 variable and 221,800 informative), and only 2.21% missing characters are available in Dryad repository doi:http://dx.doi.org/10.5061/dryad.d4d5d.

3.2. Phylogenetic analyses

A summary of the ML tree based on the analysis from ExaML recovered a well-resolved and well-supported topology (Fig. 1); the full tree including all individuals is provided as supplementary material (Appendix B). Basal relationships are highly supported, including the divergence between Tupinambinae and Teiinae and the nodes defining these subfamilies. The concatenated analysis supports a sister relationship between *Tupinambis* and *Crocodilurus* but the placement of *Dracaena* is ambiguous (BS = 59). Formerly a member of the genus *Tupinambis*, *Salvator merianae* is recovered as the sister group to a (*Dracaena* + (*Crocodilurus* + *Tupinambis*)) clade, with a well-supported *Callopistes* clade recovered as the sister group to these four genera.

Within the Teiinae, the ExaML reconstruction supports an early divergence of a strongly supported (*Dicrodon* + *Teius*) clade from the rest of the subfamily. The remaining Teiinae clade (cnemidophorines) is well supported, as are all deep (among genera) relationships. *Aurivela*, *Contomastix*, *Glaucomastix*, and *Ameivula*, all containing species formerly of the genus *Cnemidophorus*, form a strongly supported monophyletic group. The only species of *Aspidoscelis* included in the analysis is strongly supported as the sister group to *Holcosus* (formerly Central American *Ameiva*), and jointly these genera form the sister group to a well-resolved/well-supported West Indian *Pholidoscelis*. The trans-Andean *Medopheos edracantha* (formerly *Ameiva*) forms a group with a large clade of *Cnemidophorus* + *Kentropyx*. The two species of South American *Ameiva* form a well-supported group, this is the clade sister to the large (*Medopheos* + (*Cnemidophorus* + *Kentropyx*)) clade. With our sampling, the eight new teiid genera recognized by Harvey et al. (2012) and Goicoechea et al. (2016) are resolved as well-supported clades, but species within some genera (*Ameivula* and *Kentropyx*) are paraphyletic.

Species tree analyses also recovered strongly supported deep relationships within the Teiidae, including monophyletic Tupinambinae and Teiinae subfamilies. Though branching order and species relationships vary slightly, generic relationships estimated in MP-EST (Fig. 2) and ASTRAL-II (Fig. 3) are identical to one another and nearly match the ExaML concatenated analysis, the only difference being the placement of *Dracaena* and *Salvator*. The nodes supporting the position of these taxa, however, are not well supported in any of the analyses. Nodal support across the trees is generally high, except for the aforementioned placement of *Dracaena* and *Salvator* and some species relationships among West Indian *Pholidoscelis*.

4. Discussion

Taxonomic classification of the Teiidae has been controversial due to incomplete sampling and the discordance among various character types (musculature, DNA, osteology, etc.). Using 316 nuclear loci, we present a well-supported molecular phylogeny of the family that is largely in agreement with taxonomic changes proposed in a recent extensive morphological study (Harvey et al., 2012). We aim to stabilize higher-level Teiidae classification, focusing on the generic level and above. Our results suggest non-monophyly among species in both *Cnemidophorus* and *Kentropyx* (Fig. 1) though we refrain from addressing species-level taxonomy, pending more complete sampling. We define crown-group Teiidae to consist of the extant subfamilies Tupinambinae (*Callopistes*, *Crocodilurus*, *Dracaena*, *Salvator*, and *Tupinambis*) and Teiinae (*Ameiva*, *Ameivula*, *Aspidoscelis*, *Aurivela*, *Cnemidophorus*, *Contomastix*, *Dicrodon*, *Glaucomastix*, *Holcosus*, *Kentropyx*, *Medopheos*, *Pholidoscelis*, and *Teius*).

Fitzinger (1843: 20) described *Aspidoscelis* and *Pholidoscelis* but these generic names were not widely used until *Aspidoscelis* was resurrected by Reeder et al. (2002) and *Pholidoscelis* by Goicoechea et al. (2016). In both cases, the authors treated those generic names as feminine, although we consider them to be masculine. Historically, the gender of taxonomic names ending in *–scelis* has been confusing, which prompted Steyskal (1971) to write an article bringing clarity to the issue. In Greek, the ending *–scelis* is derived from *skelos* (Latin transliteration of the Greek σκέλος), which means legs. In this case, the two genera in question are Latinized compound adjectives, but are treated as singular nouns in the nominative because they are genera. As such, the ending *–scelis* denotes either masculine or feminine gender (Steyskal, 1971). According to ICZN (1999) Article 30.1.4.2. "a genus-group name that is or ends in a word of common or variable gender (masculine or feminine) is to be treated as masculine unless its author, when establishing the name, stated that it is feminine or treated it as feminine in combination with an adjectival species-group name." Because Fitzinger (1843: 20) did not state the gender of either name, and did not combine either name with its type species name (or any species-group name) to indicate gender, these genera must be treated as masculine. We provide the required emendations to the spelling of the species-group names of the genera *Aspidoscelis* and *Pholidoscelis* (Appendix D).

4.1. Tupinambinae

Recent taxonomic changes proposed elevating *Callopistes* to its own subfamily, because the placement of this genus was basal to the other subfamilies (Harvey et al., 2012), though *C. maculatus* was used to root the tree. Goicoechea et al. (2016) also suggested the need for a new subfamily, however, the position of *Callopistes* outside of Tupinambinae was only recovered in one of their four analyses. These authors also noted that this proposal contradicts many previous studies. All three methods of phylogenetic reconstruction implemented here support Pyron et al. (2013) that there is no need for changing long-standing subfamilies in the Teiidae by recognizing Callopistinae, as *C. flavipunctatus* and *C. maculatus* consistently form a clade with other Tupinambinae.

Within Tupinambinae, our dataset reveals a close relationship between *Tupinambis* and *Crocodilurus* in concordance with other studies (Harvey et al., 2012; Presch, 1974) (Figs. 1–3). This finding, however, contradicts many previous analyses (Gorman, 1970; Rieppel, 1980; Vanzolini and Valencia, 1965), which support a sister relationship between *Tupinambis* and *Dracaena*, or between *Crocodilurus* and *Dracaena* (Sullivan and Estes, 1997; Teixeira, 2003). This apparent contradiction is likely due to choice of taxa

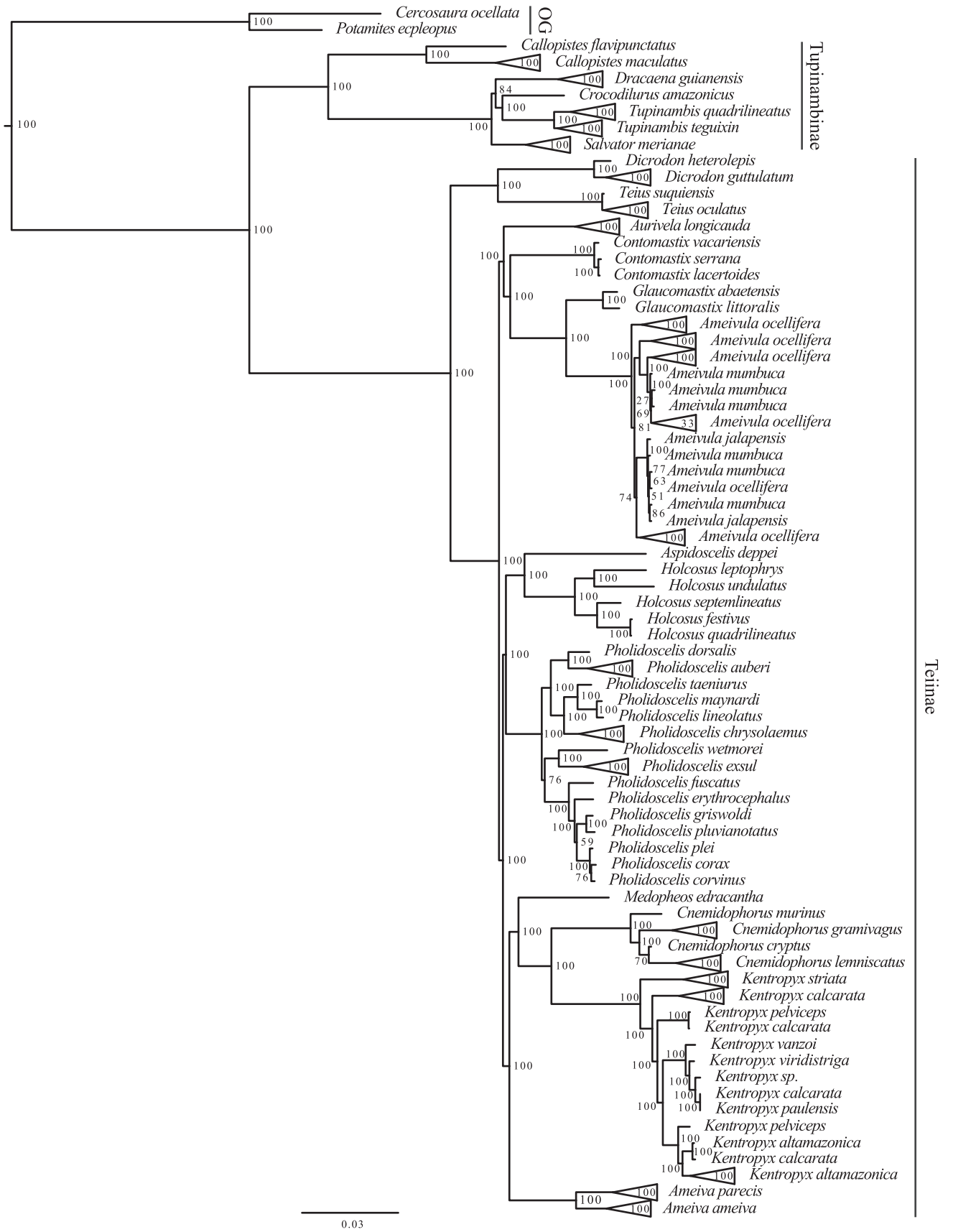

Fig. 1. Summary phylogeny of 56 teiid lizard species based on a concatenated maximum likelihood analysis of 316 loci (488,656 bp) with RaxML and ExaML. Multiple individuals per species are represented by triangles at the terminals when monophyletic. Numbers at nodes or in triangles indicate BS support values. The tree is rooted with gymnophthalmids *Cercosaura ocellata* and *Potamites ecpleopus*, eight additional outgroup species are not shown. The scale bar represents the mean number of nucleotide substitutions per site.

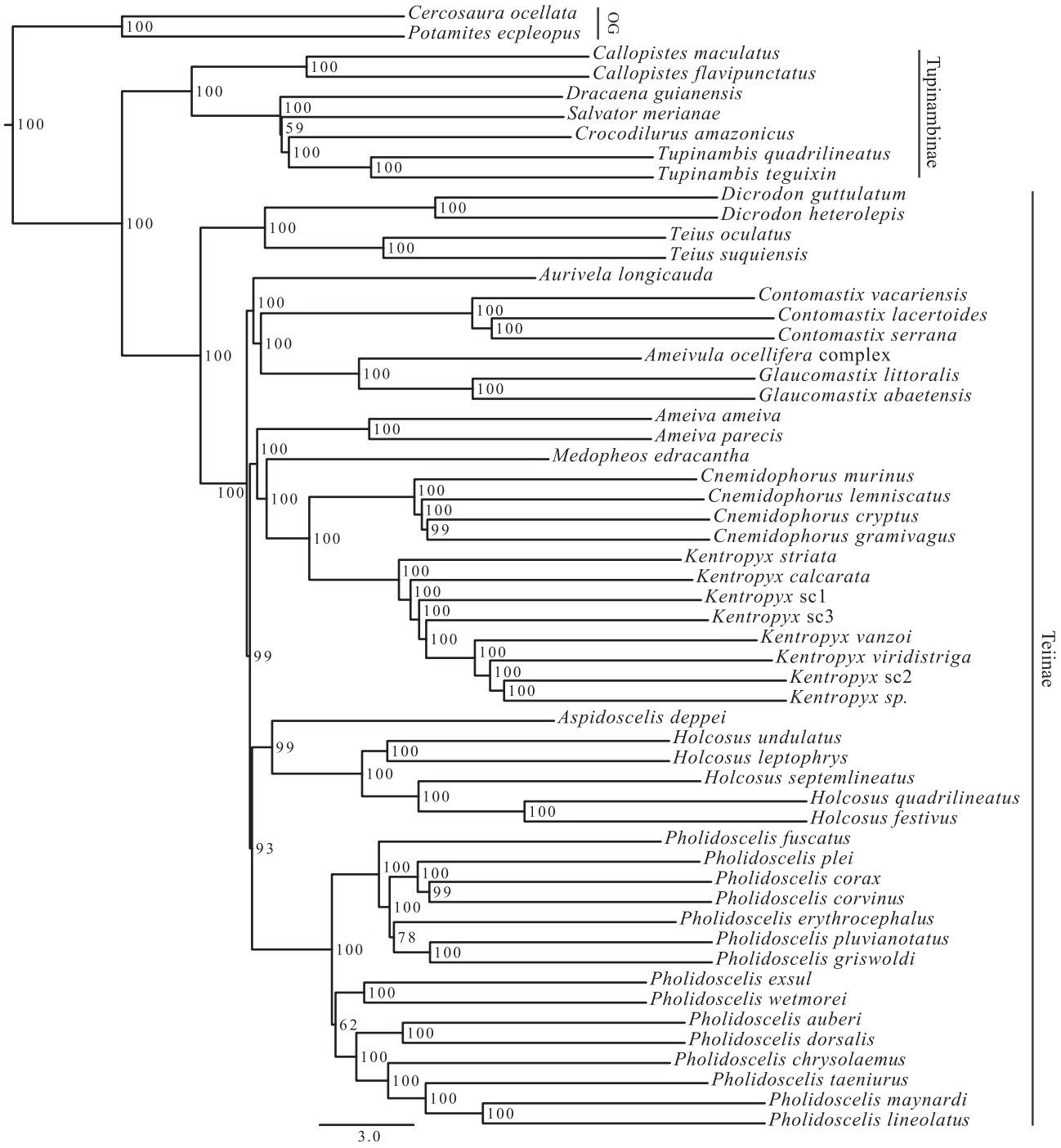

Fig. 2. Maximum clade credibility MP-EST species tree estimated from 316 loci. Numbers at nodes indicate the frequency at which each clade was supported across the gene trees. The tree is rooted with gymnophthalmids *Cercosaura ocellata* and *Potamites ecpleopus*, eight additional outgroup species are not shown. The "*Ameivula ocellifera* complex" represents the paraphyletic relationships of *A. ocellifera*, *A. jalapensis,* and *A. mumbuca*. ***Kentropyx* sc1** includes I0853_Kentropyx_pelviceps and I0608_Kentropyx_calcarata; ***Kentropyx* sc2** includes I0607_Kentropyx_calcarata and I0852_Kentropyx_paulensis; and ***Kentropyx* sc3** includes I3159_Kentropyx_pelviceps, I0595_Kentropyx_altamazonica, I0597_Kentropyx_altamazonica, I0598_Kentropyx_altamazonica, I0846_Kentropyx_altamazonica, and I0599_Kentropyx_calcarata. The scale bar represents coalescent units.

in prior studies and convergence due to the semiaquatic behavior of *Crocodilurus* and *Dracaena* (Mesquita et al., 2006). The confusing alpha taxonomy of taxa historically referred to as *Tupinambis* (Harvey et al., 2012), was also likely a factor, as many of these authors failed to provide locality data of specimens, making it unclear whether specimens of *Tupinambis* or *Salvator* were used.

Additionally, the number of recognized species within *Tupinambis* has changed considerably. Peters and Donoso-Barros (1970) recognized four species, which were later reduced to two species by Presch (1973), and re-interpreted again as four by Avila-Pires (1995). Additional taxa have been described since (Avila-Pires, 1995; Manzani and Abe, 1997, 2002), and seven species are currently recognized between *Salvator* and *Tupinambis* (Uetz and Hosek, 2016). Mitochondrial DNA shows a deep split between these two Tupinambinae genera (Fitzgerald et al., 1999), and we tentatively support the resurrection of the genus *Salvator* for the

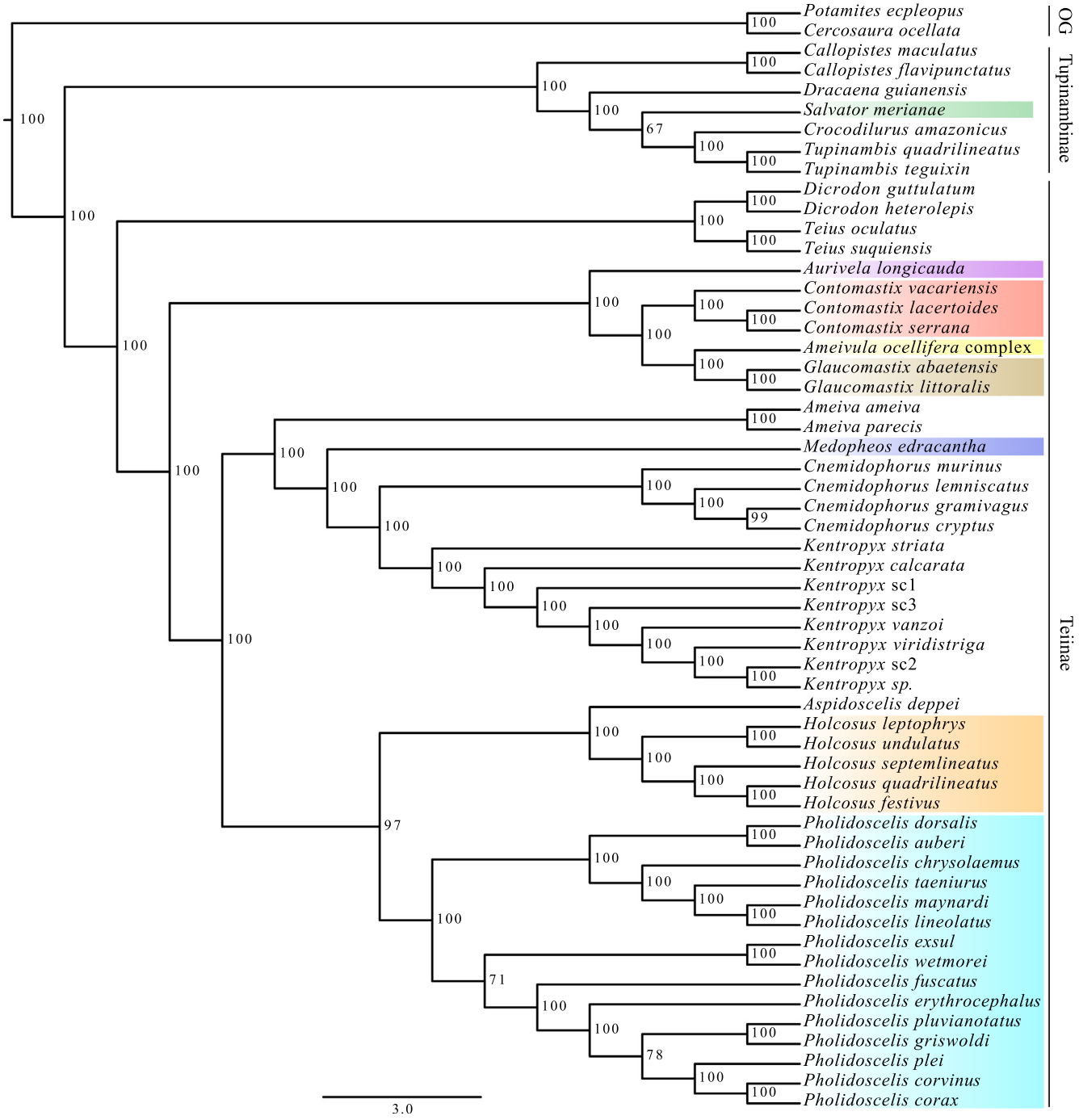

Fig. 3. ASTRAL-II species tree estimated for the Teiidae from 316 loci. Numbers at nodes indicate BS support values. Colored boxes highlight eight new genera designated by Harvey et al. (2012) and Goicoechea et al. (2016): *Salvator* (formerly *Tupinambis*), *Aurivela*, *Contomastix*, *Ameivula*, *Glaucomastix* (formerly *Cnemidophorus*), *Medopheos*, *Holcosus*, and *Pholidoscelis* (formerly *Ameiva*). The "*Ameivula ocellifera* complex" represents the paraphyletic relationships of *A. ocellifera*, *A. jalapensis*, and *A. mumbuca*. ***Kentropyx* sc1** includes I0853_Kentropyx_pelviceps and I0608_Kentropyx_calcarata; ***Kentropyx* sc2** includes I0607_Kentropyx_calcarata and I0852_Kentropyx_paulensis; and ***Kentropyx* sc3** includes I3159_Kentropyx_pelviceps, I0595_Kentropyx_altamazonica, I0597_Kentropyx_altamazonica, I0598_Kentropyx_altamazonica, I0846_Kentropyx_altamazonica, and I0599_Kentropyx_calcarata.

southern clade of *Tupinambis*, due to it being separated from *T. teguixin* and *T. quadrilineatus* in our analyses (Figs. 1–3), but also recognize that we only include one species of *Salvator* here and that more thorough taxon sampling is needed prior to fully supporting recent changes in this group. While changes in species-level taxonomy and disagreement between data types have lead to ambiguous relationships among genera, we demonstrate that some of these relationships are not easily resolved by increasing amounts of data (i.e. low nodal support for the position of *Salvator* and *Dracaena*). A rapid radiation in the history of these lineages has likely created a "hard polytomy," and increasing amounts of DNA may not resolve these relationships with current methods of phylogenetic reconstruction. Empirical studies and theory predict that adding taxa that diverge near a node of interest can have a greater effect on phylogenetic resolution than adding more characters (Prum et al., 2015; Townsend and Lopez-Giraldez, 2010). Thus, including more species of *Dracaena* and *Salvator* may improve the understanding of relationships within Tupinambinae.

4.2. Teiinae

Phylogenetic relationships within the Teiinae have long been unsatisfactory due to paraphyly and polyphyly in *Ameiva* and *Cnemidophorus* (Giugliano et al., 2006; Harvey et al., 2012; Reeder et al., 2002), but due to a lack of dense sampling, few steps have been taken to address these issues. In an examination of the phylogenetic relationships of the genus *Cnemidophorus*, Reeder et al. (2002) resurrected the genus *Aspidoscelis* to accommodate a group distributed across North and Central America. Note that while we only include a single species of *Aspidoscelis* (a genus with 42 species) here, monophyly of this group is not in question (Pyron et al., 2013; Reeder et al., 2002).

Harvey et al. (2012) further divided the South American *Cnemidophorus* by establishing three new genera (*Ameivula*, *Aurivela*, and *Contomastix*) and Goicoechea et al. (2016) erected *Glaucomastix* to address non-monophyly still remaining in this group (Fig. 3). Their *Cnemidophorus sensu stricto* includes species formerly of the "*lemniscatus* complex" distributed across Central America, northern South America, and islands of the West Indies, while the four new genera include taxa distributed south and east of the Amazon River. Our molecular data support the separation of this northern group and demonstrate a sister relationship with *Kentropyx*, but unlike findings of Harvey et al. (2012) which indicate that the three southern genera are unrelated, our data recover them as a highly-supported monophyletic group (Fig. 3), bringing into question the necessity of three new generic designations. Furthermore, our data do not support the paraphyly of *Ameivula* as in Goicoechea et al. (2016). These authors established *Glaucomastix* for the *Ameivula littoralis* group (*A. abaetensis*, *A. cyanura*, *A. littoralis*, and *A. venetecauda*) but only included two species and generated no new data for the genus. The paraphyly of this group was only recovered in one of four analyses and the nodal support was low (jackknife percentage 37).

While many new species of *Ameiva* have been described in the previous 12 years (Colli et al., 2003; Giugliano et al., 2013; Koch et al., 2013; Landauro et al., 2015; Ugueto and Harvey, 2011), few studies have examined phylogenetic relationships within the genus while including more than a few taxa, and it is clear that historically the group has been polyphyletic and ill-defined (Giugliano et al., 2006; Harvey et al., 2012; Reeder et al., 2002). Species-level polyphyly is suggested in at least *Ameivula* and *Kentropyx* here (Fig. 1), and is likely present in other genera with poorly-defined species, such as *Ameiva* and *Pholidoscelis*. However, we cannot immediately localize the sources of this discordance, which may include poor species definitions, hybridization, or misidentification of specimens in the field due to ambiguous diagnostic characters. Rangewide phylogeographic comparisons will be needed for these taxa.

Harvey et al. (2012) created the monotypic genus *Medopheos* for *Ameiva edracantha*, and resurrected *Holcosus* for ten species of *Ameiva* spread across Central America and trans-Andean South America, and a recent study suggests this group may be even more species-rich (Meza-Lázaro and Nieto-Montes de Oca, 2015). Harvey et al. (2012) elected to keep the remaining South American and West Indian species together in *Ameiva*, though this grouping was not well supported. In contrast, Goicoechea et al. (2016) resurrected *Pholidoscelis* for the Caribbean ameivas due to paraphyly of the groups. Our data support the monophyly of these genera erected to address a historically paraphyletic *Ameiva* (Figs. 1–3). The South American group (*A. ameiva* and *A. parecis*) is more closely related to a clade of South American (*Medopheos* + (*Cnemidophorus* + *Kentropyx*)), whereas West Indian *Pholidoscelis* form the sister-group to Central American (*Holcosus* + *Aspidoscelis deppei*). Relationships among West Indian *Pholidoscelis* species groups identified by Hower and Hedges (2003) vary among datasets and many have low nodal support, suggesting the need for further study in this group.

4.3. Phylogenetic methods

We used three often-cited algorithms to assess phylogenetic relationships within Teiidae: ExaML, MP-EST, and ASTRAL-II. The species tree methods recovered identical generic relationships and nearly identical species relationships in the group, the only exception being the unsupported placement of the (*Pholidoscelis exsul* + *P. wetmorei*) group from the Puerto Rican bank. In the MP-EST analysis, this group is sister to the *P. auberi* and *P. lineolatus* species groups from the Greater Antilles (Fig. 2), whereas in the ASTRAL-II analysis *P. exsul* and *P. wetmorei* form the sister group to the *P. plei* species group located in the Lesser Antilles (Fig. 3). The concatenated ExaML analysis recovers the same relationships as the ASTRAL-II analysis for this Caribbean genus and only differs in the positions of *Dracaena* and *Salvator*. The ExaML results recover a (*Salvator* + (*Dracaena* + (*Crocodilurus* + *Tupinambis*))) (BS = 84; Fig. 1) topology slightly different from the species tree analyses (*Dracaena* + (*Salvator* + (*Crocodilurus* + *Tupinambis*))) (Figs. 2 and 3). In all analyses, these four genera form a well-supported monophyletic group but the positions of *Dracaena* and *Salvator* are poorly supported in the MP-EST and ASTRAL-II trees. In support of simulation studies (Mirarab et al., 2014; Tonini et al., 2015) and empirical datasets (Berv and Prum, 2014; Pyron et al., 2014; Thompson et al., 2014) we demonstrate minimal differences among teiid relationships using concatenation and species tree methods, and note that these differences are not well supported. The concordance among methods provides support that the phylogenetic hypothesis we propose for Teiidae is robust.

5. Conclusion

We present a well-sampled and well-supported molecular phylogeny of the Teiidae and find a high degree of congruence among our genomic data and morphological data from previous analyses. While these similarities do not necessarily extend to deep relationships among taxa, we show support for the monophyly of eight genera resolved with morphology (Harvey et al., 2012) and smaller molecular datasets (Goicoechea et al., 2016). The large amount of congruence among methods of tree reconstruction (concatenation vs. species tree) was also reassuring. Very few differences were noted among our three phylogenetic trees, and those ambiguities were generally poorly supported.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2016.07.002.

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