

Molecular systematics of teioid lizards (Teioidea/ Gymnophthalmoidea: Squamata) based on the analysis of 48 loci under tree-alignment and similarity-alignment

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Abstract

We infer phylogenetic relationships within Teioidea, a superfamily of Nearctic and Neotropical lizards, using nucleotide sequences. Phylogenetic analyses relied on parsimony under tree-alignment and similarity-alignment, with length variation (i.e. gaps) treated as evidence and as absence of evidence, and maximum-likelihood under similarity-alignment with gaps as absence of evidence. All analyses produced almost completely resolved trees despite 86% of missing data. Tree-alignment produced the shortest trees, the strict consensus of which is more similar to the maximum-likelihood tree than to any of the other parsimony trees, in terms of both number of clades shared, parsimony cost and likelihood scores. Comparisons of tree costs suggest that the pattern of indels inferred by similarity-alignment drove parsimony analyses on similarity-aligned sequences away from more optimal solutions. All analyses agree in a majority of clades, although they differ from each other in unique ways, suggesting that neither the criterion of optimality, alignment nor treatment of indels alone can explain all differences. Parsimony rejects the monophyly of Gymnophthalmidae due to the position of Alopoglossinae relative to Teiidae, whereas support of Gymnophthalmidae by maximum-likelihood was low. We address various nomenclatural issues, including Gymnophthalmidae Fitzinger, 1826 being an older name than Teiidae Gray, 1827. We recognize three families in the arrangement Alopoglossidae + (Teiidae + Gymnophthalmidae). Within Gymnophthalmidae we recognize Cercosaurinae, Gymnophthalminae, Rhachisaurinae and Riolaminae in the relationship Cercosaurinae + (Rhachisaurinae + (Riolaminae + Gymnophthalminae)). Cercosaurinae is composed of three tribes—Bachiini, Cercosaurini and Ecleopodini—and Gymnophthalminae is composed of three—Gymnophthalmini, Heterodactylini and Iphisini. Within Teiidae we retain the currently recognized three subfamilies in the arrangement: Callopistinae + (Tupinambinae + Teiinae). We also propose several genus-level changes to restore the monophyly of taxa.

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Analyses of concatenated matrices of diverse genetic data are powerful tools to infer phylogenetic relationships because cladogenetic events concurrently supported by characters with different histories of change

are likely to represent the history of species (Hennig, 1966). These matrices are especially relevant today because they facilitate the analysis of legacy empirical data derived from independent studies (e.g. Driskell et al., 2004; Faivovich et al., 2005; Frost et al., 2006; McMahon and Sanderson, 2006; Grant et al., 2006; Goloboff et al., 2009; Pyron et al., 2013; Padiál et al., 2014). A limitation of these matrices, however, is that

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some terminals include only a portion of the characters potentially available for any one species. Although missing evidence can neither support nor reject relationships, accounting for this kind of missing information when optimizing available characters leads to several artefacts owing to the nature of methods. For example, empirical examples and simulations have shown that inferences can be misleading when missing data are not randomly distributed (Lemmon et al., 2009; Siddall, 2010; Simmons, 2012a,b; Simmons and Goloboff, 2013, 2014; Simmons and Norton, 2013), and although biases are especially acute in parametric methods that extrapolate estimations of branch length among partitions or that implement poor tree searches (e.g. Siddall, 2010; Simmons, 2012a,b; Simmons and Goloboff, 2013, 2014; Simmons and Randle, 2014), parsimony analyses are also susceptible to these artefacts when tree searches are superficial (Simmons and Goloboff, 2013, 2014; Goloboff, 2014). Missing comparative data can also lead to ambiguous optimization at internal nodes, which render the various positions of incomplete taxa equally costly in most parsimonious trees (i.e. wildcards or rogue taxa; Nixon and Wheeler, 1993; Kearney, 2002; Pol and Escapa, 2009). This ambiguity is made evident by the collapse of the affected areas in the strict consensus of most parsimonious trees, but ambiguity can also be concealed under apparent resolution with high branch support values in maximum-likelihood analyses (e.g. Padial et al., 2014; Simmons and Goloboff, 2014; Simmons and Randle, 2014). Regardless of potential biases, the simultaneous analysis of all data at hand is a prerequisite to assess the strength and weakness of evidence (Kluge, 1997; Grant and Kluge, 2003).

The objective of this study was to perform a strong test of the relationships of teioid lizards (Teioidea) using legacy (GenBank) and newly produced molecular data. To do so we compiled gene sequences for all species of teioids stored in GenBank and added ca. 5575 bp of newly produced sequences of nine loci (three of mitochondrial DNA and six of nuclear DNA) for 33 species. These data were assembled into a matrix with 299 terminals representing 57 genera and 185 teioid species (93 and 47% of currently recognized genera and species, respectively) and 40 out-group species sampled for a maximum of 32 695 unaligned base pairs of 48 loci. This far surpasses the largest analysis to date (Pyron et al., 2013), which used 7035 bp of 12 loci for 144 species of teioids. Thus, to rigorously assess whether available empirical data can actually refute previously inferred relationships of Teioidea, we implemented several analytical strategies that rely on different approaches to alignment and tree searches. First, we analysed our data under two different alignment methods: tree-alignment (also referred to as direct optimization or dynamic homology; see Sank-

off, 1975; Wheeler, 1996, 2001; Wheeler et al., 2006) and the more traditional similarity-alignment optimization, which in our case is based on an iterative refinement using the weighted sum-of-pairs score (WSP) and a series of consistency scores (i.e. MAFFT, Katoh and Standley, 2013). Second, we compared the results of phylogenetic analyses using different optimality criteria, equally weighted parsimony and maximum-likelihood, and the results of analyses in which indels are a class of evidence versus those in which indels are treated as nucleotides of unknown identity (i.e. evidence of absence is treated as absence of evidence; see Padial et al., 2014). These different strategies were implemented with the goal of identifying and discussing the possible contribution of optimality criteria, alignment methods, missing data and treatment of indels to similarities and differences observed among optimal trees of teioids.

The phylogenetic relationships of Teioidea

Teioidea includes ca. 397 species of Nearctic and Neotropical lizards in two families, Teiidae and Gymnophthalmidae (Estes et al., 1988), and 61 genera (Uetz and Hošek, 2015), which are informally known as macroteids and microteids, respectively, due to the marked difference in body size (Ruibal, 1952; Estes et al., 1988). A close relationship between Teiidae and Gymnophthalmidae has long been recognized (Boulenger, 1885; Camp, 1923) and, indeed, for most of the taxonomic history of the group they have been treated as a single family, Teiidae. The first internal classification of the Teioidea was proposed by Boulenger (1885), who recognized four (I–IV) informal groups of teiid lizards (*sensu lato*) based on external morphological characters, and provided a family-group taxonomy that lasted for nearly 100 years. MacLean (1974) recognized Teiinae (Boulenger's Group I) and Gymnophthalminae (Boulenger's Groups II–IV) as subfamilies within a monophyletic Teiidae. Presch (1983) elevated MacLean's two subfamilies to family level on the basis of the morphology of the abductor musculature (Rieppel, 1980), chromosome morphology (Gorman, 1970, 1973) and Northcutt's (1978) evidence from brain anatomy that suggested that the two groups were not each other's closest relatives; teiids were thought to be more closely related to iguanians and gymnophthalmids more closely related to lacertids, and hence the need to recognize two separate families. Estes (1983), in his catalogue of fossil lizards, continued to consider Teiidae and Gymnophthalmidae as sister groups, but followed Presch in his family-level nomenclature. Northcutt's (1978) and Presch's (1983) hypothesis of diphily was first rejected by Harris (1985) on the basis of tongue morphology. Subsequently, Estes et al. (1988), in a

major study of squamate relationships that applied and augmented the morphological evidence provided by Camp (1923), Rieppel (1980) and Harris (1985), recovered gymnophthalmids and teiids as sister taxa, but retained the two groups as coordinate families, as did Presch (1988), even though rejecting Presch's rationale for the rank elevation of *Gymnophthalmiinae* and *Teiinae*.

Regardless, since the work of Presch (1988) and Estes et al. (1988), no specific attempts have been made to rigorously test the overall relationships of *Teioidea* via dense taxon sampling. By contrast, although their sister-taxon status is widely accepted, some studies noted the paucity of corroboration for the familial division (Harris, 1985; Myers and Donnelly, 1996, 2001; Hoyos, 1998). In fact, most workers who addressed within-family relationships within *Teioidea* (e.g. *Gymnophthalmidae*: Pellegrino et al. (2001), Castoe et al. (2004); *Teiidae*: Giugliano et al. (2007), Harvey et al. (2012)], assumed the monophyly of either group, and employed several outgroups from the assumed monophyletic sister family. The only study that has provided a general test of teioid monophyly (Pyron et al., 2013) did so within the framework of an extensive maximum-likelihood analysis of similarity-aligned nucleotide sequences within a supermatrix of *Squamata*, and found the families *Gymnophthalmidae* and *Teiidae* to be monophyletic and sister taxa, although their recovered relationships among teiids and gymnophthalmids were novel.

Current understanding of the phylogenetic relationships within Teiidae

The family *Teiidae* (*sensu stricto*: macroteids) comprises 150 species in 16 genera (Uetz and Hošek, 2015). Teiids occupy a wide variety of environments, from Amazon rainforests to North American deserts, inhabiting beaches and desert flats, tropical dry forests and edges of closed habitats, from Argentina north to well into the United States (Krause, 1985; Pough et al., 1998). Although most species are terrestrial, the family includes the semi-aquatic genera *Crocodylurus* and *Dracaena* (Ávila-Pires, 1995; Mesquita et al., 2006). Teiids vary greatly in body size, ranging from *Aspidoscelis inornata* [72 mm maximum snout-to-vent ratio (SVL); Walker et al., 2012;] to large tegus, *Tupinambis* (500 mm SVL; Campos et al., 2011) and *Dracaena* (450 mm SVL; Harvey et al., 2012). Although most genera comprise bisexual (i.e. dioecious) species, some members of *Aspidoscelis*, *Cnemidophorus*, *Kentropyx* and *Ameivula* include parthenogenetic species, such as *Aspidoscelis uniparens*, *Cnemidophorus cryptus* (Cole and Dessauer, 1993), *Kentropyx borekiana* (Cole et al., 1995) and *Ameivula nativo* (Rocha et al., 1997).

Several aspects of teiid systematics remain contentious. Evidence from chromosomes (Gorman, 1970), external morphology (Vanzolini and Valencia, 1965), hemipenes (Böhme, 1988), osteology (Presch, 1974, 1983; Veronese and Krause, 1997), myology (Rieppel, 1980; Abdala and Moro, 1999), neuro-anatomy (Northcutt, 1978) and DNA sequences (Giugliano et al., 2007; Pyron et al., 2013) corroborates the division of *Teiidae* into two clades recognized by most authors as subfamilies: *Tupinambinae* (containing *Callopiestes*, *Crocodylurus*, *Dracaena*, *Salvator* and *Tupinambis*) and *Teiinae* (containing *Ameiva*, *Ameivula*, *Aspidoscelis*, *Cnemidophorus*, *Contomastix*, *Dicrodon*, *Holcosus*, *Kentropyx*, *Medopheos* and *Teius*). On the basis of morphological data and an implicit differential weighting scheme, Harvey et al. (2012) recovered *Tupinambinae* as paraphyletic with respect to the second large group, *Teiinae*. But given that they used *Callopiestes maculatus* (Harvey et al., 2012; : 6, line 5) to root their trees, it was impossible for them to discover any alternative to this assumption in their final topology. To recognize this rooting artefact extending from their assumption that *Callopiestes* is the sister taxon of the rest of teiids, they recognized *Callopiestes* to form its own subfamily, which they named *Callopiestinae*, apparently unaware that the name was already available, coined by Fitzinger (1843). Within their *Tupinambinae* they recovered *Tupinambis* as non-monophyletic, which they remedied by resurrecting the name *Salvator* Duméril and Bibron, 1839 for former *Tupinambis duseni*, *T. merianae* and *T. rufescens*. Within *Teiinae*, formerly composed of *Ameiva*, *Aspidoscelis*, *Cnemidophorus*, *Dicrodon*, *Kentropyx* and *Teius*, Harvey et al. (2012) remedied the wildly non-monophyletic *Ameiva* and *Cnemidophorus* by recognizing several new or resurrected genera: *Ameivula* Harvey et al., 2012; *Aurivela* Harvey et al., 2012; *Contomastix* Harvey et al., 2012; *Holcosus* Cope, 1862, and *Medopheos* Harvey et al., 2012. However, this arrangement remains contradicted by molecular evidence (Giugliano et al., 2007) and apparently as well by the “internal morphological data not included in our study” noted by Harvey et al. (2012: 76).

The phylogenetic relationships and the genus-level systematics within the “cnemidophorines” (a collective name coined by Reeder et al., 2002), a diverse group of species of the subfamily *Teiinae* now containing *Ameiva*, *Ameivula*, *Aspidoscelis*, *Aurivela*, *Cnemidophorus*, *Contomastix*, *Holcosus*, *Kentropyx* and *Medopheos*, are also disputed. Harvey et al. (2012) found cnemidophorines to be paraphyletic on the basis of external morphology because *Dicrodon* and *Teius* were recovered deeply nested within the group near *Ameivula*. Also, whereas some molecular data (Reeder et al., 2002; Giugliano et al., 2007) support the monophyly of this group, Pyron et al.'s (2013) analysis of a more

extensive dataset did not recover the cnemidophorines as monophyletic, but instead found *Dicrodon guttulatius* nested within *Ameiva*.

Current understanding of phylogenetic relationships of *Gymnophthalmidae*

The family *Gymnophthalmidae* comprises 253 species in 45 genera (Uetz and Hošek, 2015), and ranges from southern Mexico to Argentina, the Caribbean, and some islands on the continental shelves of South and Central America (Pellegrino et al., 2001; Doan and Castoe, 2005). *Gymnophthalmids* occur in habitats ranging from open areas of the high Andes [such as *Pholidobolus macbrydei* (Montanucci, 1973; Hillis, 1985) and some *Proctoporus* (Uzzell, 1970; Doan and Castoe, 2005; Doan et al., 2005; Goicoechea et al., 2012, 2013)] to lowland tropical rainforests. Most species are terrestrial but some are semi-aquatic, such as those in the genera *Neusticurus* and *Potamites* (Ávila-Pires, 1995; Pellegrino et al., 2001). The genus *Bachia* is fossorial (Pellegrino et al., 2001; Kohlsdorf and Wagner, 2006; Galis et al., 2010; Kohlsdorf et al., 2010), and several species in the genus *Anadia* (Ofstedal, 1974; Pellegrino et al., 2001) and *Euspondylus acutirostris* (Ofstedal, 1974) are partly arboreal. Although most species are bisexual/dioecious, the genera *Leposoma* and *Gymnophthalmus* include unisexual species, such as *Leposoma percarinatum* (Uzzell and Barry, 1971; Hoogmoed, 1973; Pellegrino et al., 2011) and *Gymnophthalmus underwoodi* (Thomas, 1965; Hardy et al., 1989; Yonenaga-Yassuda et al., 1995; Kizirian and Cole, 1999). Unlike most teiids, *gymnophthalmids* are small (SVL 40–150 mm) (Pellegrino et al., 2001).

In recent decades, a few attempts were made to infer the phylogeny of *gymnophthalmids* using morphological evidence (Presch, 1980; Hoyos, 1998; Colli et al., 2015 [in part]). Presch (1980) supported the monophyly of *Gymnophthalmidae*, and recognized six groups within the family: Group 1, containing *Alopoglossus*, *Opipeuter* (now part of *Proctoporus*; Goicoechea et al., 2012), *Prionodactylus* (now part of *Cercosaura*; Doan, 2003), *Proctoporus* and *Ptychoglossus*; Group 2, containing *Euspondylus* and *Pholidobolus*; Group 3, containing *Anadia*, *Ecleopus* and *Placosoma*; Group 4, containing *Cercosaura*, *Echinosaura*, *Leposoma*, *Neusticurus* and *Arthrosaura*; Group 5, containing *Pantodactylus* (*Cercosaura sensu* Doan, 2003); and Group 6, containing *Bachia*, *Gymnophthalmus*, *Heterodactylus*, *Iphisa* and *Tretioscincus*. Presch's Groups 1–5 correspond to Boulenger's (1885) Group II, while Group 6 corresponds to Boulenger's Groups III and IV. Hoyos (1998) examined the relationships of 16 species of *gymnophthalmids* based on osteological and myological characters using three teiids and one scincid as out-

groups. His results differ greatly from those of Presch (1980), and he failed to find a synapomorphy for *Gymnophthalmidae* among the characters studied.

The first contribution to the systematics of microteiid lizards using genetic data was the study by Pellegrino et al. (2001) of 51 species representing 26 genera of *gymnophthalmids*. These authors erected four subfamilies and four tribes: the subfamily *Alopoglossinae* consisted solely of *Alopoglossus*; the subfamily *Gymnophthalminae*, divided into two tribes, *Heterodactylini* (a junior synonym of *Iphisini* Gray, 1851, in this application) and *Gymnophthalmini*; the monotypic subfamily *Rhachisaurinae*, consisting solely of *Rhachisaurus*, a new genus separated from *Anotosaura*; and *Cercosaurinae*, which consists of 20 genera in the tribes *Cercosaurini* and *Ecleopodini*. Genera not represented in that study [*Adercosaurus*, *Amapasaurus*, *Anadia*, *Echinosaura*, *Euspondylus*, *Macropholidus*, *Opipeuter* (*Proctoporus sensu* Goicoechea et al., 2012), *Proctoporus*, *Riolama*, *Stenolepis* and *Teuchocercus*] were tentatively allocated to the recognized clades on the basis of morphology. Castoe et al. (2004) increased sampling (12 additional species and one more genus) and reanalysed Pellegrino et al. (2001) data using a Bayesian approach. Their results were generally consistent with those obtained by Pellegrino et al. (2001), but the following taxonomic changes were proposed: *Ptychoglossus* was included in *Alopoglossinae*; *Heterodactylini* and *Gymnophthalmini* were combined into *Gymnophthalminae* without tribal divisions; *Ecleopodini* was considered a subfamily; and *Bachia* was allocated to the new tribe, *Bachini*, within *Cercosaurinae*. Castoe et al. (2004) also suggested that *Neusticurus* and *Proctoporus* were polyphyletic. Subsequently, Doan and Castoe (2005) addressed those polyphyletic relationships and erected two new genera, *Potamites* and *Petracola*, to accommodate a group of species formerly included in *Neusticurus* and *Proctoporus*, and resurrected *Riama* to allocate another species group of *Proctoporus*. Goicoechea et al. (2012) supported the generic subdivision proposed by Doan and Castoe (2005) and found *Opipeuter* nested within *Proctoporus*, which they remedied by considering *Opipeuter* a junior synonym of *Proctoporus*.

Very late in the development of this manuscript (while finalizing the final submission) three papers appeared which bear on our overall objective, the first of which, Kok (2015), recognized on the basis of molecular and morphological data that *Riolama* is not part of *Cercosaurinae*, but relatively basal in the *gymnophthalmid* tree. He recognized a new subfamily, *Riolaminae*, for this taxon.

The second paper, Torres-Carvajal et al. (2015), found *Cercosaura* to be paraphyletic based on the Bayesian reconstruction of the relationships between most species of *Cercosaura* and other genera within

Cercosaurini based on three mitochondrial (12S, 16S and ND4) genes and one nuclear (*c-mos*) gene. Subsequently, they placed *C. dicra* and *C. vertebralis* within *Pholidobolus* and redelimited *Cercosaura*. Their topology also supports recognition of *C. ocellata bassleri* as a distinct species, *C. bassleri*, and recognition of *C. argulus* and *C. oshaughnessyi* as two different species (previously synonymized by Doan and Lamar, 2012).

The third paper, Colli et al. (2015) named a new genus, *Rondonops*, for which genetic samples had not been previously available, although according to their analyses was the likely sister taxon of *Iphisia*. To place this genus, they analysed 77 characters of morphology from Rodrigues et al. (2005, 2007a,b) for two outgroups (*Alopoglossus* and *Rhachisaurus*) and 17 ingroup representatives of the major groups, excluding Ecleopodinae, Bachiinae and *Riolama*, in addition to genetic data [nuDNA (*c-mos*), mtDNA (12S, 16S, ND4) for 70 terminals, with the exception of *Rondonops* all downloaded from GenBank and primarily provided by Castoe et al. (2004) and Pellegrino et al. (2001)]. Their genetic dataset, with the exception of *Rondonops*, is a subset of our genetic dataset. Employing similarity-alignment and parsimony, Bayesian and maximum-likelihood analyses of their datasets, all rooted on Alopoglossinae, they concluded that Gymnophthalmidae (*sensu lato*) is composed of six subfamilies (Alopoglossinae, Ecleopodinae, Cercosaurinae, Bachiinae, Rhachisaurinae, Gymnophthalminae) that are reasonably stable with respect to content, but which vary substantially in topology depending on whether employing Bayesian, parsimony or maximum-likelihood optimality criteria. Following Pellegrino et al. (2001), they recognized Alopoglossinae as the sister taxon of all other gymnophthalmids, but because this part of the topology was also an assumption of their analysis it was impossible to find another relationship. The topology(s) of the ingroup were substantially different than Pellegrino et al. (2001). Unlike Pellegrino et al. (2001), they considered Ecleopodinae to be the sister taxon of all other gymnophthalmids excluding Alopoglossinae, whereas Pellegrino et al. (2001) regarded this group (as a tribe) to be the sister taxon of their Cercosaurini. Among other modifications, they considered Bachiinae to be the sister taxon of Gymnophthalminae whereas Pellegrino et al. (2001) considered it to be part of their Cercosaurini. They did not include *Riolama* in their analysis. Bayesian analysis of morphology (data and optimal result undisclosed in their paper) and molecules + molecular evidence formed similar topologies, with Alopoglossinae + Rhachisaurinae being the sister taxon of Gymnophthalminae (Cercosaurinae not being studied for morphology), and with Iphisini being attached to Heterodactylini (their Chirocolini) in morphology-only and attached to Gymnophthalmini in

their pruned morphology + molecules tree. A maximum-likelihood tree of their molecular-only terminals results in a topology of Alopoglossinae + (Ecleopodinae + (Cercosaurinae + (Bachiinae + (Gymnophthalminae + Rhachisaurinae))), with Gymnophthalminae composed of three tribes in the topology Chirocolini [our Heterodactylini] + (Iphisini + Gymnophthalmini).

Because of its very late appearance, its primary focus on placing phylogenetically a single new genus *Rondonops*, and the lower taxon and data sampling than in our study, we do not address this study in detail, although we do in passing at various points, particularly with respect to some nomenclatural issues.

Despite major improvements in the knowledge of relationships of gymnophthalmids, several systematics issues remain problematic. For example, Rodrigues et al. (2005, 2007b, 2009) and Peloso et al. (2011) agreed with the reallocation of *Ptychoglossus* to Alopoglossinae, but did not address the other changes proposed by Castoe et al. (2004) and continued to follow Pellegrino et al. (2001) classification. Pyron et al. (2013) found strong support for the monophyly of the previously recognized subfamilies with the exception of Cercosaurinae, as did Colli et al. (2015). Pyron et al. (2013) elevated the tribes Bachini, Cercosaurini and Ecleopodini to subfamilies and this was followed by Colli et al. (2015). By contrast, the monophyly of some of the more species-rich genera in the family has not been assessed hitherto (Pellegrino et al., 2001; Peloso et al., 2011).

Materials and methods

Locus sampling and laboratory protocols

Phylogenetic analyses in this study employ gene sequences of all species of Teioidea available in GenBank as of 15 May 2014, as well as new sequences produced for 33 terminals representing 33 species. Sequences of a total of 48 genes were sampled, representing all species used by previous studies to infer relationships of members of Teioidea (see below for new sequences produced for this study). Non-coding mitochondrial genes include 12S and 16S rRNA genes of the heavy strand transcription unit 1 fragment. Protein-coding mitochondrial genes include cytochrome b (*cytb*), and NADH dehydrogenase subunit I (ND1), subunit II (ND2) and subunit 4 (ND4). Nuclear protein-coding genes include activity-dependent neuroprotector (ADNP), aryl hydrocarbon receptor (AHR), BTB and CNC homology 1 (BACH1), brain-derived neurotrophic factor (BDNF), basic helix–loop–helix domain-containing protein class B2 (BHLHB2), bone morphogenetic protein 2 (BMP2), caspase recruitment domain family member 4 (CARD4), cartilage interme-

diate layer protein (CILP), oocyte maturation factor (C-MOS), cullin-associated and neddylation-dissociated protein 1 (CAND1), chemokine C-X-C motif receptor 4 (CXCR4), distal-less (DLL), dynein axonemal heavy chain 3 (DNAH3), endothelin converting enzyme-like protein 1 (ECE1), ectodermal neural cortex 1 (ENC1), follicle stimulating hormone receptor (FSHR), follistatin-like protein 5 (FSTL5), galanin receptor 1 (GALR1), growth hormone secretagogue receptor (GHSR), G protein-coupled receptor 37 (GPR37), inhibin beta A (INHBA), leucine zipper tumor suppressor 1 (LZTS1), leucine rich repeat neuronal 1 (LRRN1), megakaryoblastic leukaemia translocation 1 (MKL1), myeloid/lymphoid or mixed-lineage leukaemia (MLL), mutS protein 6 (MSH6), nerve growth factor beta polypeptide (NGFB), neurotrophin-3 (NTF3), pinin (PNN), prostaglandin E receptor 4 (PTGER4), protein tyrosine phosphatase non-receptor type 12 (PTPN12), 35 G protein-coupled receptor 149 (R35), recombination activating protein 1 (RAG1), solute carrier family 8 member 1 (SLC8A1), solute carrier family 8 member 3 (SLC8A3), solute carrier family 30 member 1 (SLC30A1), synuclein alpha interacting protein (SNCAIP), receptor-associated factor 6 (TRAF6), valosin-containing protein p97/p47 complete-interacting protein 1 (VCP1), zinc finger homeobox protein (ZEB2) and zinc finger protein 36 C3H type-like 1 (ZFP36L1). Non-coding nuclear genes include only the 18S rRNA gene. Novel sequences include three mitochondrial genes (approximately 550 bp of the 16S, 350 bp of the cytb and 800 bp of the ND4, including three tRNAs) and six nuclear genes (400 bp of the C-MOS, 721 bp of the NADH3, 753 bp of the FSHR, 576 bp of the NT3, 543 bp of the SLC30A1 and 882 bp of the ZEB2: list of primers given in Table 1).

Total genomic DNA was extracted from frozen tissues (liver or muscle) or tissues preserved in 95% ethanol with a Qiagen (Valencia, CA) DNeasy tissue extraction kit or following the protocol developed by Fetzner (1999). Extraction products were checked in a 1% agarose to estimate the quality and amount of genomic DNA, and PCRs for the nine different gene regions were performed using the primers and protocols listed in Table 1. The size of the target region was estimated by electrophoresis on a 1% agarose gel, followed by direct purification of the PCR products using a vacuum drier or enzymatically with Exonuclease I and Shrimp Alkaline Phosphatase (Fermentas, Burlington, Ontario, Canada). Double stranded DNA was sequenced using the Perkin Elmer ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction (PE Applied Biosystems, Foster City, CA). Excess Dye Terminator was removed with plate sephadex columns (Princeton Separations, Adelphia, NJ), and sequences run on an ABI PRISM 3730XL or 3170 automated

Genetic Analyzers (Applied Biosystems) at the DNA Sequencing Center at Brigham Young University (UT, USA) and Instituto de Química (Universidade de São Paulo, SP, Brazil), respectively. Raw sequence chromatographs for sequences generated in this study were edited using Sequencher 3.1 (Gene Codes, Ann Arbor, MI). All sequences were deposited in GenBank and accession numbers are listed in Supplementary Table S1. Voucher information is provided in Table 2.

Taxon sampling

Our datasets are composed of gene sequences for 299 terminals representing 225 nominal species and eight unnamed species, of which 58 terminals of 40 species are part of the outgroup. We sampled multiple outgroups successively distant to the ingroup, and guided by relationships recovered by previous studies (Townsend et al., 2004; Vidal and Hedges, 2005; Fry et al., 2006; Wiens et al., 2010, 2012; Pyron et al., 2013; Reeder et al., 2015). Rather than testing previously inferred relationships among outgroup taxa (which would require a character and taxon sampling larger than those used in the same studies that guided our outgroup selection), our goal was to capture enough variation in DNA sequence of outgroups to provide a strong test of the monophyly of the ingroup (Nixon and Carpenter, 1993).

Townsend et al.'s (2004) maximum-likelihood analysis of 4600 bp of similarity-aligned sequences of nuclear (RAG-1 and C-MOS) and mitochondrial (ND2) genes of 69 terminals recovered Teioidea as the sister group of a clade containing Amphisbaenia and Lacertidae, the inclusive clade forming Lacertoidea. Toxicofera, a clade containing Iguania, Anguimorpha and Serpentes, was the sister of Lacertoidea, together comprising Episquamata. Townsend et al. (2004) also recovered Scinciformata, comprising the infraorder Scincomorpha and the families Cordylidae, Gerrosauridae and Xantusiidae, the sister of Episquamata, and dibamids and gekkotans together as the sister group of all other squamates. Maximum-likelihood and Bayesian analyses of 6192 bp of similarity-aligned sequences of nine nuclear coding genes of 19 taxa (Vidal and Hedges, 2005), Fry et al. (2006) maximum-likelihood and Bayesian analyses based on five nuclear coding genes of 15 taxa, and Wiens et al. (2012) analysis based on 33 717 bp analysis of 161 taxa of 44 nuclear genes under the same optimality criteria recovered the same relationships. Also, the maximum parsimony, maximum-likelihood and Bayesian inferences of Wiens et al. (2010) based on a combined analysis of 363 morphological characters and 15 794 bp of 22 nuclear genes are congruent with this topology. Pyron et al. (2013) in a maximum-likelihood

Table 1
List of PCR and sequencing primers used in this study and a summary of the PCR conditions.

Gene region	Primer Name	Sequence (5'–3')	References	PCR conditions
16S	16SF.1 16SR.0	TGTTTACCAAAAACATAGCCTTTAGC TAGATAGAAACCGACCTGGATT	Whiting et al. (2003)	94 °C (1 : 00), 45–48 °C (1 : 00), 72 °C (1:00) × 40
Cyt-b	LGL765 H15149 CB1-L CB2-H CB3-H	GAAAAACCAAYCGTTGTWATTCAACT TGCAGCCCCTCAGAATGATATTTGCTCTCA CCATCCAACATCTCAGCATGATGAAA CCCTCAGAATGATATTTGCTCTCA GGCGAATAGGAAAGTATCATTC	Bickham et al. (1995) Kocher et al. (1989) Palumbi (1996)	95 °C (:25), 48 °C (1:00), 72 °C (2:00) × 40
ND 4	ND4L Leu	CACCTATGACTACCAAAAGCTCATGTAGAAGC CATTACTTTTACTTGGATTTGCACCA	Arévalo et al. (1994)	95 °C (:25), 52 °C (1:00), 72 °C (2:00) × 40
C-MOS	G73 G74 Mos-F Mos-R	GCGGTAAAGCAGGTGAAGAAA TGAGCATCCAAAGTCTCCAATC CTC TGG KGG CTT TGG KKC TGT STA CAA GG GGTGATGGCAAANGAGTAGATGTCTGC	Saint et al. (1998) Godinho et al. (2005)	95 °C (:45), 53 °C (:45), 72 °C (1:00) × 45 or 94 °C (3:00), 48 °C (:45), 72 °C (1:00) × 1 and 94 °C (:45), 48 °C (:45), 72 °C (1:00) × 37
NT3	NT3-F1 NT3- R3	ATG TCC ATC TTG TTT TAT GTG ATA TTT TTA CAY CKY GTT TCA TAA AAA TAT T	Noonan and Chippindale (2006)	94 °C (2:00), 94 °C (:15), 51 °C (:20) [–0.1 °C/cycle], 72 °C (1:00) × 40
DNAH3	DNAH3-F1 DNAH3-R6	GGTAAAATGATAGAAGAYTACTG CTKGAGTTRGAHACAATKATGCCAT	Townsend et al. (2008)	94 °C (2:00), 94 °C (:15), 51 °C (:20) [–0.1 °C/cycle], 72 °C (1:00) × 40
FSHR	FSHR-F1 FSHR-R2	CCDGATGCCTTCAACCCVTGTGA RCCRAAYTTRCTYAGYARRATGA	Townsend et al. (2008)	94 °C (2:00), 94°C (:15), 51°C (:20) [–0.1°C/cycle], 72°C (1:00) × 40
SLC30A1	SLC30A1-F1 SLC30A1-R2	AAYATGCGWGGAGTKTTTCTGC AAAGATGATTCRGRYTGAYGTTT	Townsend et al. (2008)	94°C (2:00), 94°C (:15), 51°C (:20) [–0.1°C/cycle], 72°C (1:00) × 40
ZEB2	ZFH1B –F1 ZFH1B –R2	TAYGARTGYCCAAACTGCAAGAAACG AGTACAGACATGTGGTCTTGTATGGGT	Townsend et al. (2008)	94°C (2:00), 94°C (:15), 51°C (:20) [–0.1°C/cycle], 72°C (1:00) × 40

analysis of similarity-aligned sequences based on 12 896 bp of seven nuclear and five mitochondrial genes for 4161 terminals also corroborated previous results. More recently, Reeder et al. (2015) performed a maximum-likelihood analysis of 210 species of Squamata using 691 morphological characters and 46 genes, and corroborated the position of Teioidea as the sister group of Amphisbaenia + Lacertidae, and this clade was found sister to Toxicofera.

Our outgroup includes four species of Amphisbaenia (*Amphisbaena silvestri*, *A. fuliginosa*, *Geocalamus acutus* and *Rhineura floridana*) and five species of Lacertidae (*Adolfus jacksoni*, *Lacerta viridis*, *Mesalina guttulata*, *Psammodromus algirus* and *Takydromus sexlineatus*). We also include more distantly related taxa, such as Anguimorpha (*Anniella pulchra*, *Lanthanotus borneensis* and *Shinisaurus crocodilurus*), Cordylidae (*Namazonurus namaquensis*, *Smaug warreni*, *S. warreni depressus* and *Platysaurus pungweensis*), Iguania (*Ano-*

lis carolinensis, *Dipsosaurus dorsalis*, *Gambelia wislizenii*, *Microlophus thoracicus*, *Polychrus marmoratus*, *Uromastix aegyptia* and *U. bentii*), Scincidae (*Amphiglossus astrolabi*, *Emoia cyanura*, *Eutropis macularia*, *Feylinia grandisquamis*, *F. polylepis*, *Plestiodon egregius*, *P. fasciatus*, *P. laticeps*, *Sphenomorphus simus*, *S. solomonis*, *Trachylepis capensis* and *T. quinquetaeniata*), Serpentes (*Bungarus ceylonicus*, *B. fasciatus* and *Naja kaouthia*) and Xantusiidae (*Lepidophyma sylvaticum* and *Xantusia vigilis*). *Coleonyx variegatus* (Gekkota) was used to root the trees.

The ingroup includes 95 terminals representing 68 nominal and two unnamed species of Teiidae in 16 genera (*Ameiva*, *Ameivula*, *Aspidoscelis*, *Aurivela*, *Callopietes*, *Cnemidophorus*, *Contomastix*, *Crocodylurus*, *Dicrodon*, *Dracaena*, *Holcosus*, *Kentropyx*, *Medophaeos*, *Salvator*, *Teius* and *Tupinambis*), and 146 terminals representing 117 nominal and six unnamed species of Gymnophthalmidae in 41 genera (*Acratosaura*, *Alexan-*

Table 2
Localities and field numbers for the species sequenced in this study

Species	Locality	Field number
<i>Acratosaura mentalis</i>	Morro do Chapéu, BA	MTR 906448
<i>Acratosaura spinosa</i>	Mucugê, BA	MTR 13999
<i>Alexandresaurus camacan</i>	Una, BA	MTR (MD1771)
<i>Alopoglossus angulatus</i>	Guajará Mirim, RO	MTR (LG 1026)
<i>Arthrosaura kockii</i>	Vila Rica, MT	MTR 978011
<i>Calyptommatus confusionibus</i>	Serra das Confusões, PI	MRT 4623
<i>Calyptommatus leiolepis</i>	Queimadas, BA	MTR 05055
<i>Calyptommatus nicterus</i>	Vacaria, BA	MTR 05053
<i>Calyptommatus sinebrachiatus</i>	Santo Inácio, BA	MTR 05054
<i>Caparaonia itaquara</i>	Parque Nacional do Caparaó, MG	MTR10848
<i>Colobodactylus dalcyanus</i>	Campos de Jordão, SP	MTR (LG 761)
<i>Colobodactylus taunayi</i>	Serra da Prata, PR	MTR (LG 646)
<i>Colobosaura modesta</i>	Niquelândia, GO	MTR (LG 1145)
<i>Ecleopus gaudichaudii</i>	Boiçucanga, SP	MTR (LG1356/MCL0152)
<i>Gymnophthalmus leucomystax</i>	Fazenda Salvamento, RR	MTR 946613
<i>Gymnophthalmus underwoodi</i>	Ilha de Maracá, RR	MTR 946590
<i>Gymnophthalmus vanzoi</i>	Fazenda Salvamento, RR	MTR 946639
<i>Heterodactylus imbricatus</i>	Serra da Cantareira, SP	MTR (LG1504)
<i>Iphisa elegans</i>	Aripuanã, MT	MTR 977426
<i>Leposoma rugiceps</i>	Colombia, Depto de Sucre, municipio de Gabras, Finca La Esmeralda	MTR (EH 346)
<i>Micrablepharus atticolus</i>	Santa Rita do Araguaia, GO	MRT 946141
<i>Micrablepharus maximiliani</i>	Barra do Garças, MT	MTR (LG1017)
<i>Nothobachia ablephara</i>	Petrolina, PE	MTR (LG897)
<i>Placosoma glabellum</i>	Iguaape, SP	MTR (LG940)
<i>Procellosaurinus erythrocerus</i>	Queimadas, BA	MTR 05057
<i>Procellosaurinus tetradactylus</i>	Alagoado, BA	MTR 05056
<i>Psilophthalmus paeminus</i>	Santo Inácio, BA	MTR 05058
<i>Rhachisaurus brachylepis</i>	Serra do Cipó, MG	MTR 887336
<i>Scriptosaura catimbau</i>	Catimbau, PE	MRT15353
<i>Stenolepis ridleyi</i>	Ibiapaba, CE	MTR (LG2124)
<i>Tretioscincus agilis</i>	Vila Rica, MT	MTR 978177
<i>Tretioscincus oriximinensis</i>	Poção, PA	MTR 926415
<i>Vanzosaura multiscutatus</i>	Vacaria, BA	MTR 05059

Political units (under 'localities') of Brazil are: Bahia (BA); Ceará (CE); Goiás (GO); Mato Grosso (MT); Minas Gerais (MG); Pará (PA); Paraná (PR); Pernambuco (PE); Piauí (PI); Roraima (RR); Rondônia (RO); São Paulo (SP). Field number acronyms are as follows: MTR and MRT: Miguel Trefaut Rodrigues (Universidade de São Paulo, São Paulo, Brazil). All vouchers in parentheses are in M.T.R.'s collection.

dresaurus, *Alopoglossus*, *Anadia*, *Anotosaura*, *Arthrosaura*, *Bachia*, *Calyptommatus*, *Caparaonia*, *Cercosaura*, *Colobodactylus*, *Colobosaura*, *Colobosauroides*, *Dryadosaura*, *Echinosaura*, *Ecleopus*, *Gymnophthalmus*, *Heterodactylus*, *Iphisa*, *Kaieteurosaurus*, *Leposoma*, *Macropholidus*, *Marinussaurus*, *Micrablepharus*, *Neusticurus*, *Nothobachia*, *Pantepuisaurus*, *Petracola*, *Pholidobolus*, *Placosoma*, *Potamites*, *Procellosaurinus*, *Proctoporus*, *Psilophthalmus*, *Ptychoglossus*, *Rhachisaurus*, *Riama*, *Riolama*, *Scriptosaura*, *Stenolepis*, *Tretioscincus* and *Vanzosaura*). The only genera of teioids not represented among available gene sequences are *Adercosaurus*, *Amapasaurus*, *Euspondylus*, *Rondonops* (named after our analyses were completed) and *Teuchocercus*, all gymnophthalmids.

Due in part to the lack of secondary literature to aid in identifications and in part because of the rapid evolution of understanding in the group, a considerable number of gene sequences used in previous phylogenetic analyses are re-identified. In total, 45 GenBank

sequences required re-identification or updating of generic names to bring them into current nomenclature, and another five cannot be identified beyond genus level. New identifications were performed by cross-checking GenBank identifications with updated identifications provided in the papers for which sequences were originally submitted, and with new identifications provided in subsequent literature (see Appendix 1).

Tree-alignment + parsimony analysis

Sequences were first aligned in MAFFT (see below) and partitioned into fragments of equal length separated by conserved regions with no gaps and few or no nucleotide substitutions. This strategy generated putatively homologous fragments where length variation among DNA sequences was assigned to insertions and/or deletions of nucleotides, which is a requisite for tree alignment in POY (Wheeler et al., 2006). After the removal of gaps implied by MAFFT from

sequence fragments, tree alignment of unaligned sequences was performed under parsimony with equal weights for all classes of transformations using direct optimization (DO; Wheeler, 1996; Wheeler et al., 2006) and iterative pass optimization (IPO; Wheeler, 2003) algorithms in POY 5.1.1 (Wheeler et al., 2015). Tree searches were first conducted using DO under the command “search”, which implements an algorithm based on random addition sequence Wagner builds, subtree pruning and regrafting (SPR), and tree bisection and reconnection (TBR) branch swapping (see Goloboff, 1996, 1999), parsimony ratcheting (Nixon, 1999) and tree fusing (Goloboff, 1999), running consecutive rounds of searches within a specified run-time, storing the shortest trees of each independent run and performing a final round of tree fusing on the pooled trees. Some searches implemented the command “auto_static_approx”, which evaluates sequence fragments and transforms characters into static homologies when the number of indels is low and stable between topologies. This command was applied to the last set of searches and was not implemented during the last round of swap under iterative pass. The optimal tree found during driven searches was swapped using IPO (Wheeler, 2003).

Tree searches were carried out using the American Museum of Natural History’s high performance computing cluster ENYO (a cluster of 33 Intel Xeon 3.0-GHz dual-core, 128 dual-processors, L2 cache, 64-bit and 1TB shared storage and 16 GB RAM per node). Details about the duration and intensity of tree searches are listed on Table 3. As we have observed that POY 4.1.2 or POY 5.1.1 does not always report all equally parsimonious trees when large datasets are analysed, the optimal alignment resulting from IPO was converted into a data matrix (i.e. implied alignment: Wheeler, 2003) and driven searches were conducted in TNT (Goloboff et al., 2008) until a stable

strict consensus was reached at least three times (see below for details of driven searches in TNT). We calculated Goodman–Bremer (GB) values (Goodman et al., 1982; Bremer, 1988; see Grant and Kluge, 2008) for each supported clade in TNT using the optimal tree-alignment matrix and the parameters specified in the bremer.run macro (available at <http://www.zmuc.dk/public/phylogeny/tnt/>), which begins by searching for trees N steps longer than the optimum (ten random addition sequence Wagner builds and TBR swapping saving two trees per replicate), using inverse constraints for each node of the most parsimonious tree. Swapping of each constrained search was limited to 20 min and constrained searches were repeated three times as specified in the default settings of the bremer.run macro. We also calculated parsimony jackknife frequencies (Farris et al., 1996) for each supported clade by resampling the tree-alignment matrix. We caution that, as in analyses of similarity-alignment matrices, the resulting clade frequencies are conditional on this particular alignment and not the data themselves. Given that the tree-alignment matrix is derived from the optimal tree, the resulting clade frequencies are expected to be higher than would be obtained from matrices aligned according to different guide trees (e.g. a UPGMA or neighbor-joining tree, as in MAFFT and Clustal, respectively). We calculated jackknife frequencies from 500 pseudoreplicate searches using driven searches (see below), gaps treated as fifth state and removal probability of 0.36 ($\approx e^{-1}$), which reportedly renders jackknife and bootstrap values comparable (Farris et al., 1996).

Similarity-alignment + parsimony analysis

Similarity-alignments for parsimony and maximum-likelihood analyses of static matrices were performed in MAFFT online version 7 using the G-INS-i strategy,

Table 3

Details of ten independent parsimony tree searches performed under tree-alignment in POY 5.1.1 (Wheeler et al., 2015) using the computer cluster ENYO

	No. of CPUs	CPU per hours	Builds + TBR	Fuse	Ratchet	Tree length	Hits
	32	1536	83	81	31	67 326	1
	32	1536	81	65	32	67 326	8
	32	1536	88	77	35	67 326	8
	32	3072	162	195	72	67 325	1
	64	7680	421	542	163	67 324	1
	32	1536	123	104	48	67 325*	1
	32	1536	124	129	48	67 320*	6
	32	4608	387	444	179	67 320*	41
	32	3072	254	313	112	67 320*	25
	32	4608	387	450	191	67 320*	33
Total	352	30720	2110	2400	911	67 320	105 [†]

Fuse and Ratchets refer to rounds of fusing and ratcheting performed under driven searches implemented by the command “search”.

*Searches implementing the command “auto_static_approx”.

[†]Number of hits for the best tree length of 67 320 steps.

which is considered appropriate for alignments that consist of large numbers of sequences (Kato et al., 2005; Kato and Standley, 2013). The G-INS-i strategy performs global alignment with a fast Fourier transform (FFT) approximation progressively on a phenetic (modified UPGMA) guide tree followed by iterative edge refinement that evaluates the consistency between the multiple alignment and pairwise alignments. The iterative refinement is repeated until no improvement is observed in the weighted sum-of-pairs score or 1000 cycles are completed (maxiterate = 1000). We applied the default transition/transversion cost ratio of 1:2 but changed the gap opening penalty from three times substitutions to one time substitutions to avoid penalizing insertions and deletions more than we did in the tree-alignment analysis.

For parsimony analyses of the MAFFT similarity-aligned dataset, we weighted all transformations equally and treated gaps as a fifth state. Alternatively, in a second analysis gaps were treated as missing data. This last analysis was performed to parse for the effect of optimality criteria (parsimony and maximum-likelihood) when comparing trees inferred from the same similarity-alignment (see Peloso et al., 2015). We implemented driven searches in TNT (Goloboff et al., 2008), consisting of several rounds of tree-drifting, sectorial searches, parsimony ratchet and tree fusing until a stable strict consensus was reached at least three times. We modified several search parameters that allow a more efficient exploration of the tree space in matrices with large amounts of missing data (Goloboff, 2014). These included, implementing informative addition sequence (IAS) instead of standard random simple sequence addition during Wagner-tree building, accepting trees of equal score during sectorial searches, allowing the perturbation phase of tree-drifting and ratchet to perform many changes to trees before starting a new round of TBR. We also calculated the strict consensus using TBR-collapsing, as this strategy has proved useful to uncover cases where apparently resolved relationships lack support by evidence (Simmons and Goloboff, 2013). GB and jackknife frequencies were estimated as explained above.

Similarity-alignment + maximum-likelihood analysis

We used PartitionFinder v1.0.1 (Lanfear et al., 2012) to select the optimal partition scheme and substitution models for our dataset under the Akaike information criterion (AIC), the Bayesian information criterion (BIC), and the corrected AIC (cAIC). Due to computational limitations related to the size of our dataset, comparisons were limited to three partitions schemes: (i) all data combined, (ii) a two-partition, mtDNA/nuDNA, scheme and (iii) a 48-partition scheme (each partition corresponding to individual loci mentioned above). Additional partition schemes by codon position

were attempted but the software consistently crashed during the evaluation of more diverse partition schemes under both greedy heuristic and greedy searches.

Maximum-likelihood analyses (maximum average likelihood in the sense of Barry and Hartigan, 1987) were performed in GARLI 2.0 (Zwickl, 2006). This software was preferred because it allows a more thorough search of the tree space than RAxML (Stamatakis, 2006; Morrison, 2007). The first 100 tree searches employed an enhanced strategy consisting of the modification of a set of default parameters that, according to Zwickl (2006), should improve tree searches, albeit at the expense of computational time: random addition sequence starting trees (streefname = random; default = stepwise) with 100 attachments per terminal (attachmentspertaxon = 100; default = 50), a lower strength of selection of individual trees found during swapping set at 0.01, which helps to scape local optima (selectionintensity = 0.01; default = 0.5), and maximum SPR distance of 30 branches away from original location (limsprange = 50; default = 6). An additional 1000 tree searches were performed under default parameters but with random addition sequence starting trees. Node support was evaluated through 1000 bootstrap replicates using default parameters but with random addition sequence starting trees. Analyses were performed in the GARLI Web Server (Bazin et al., 2014).

Finally, we compared the total number of clades shared among optimal trees in Mesquite using the TSV package (Maddison and Maddison, 2011).

Results

Tree-alignment + parsimony

Tree searches in POY identified an optimal tree of 67 320 steps that was visited 105 times (Table 3). A final round of swapping under IPO recovered a single tree of 67 252 steps. Additional driven searches of the optimal tree-alignment matrix in TNT produced 170 most parsimonious trees of equal length (67 252 steps), the strict consensus of which had 266 nodes. The resulting tree-alignment consists of 36 267 columns, 4850 of which contain gaps (13.4%) (tree-alignment matrix and consensus tree deposited in TreeBase under accession number S17936).

Although the lack of taxon-sampling density prevents reading too much into the outgroup structure, tree-alignment + parsimony (TA + PA) recovered Teioidea as the sister group of Serpentes (Fig. 1), together forming the sister group of a clade composed of a paraphyletic Amphisbaenia and a monophyletic Lacertidae. This topology renders Lacertoidea (Amphisbaenia, Lacertidae and our Teioidea) and Toxicofera (Anguimor-

pha, Iguania and Serpentes) polyphyletic. The monophyly of Amphisbaenia (Rhineuridae and Amphisbaenidae in our analyses) was also rejected, inasmuch as Rhineuridae was found to be the sister of the remainder of Amphisbaenidae + Lacertidae (Fig. 1). The sister of the clade composed of Teioidea + Serpentes + Amphisbaenia + Lacertidae is a clade composed of Iguania and Anguimorpha. The sister of this inclusive clade is Scincoidea. Within Iguania the essentially monospecific genus *Dipsosaurus* was recovered as non-monophyletic (suggesting a lack of overlap between loci, or the possibility of misidentified sequences assigned to this taxon in GenBank, although these individually do BLAST as *Dipsosaurus dorsalis*). Scinciformata, comprising Cordylidae, Xantusiidae and Scincomorpha, was recovered as monophyletic. Within Scincomorpha, the superfamilies Lygosomatoidea and Scincoidea, and the families Mabuyidae, Scincidae and Sphenomorphidae were recovered as paraphyletic. *Sphenomorphus* was also recovered as paraphyletic.

Because of the dense taxon sampling within our ingroup, those results are evidentially compelling. Within Teioidea, Gymnophthalmidae is recovered as paraphyletic, with Pellegrino et al. (2001) Alopoglossinae as the sister group of a group composed of a monophyletic Teiidae and the rest of Gymnophthalmidae excluding Alopoglossinae (support values for ingroup taxa are listed in Table 4). Within Teiidae, Callopiinae of Harvey et al. (2012) was recovered as monophyletic and sister to the rest of teiids. Tupinambinae *sensu* Estes (1983) was also found to be monophyletic, and sister to Teiinae of Estes et al. (1988), but with *Tupinambis* collapsing into a polytomy with *Dracaena* and *Crocodylus*. Teiinae was also found to be monophyletic, with *Dicrodon* as the sister taxon of the remaining species of the clade, and *Teius* as the sister group of Reeder et al. (2002) “cnemidophorines” (comprising the genera *Ameiva*, *Ameivula*, *Aspidoscelis*, *Aurivela*, *Cnemidophorus*, *Holcosus* and *Kentropyx*). Within the “cnemidophorines”, *Ameiva* is polyphyletic, with cis-Andean species (Hower and Hedges, 2003; Harvey et al., 2012) forming the sister group of the remaining “cnemidophorines”, and West Indies *Ameiva* (Hower and Hedges, 2003) forming the sister group of *Aurivela*. *Contomastix* was found as the sister group of a clade including a paraphyletic *Ameivula* with *A. ocellifera* forming the sister of a clade with *Ameivula abaetensis* plus a monophyletic taxon composed of *Cnemidophorus* + *Kentropyx*. *Holcosus* is monophyletic and the sister of a large clade including *Medopheos* as sister to *Aspidoscelis*, and this *Medopheos* + *Aspidoscelis* clade is the sister group of *Aurivela* plus West Indies *Ameiva*. Within *Aspidoscelis* our analysis corroborated the monophyly of the *A. deppii*, *A. sexlineata* and *A. tigris* species groups (Fig. 2). Within the *A. sexlineata* group, our analyses

did not recover the monophyly of the samples of *A. sexlineata*, as *A. inornata* is recovered as nested among the samples of *A. sexlineata*, something that requires further study. Also, *Aspidoscelis c. costata* forms the sister taxon of *Aspidoscelis gularis gularis* + *Aspidoscelis g. septemvittata*, again something that should not be rejected out of hand inasmuch as the large-bodied, fine-scaled members of the *Aspidoscelis sexlineata* group remain poorly understood. Within the West Indies “*Ameiva*” clade, reciprocally monophyletic sister clades were recovered. The first contains species of the *Ameiva exul* group (consisting of *A. exul*, *A. polops* and *A. wetmorei* from Puerto Rico; Hower and Hedges, 2003), and its sister clade, including species in the *A. auberi* group (comprising *A. auberi* and *A. dorsalis* from Cuba, Bahamas and Jamaica; Hower and Hedges, 2003) and the *A. plei* group (or Lesser Antillean clade, containing *A. corax*, *A. erythrocephala*, *A. fuscata*, *A. grisworldi*, *A. plei* and *A. pluvianotata*; Hower and Hedges, 2003). The second clade includes species of the *Ameiva lineolata* group (*A. chrysoleama*, *A. lineolata*, *A. mainardy* and *A. taeniura*). Within the *A. lineolata* group we found our samples of *A. chrysoleama* to form a non-monophyletic series, inasmuch as *A. c. umbratilis* was found as sister to (*A. taeniura* (*A. lineolata* + *A. maynardi*)).

The rest of Gymnophthalmidae (excluding Alopoglossinae) forms a monophyletic group composed of two major clades (Figs 3 and 4). The first clade is composed of *Riolama leucosticta* [placed in Cercosaurinae by Pellegrino et al. (2001), unstudied by Pyron et al. (2013) and Colli et al. (2015), and placed in Riolaeminae by Kok (2015) for reason of it being phylogenetically distant from Cercosaurinae], which forms the sister group of a clade composed of *Rhachisaurus* (Rhachisaurinae) and Gymnophthalminae as sister groups. Within Gymnophthalminae, our analyses support the tribes Gymnophthalmini and Heterodactylini *sensu* Pellegrino et al. (2001), and Heterodactylini and Iphisini as outlined by Rodrigues et al. (2009). The position of *Scriptosaura* within Gymnophthalmini is corroborated, with *S. catimbau* being the sister of *Nothobachia ablephara*.

The second clade includes a monophyletic *Bachia*, the sister of a clade containing Ecleopodinae and Cercosaurinae except for *Riolama*. Within the genus *Bachia*, Dixon’s (1973) species groups were found to be non-monophyletic, and with the samples of *B. monodactylus* and *B. heteropa* resolved as paraphyletic.

The sister of *Bachia* includes Ecleopodinae (*sensu* Castoe et al., 2004) as the sister group of Cercosaurinae except for *Riolama*, a result that renders Pellegrino et al. (2001) Cercosaurinae (comprising Cercosaurini and Ecleopodini) paraphyletic. Within Ecleopodinae, the genera *Arthrosaura* and *Leposoma* were both recovered as non-monophyletic. Part of *Arthrosaura* (*A. kockii* and *A. reticulata*) is the sister of the remain-

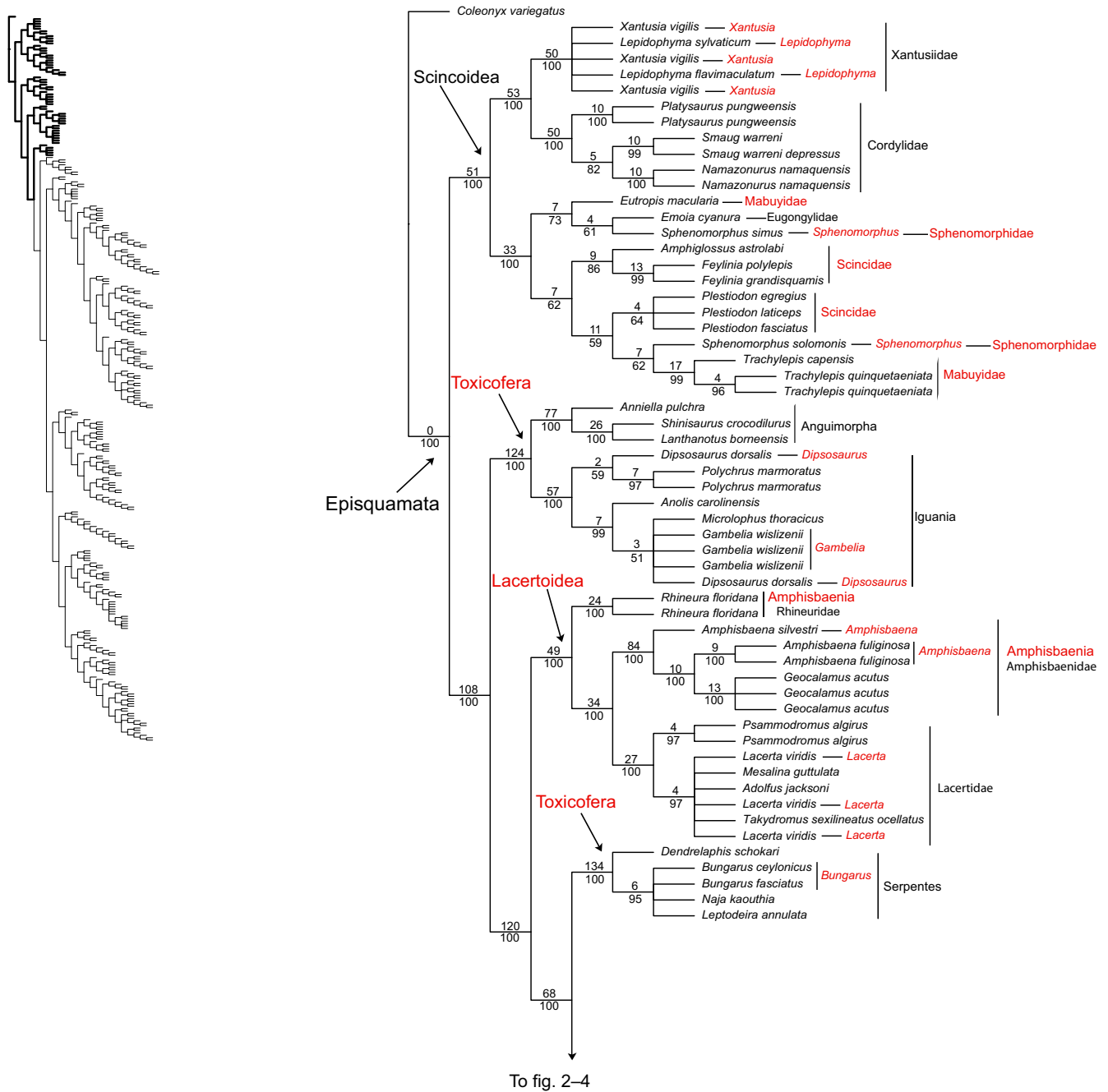


Fig. 1. Tree-alignment + parsimony: strict consensus of 105 most parsimonious trees of 67 320 steps showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodman-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

ing ecleopodines, while the other part is embedded in a clade within the *Leposoma parietale* group, part of which collapses in a polytomy with *Arthrosaura*. The *Leposoma scincoides* group is found to be monophyletic and the sister to all ecleopodines except for *Arthrosaura kockii* and *A. reticulata*. Within Cercosaurinae, the only non-monophyletic genus is *Cercosaura*, with *C. quadrilineata* as the sister group of

a clade containing *Anadia*, *Potamites*, *Proctoporus* and the remaining *Cercosaura*.

Similarity-alignment + parsimony

The optimal MAFFT similarity-alignment comprises 34 296 columns, of which 2180 cells (6.4%) contain gaps (matrix and consensus tree deposited in TreeBase

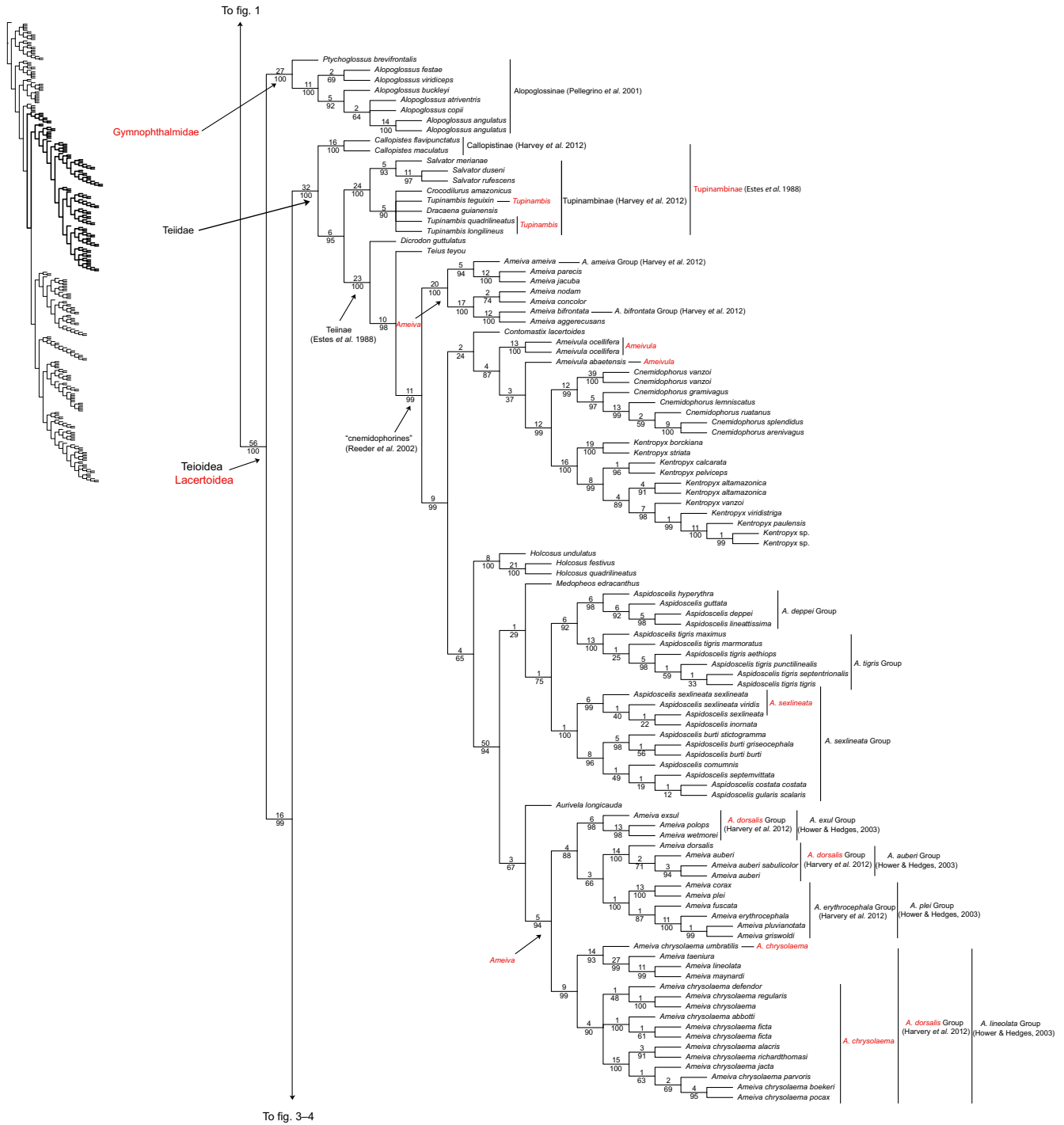


Fig. 2. Tree-alignment + parsimony: strict consensus of 105 most parsimonious trees of 67 320 steps showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodman-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

under accession number S17936). Driven searches of this matrix with gaps as a fifth state (SA + PA) resulted in 151 optimal trees of 69 472 steps (requiring 2220 more steps than the tree-alignment parsimony tree), the strict consensus of which has 252 nodes (Figs 5–8).

Within the outgroup, *Shinisaurus crocodilurus* is found near the root, making Anguimorpha, Toxicofera and Episquamata paraphyletic. Amphisbaenia, Mabuyidae and Scincidae are also paraphyletic, and the position of Serpentes as the sister group of

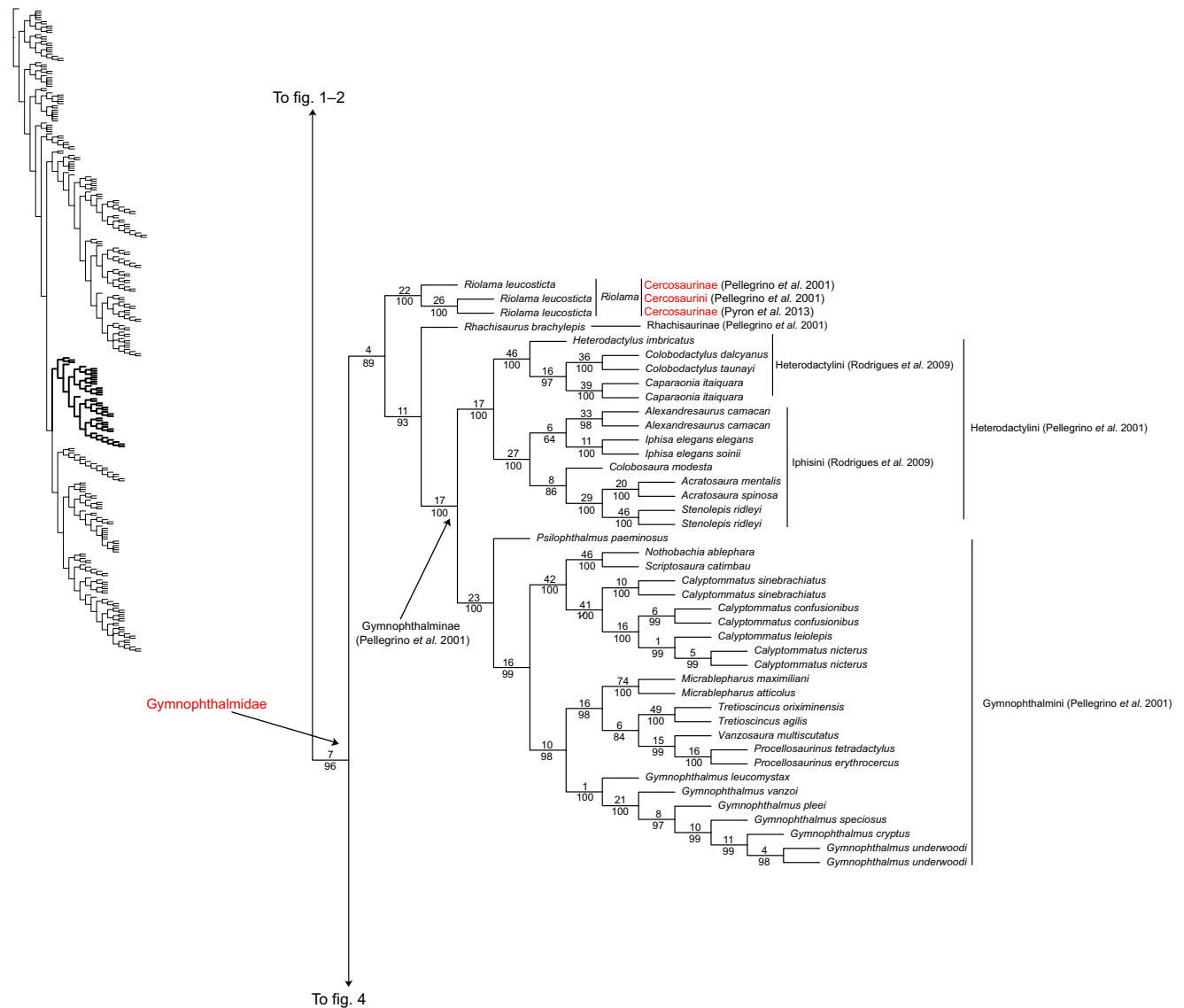


Fig. 3. Tree-alignment + parsimony: strict consensus of 105 most parsimonious trees of 67 320 steps showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodman-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

Teioidea also renders Toxicofera paraphyletic (Fig. 5).

Gymnophthalmidae is non-monophyletic because the position of Alopoglossinae (*Alopoglossus* + *Ptychoglossus*) is recovered in a consensus polytomy with Teiidae and the remainder of Gymnophthalmidae (Figs 6–8). Teiidae is nonetheless monophyletic although the support for this hypothesis is relatively low. Within Teiidae, Harvey et al.’s (2012) Callopestinae is recovered in a consensus polytomy of Tupinambinae (*sensu* Harvey et al., 2012) and Teiinae (*sensu* Estes et al., 1988). Resolution is reduced to a completely unresolved polytomy within Tupinambinae compared with the tree-alignment results, with none of the nominal multi-species genera being recovered as

monophyletic, a huge reduction in resolution from the tree-optimized alignment tree.

Teiinae is monophyletic, and *Teius teyou* was found to be the sister taxon of the remainder of the group (Fig. 6) rather than *Dicrodon* as in the tree-alignment results. All genera of Teiinae represented by two or more species are monophyletic although the recovered relationships among the genera are strikingly different from those recovered in the tree-alignment analysis. The monophyly of Reeder et al. (2002) “cnemidophorines” is also supported. *Holcosus* is recovered in a consensus polytomy with (a) *Cnemidophorus*, (b) a group composed of *Ameivula* and *Kentropyx*, and (c) the remaining teiines.

The remaining teiines are parsed into two widely separated parts of *Ameiva*, the cis-Andean group

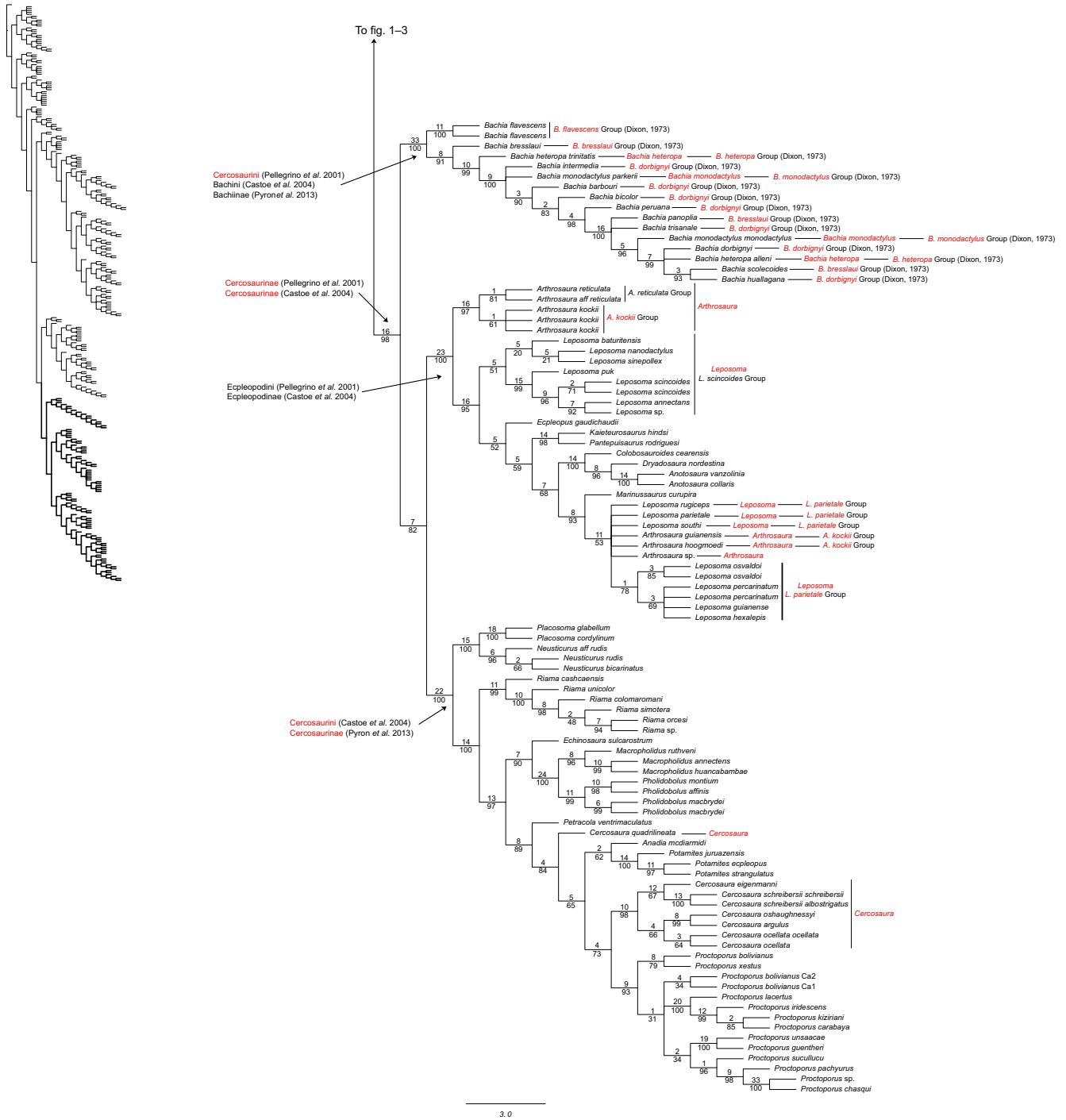


Fig. 4. Tree-alignment + parsimony: strict consensus of 105 most parsimonious trees of 67 320 steps showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodman-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

forms the sister taxon of the rest and, within this group, *Contomastix* forms the sister taxon of *Medopheos* + West Indian *Ameiva* + a group composed of *Aurivela* and *Aspidoscelis*.

Within West Indian *Ameiva*, the analytical monophyly of the *A. exul*, *A. auberi*, *A. plei* and *A. lineolata* groups

is corroborated, but the *A. dorsalis* group of Harvey et al. (2012) is resolved as paraphyletic. Within the *A. lineolata* group, one sample of *A. chrysolaema*, *A. c. umbratilis*, is recovered as the sister of a clade including *A. taeniura*, *A. lineolata* and *A. maynardi*. Within *Aspidoscelis*, the *A. deppii*, *A. sexlineata* and *A. tigris* groups

Table 4

Ingroup taxa of Teioidea/Gymnophthalmoidea and named taxa above the genus level for which the monophyly was tested

	TA+PA (GB/JK)	SA+PA (GB/JK)	SA+PA _{4th} (GB/JK)	SA+ML (BSS)
<i>Acratosaura</i>	29/100	33/100	22/99	100
Alopoglossinae	27/100	17/100	11/99	93
<i>Alopoglossus</i>	11/100	11/99	1/98	88
<i>Ameiva</i>	–	–	–	–
<i>Ameivula</i>	–	5/52	1/–	80
<i>Anotosaura</i>	14/100	15/96	22/87	88
<i>Arthrosaura</i>	–	–	–	52
<i>Aspidoscelis</i>	1/75	7/88	12/59	81
<i>Bachia</i>	33/100	29/99	12/22	99
Bachiini	33/100	29/99	12/22	99
<i>Callopietes</i>	16/100	12/99	10/91	99
Callopietinae (Harvey et al., 2012)	16/100	12/99	10/91	99
<i>Calyptommatius</i>	16/100	40/100	39/100	100
“cnemidophorines”	11/99	5/51	–	–
<i>Cercosaura</i>	–	3/5	–	84
Cercosaurinae	–	–	–	–
<i>Cnemidophorus</i>	12/99	11/97	1/63	11
<i>Colobodactylus</i>	16/97	38/100	28/100	100
Eupleopodinae	23/100	16/94	1/93	99
Gymnophthalmidae	–	–	–	35
Gymnophthalminae	17/100	–	16/74	100
Gymnophthalmini	23/100	16/99	7/74	100
<i>Gymnophthalmus</i>	1/100	24/100	23/99	100
Heterodactylini (Rodrigues et al., 2009)	49/100	21/100	23/100	100
<i>Holcosus</i>	8/100	1/42	1/–	45
Iphisini (Rodrigues et al., 2009)	27/100	–	18/74	100
<i>Kentropyx</i>	16/100	16/100	1/–	100
<i>Leposoma</i>	–	–	–	–
<i>Macropholidus</i>	8/96	13/100	11/91	94
<i>Micrablepharus</i>	74/100	1/100	67/100	100
<i>Neusticurus</i>	6/96	13/97	18/79	92
<i>Pholidobolus</i>	11/99	1/55	4/64	76
<i>Placosoma</i>	18/100	35/100	17/100	100
<i>Potamites</i>	14/100	6/96	13/90	94
<i>Procellosaurinus</i>	16/100	46/100	56/100	100
<i>Proctoporus</i>	9/93	9/63	–	14
<i>Riama</i>	11/99	23/100	13/78	67
<i>Salvator</i>	5/93	–	–/37	98
Teiidae	68/100	1/99	–	39
Teiinae	23/100	20/100	9/94	90
Teioidea	56/100	82/100	71/100	98
<i>Tretioscincus</i>	49/100	48/100	78/100	100
Tupinambinae (Harvey et al., 2010)	24/100	1/99	12/99	98
<i>Tupinambis</i>	–	–	–	–

GB refers to Goodman–Bremer values, JK to jackknife frequencies and BSS to bootstrap frequencies. Dashes indicate that monophyly was rejected.

are all recovered as monophyletic. Within the *A. sexlineata* group the monophyly of the nominal terminals of *A. sexlineata* were non-monophyletic, with *A. inornata* nested with *A. sexlineata*, as in the tree-alignment results. *Aspidoscelis c. costata* is in a group with *A. g. gularis* and *A. g. septemvittata* (Fig. 6).

The sister taxon of Teiidae, the clade of Gymnophthalmidae excluding Alopoglossinae, is divided into two large reciprocally monophyletic groups (Figs 7 and 8). The first of these contains *Rhachisaurus* as the sister of a large group of microteiids, itself composed of two reciprocally monophyletic clades. The

first of these is, as in the tree-alignment analysis, composed of *Heterodactylus* + a group composed of *Caparaonia* + *Colobodactylus*, and sister of that group, a resolved group composed of *Alexandresaurus* + *Riolama*, and the sister taxon of that small group, an asymmetrically resolved group composed of *Iphisa*, *Colobosaura*, *Acratosaura* and *Stenolepis*. In this less-than-parsimonious result *Riolama* is found embedded within Gymnophthalminae as the sister group of *Alexandresaurus* (with low support, GB = 1) (Fig. 7), a major positional change for *Riolama* from the more parsimonious tree-align-



Fig. 5. Similarity-alignment + parsimony: strict consensus of 151 most parsimonious trees of 69 472 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodman-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

ment result. This renders Cercosaurinae (or Cercosaurini), Gymnophthalminae and Iphisini paraphyletic.

The second clade includes *Psilophthalmus* + a large group itself composed of two groups, *Calyptommatius* + (*Nothobachia* + *Scriptosaura*), and *Gymnophthalmus*

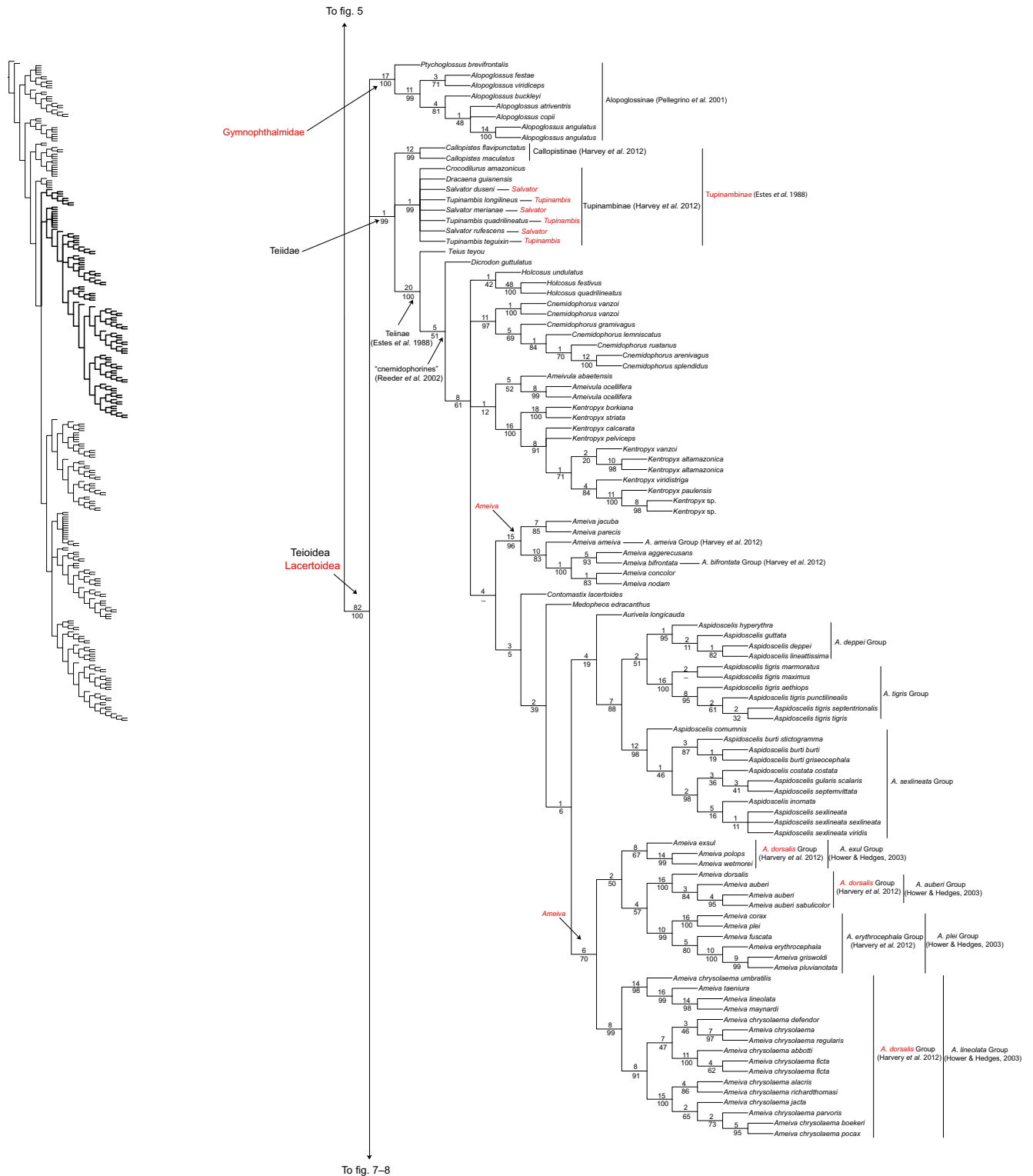


Fig. 6. Similarity-alignment + parsimony: strict consensus of 151 most parsimonious trees of 69 472 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodman-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

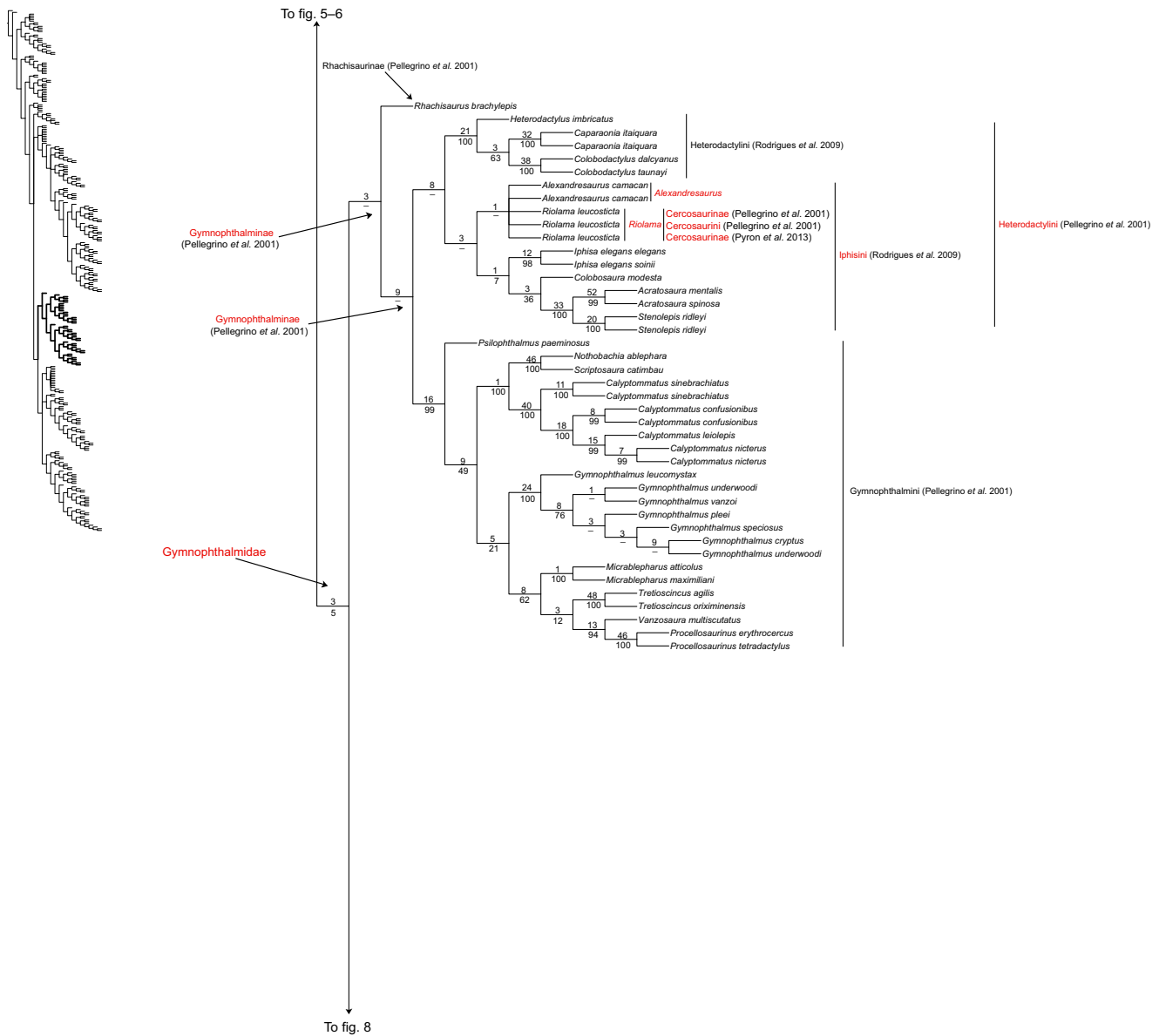


Fig. 7. Similarity-alignment + parsimony: strict consensus of 151 most parsimonious trees of 69 472 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodman-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

plus an asymmetrically resolved group composed of *Micrablepharus*, *Tretioscincus*, *Vanzosaura* and *Procellosaurinus*. The second of the major groups within Gymnophthalminae excluding Alopoglossinae has a basal trichotomy, composed of *Bachia* (which has lost all resolution in the consensus), as sister of a clade containing the ecleopodines and the cercosaurines (Fig. 8), supporting Pellegrino et al. (2001) Cercosaurinae, but not the subdivision of this subfamily into the tribes Cercosaurini and Ecleopodini. Castoe et al. (2004) Ecleopodinae and Pyron et al. (2013) Bachiinae are supported. The position of Ecleopodinae is also unre-

solved. Within Ecleopodinae, *Arthrosaura* is paraphyletic. *Leposoma* itself is recovered as non-monophyletic as the *L. scincoides* and *L. parietale* groups are placed in separated clades. Within the Cercosaurinae (excluding *Riolama*), all genera are monophyletic.

Similarity alignment + parsimony, but excluding indels as evidence

Driven searches of the same similarity-alignment matrix but with length variation/gaps treated as miss-



Fig. 8. Similarity-alignment + parsimony: strict consensus of 151 most parsimonious trees of 69 472 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa. Numbers above branches are Goodson-Bremer values and those below branches are jackknife percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

ing data (SA + PA_{4th}) resulted in 129 optimal trees of 65 218 steps and a strict consensus of 249 nodes, three fewer than with gaps as evidence (matrix and consensus tree deposited in TreeBase under accession number S17936; see Figs S1–S4). Within the outgroup, Anguimorpha is now monophyletic, with *Shinisaurus* as sister of *Anniella* and *Lanthanotus*. Teioidea is monophyletic, but Gymnophthalmidae remains paraphyletic, with Alopoglossinae as sister of the remaining teioids. Furthermore, in this analysis Gymnophthalmidae and Teiidae are also paraphyletic due to the position of *Riolama*, which is recovered embedded within Teiidae and as the sister group of Teiinae (support values for ingroup taxa are listed in Table 4). The relationships of Tupinambinae are better resolved, and *Tupinambis* is recovered as monophyletic, while *Salvator* is paraphyletic with respect to *Dracaena* and *Crocodylurus*. Teiinae is monophyletic and better resolved, with *Cnemidophorus* and *Kentropyx* as sister taxa and these as sister to *Ameivula*. Nonetheless, *Teius* and *Dicrodon* are found as sister taxa and nested within the West Indies *Ameiva*, rendering both the “cnemidophorines” and *Ameiva* paraphyletic. Within Gymnophthalmidae (excluding Alopoglossinae and *Riolama*), the relationships of *Bachia* are almost fully resolved, but the non-monophyly of groups remains. Bachiinae and Gymnophthalminae are recovered as sister groups and the genera are monophyletic. Within Ecleopodinae, *Leposoma* is paraphyletic for several reasons. *Leposoma baturitensis* is found as sister to *Ecleopus*, and part of *Arthrosaura* is nested within the *L. parietale* group, while the rest of the *L. scincoides* group is placed on a different part of the Ecleopodinae clade. Within the Cercosaurinae, *Cercosaura* is paraphyletic, with *C. quadrilineata* as sister group of *Macropholidus* and *Pholidobolus*, and *Proctoporus* is also paraphyletic because *Anadia* is recovered as sister to *Proctoporus bolivianus*.

Similarity-alignment + maximum-likelihood

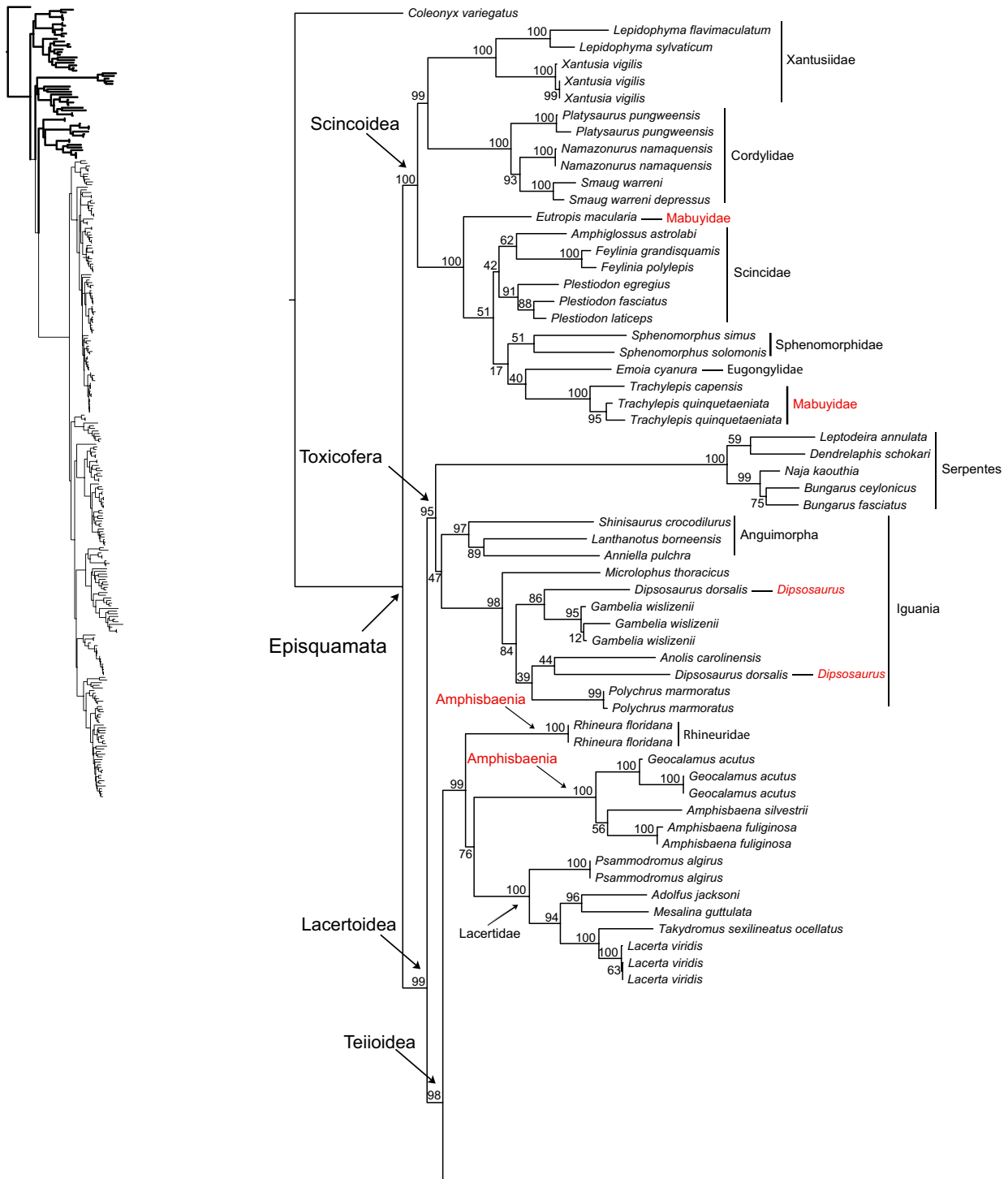
Partition Finder identified the two-partition (mtDNA/nuDNA) scheme with GTR + I + G substitution model for both partitions to be the optimal model. Under this partition scheme and model, the best GARLI's maximum log likelihood score was $-319\,701.933995$, and the corresponding topology (Figs 9–12) was found only once among the 1100 replicates (log likelihood scores range: $-319\,744.1$ to $-319\,701.9$) (matrix and best tree deposited in TreeBase under accession number S17936).

The optimal tree of maximum-likelihood analyses under similarity alignment (SA + ML) supports a monophyletic Teioidea (composed of monophyletic Teiidae and Gymnophthalmidae), sister of a clade formed

by Amphisbaenia and Lacertidae (Fig. 9), the inclusive clade forming Lacertoidea of Estes (1983). Amphisbaenia is recovered as non-monophyletic as Rhineuridae was the sister of the clade formed by Lacertidae and Amphisbaenidae. Toxicofera is monophyletic and sister of the clade formed by Lacertoidea and Teioidea. Anguimorpha is the sister of Iguania and this clade, in turn, is sister of Serpentes. Within Iguania, two samples of *Dipsosaurus dorsalis* are recovered in different parts of the tree, one as the sister of *Anolis*, and the other as the sister of *Gambelia* (suggesting, as noted earlier, a lack of overlap between loci or the possibility of sequence misidentification). This analysis also recovered the monophyly of Scinciformata, consisting of Scincomorpha, Xantusiidae and Cordylidae, but Mabuyidae and Lygosomoidea were paraphyletic.

Within Teiidae the monophyly of the subfamilies Tupinambinae and Teiinae *sensu* Estes et al. (1988) is supported by the optimal tree, as well as Tupinambinae and Callopidinae of Harvey et al. (2012) (Fig. 10). *Tupinambis* is not recovered as monophyletic as *Dracaena guianensis* and *Crocodylurus amazonicus* are nested within this genus, but *Salvator* is found to be monophyletic. Within the subfamily Teiinae, *Dicrodon* is the sister taxon of a large clade that includes the “cnemidophorines” with *Teius* embedded within (Fig. 10). This large clade comprises two major clades. The first clade contains *Contomastix* as sister to *Holcosus*, and these as sister of cis-Andean *Ameiva* (Hower and Hedges, 2003; Harvey et al., 2012), forming the sister group of a clade containing the genera *Ameivula*, *Cnemidophorus* and *Kentropyx*. The second clade contains the genus *Teius* as the sister of a clade formed by *Aspidoscelis*, *Aurivela*, *Medopheos* and West Indian *Ameiva* (Hower and Hedges, 2003; Harvey et al., 2012). Thus, *Ameiva* is paraphyletic in this analysis. Within *Aspidoscelis*, the *A. deppii*, *A. sexlineata* and *A. tigris* groups are monophyletic (Fig. 10). As in other analyses, the monophyly of nominal *A. sexlineata* samples is not recovered because *A. inornata* is nested within it. *Aspidoscelis gularis* was also nominally paraphyletic as *A. c. costata* is more closely related to *A. gularis scalaris* than either is to *A. g. gularis*. Within the West Indies *Ameiva* clade, the monophyly of the *A. auberi*, *A. exul*, *A. lineolata* and *A. plei* groups (*sensu* Hower and Hedges, 2003) was recovered. The *A. dorsalis* group of Harvey et al. (2012) is paraphyletic.

The second clade of Teioidea corresponds to Gymnophthalmidae (Figs 11 and 12). Within this clade the first split separates a clade with Alopoglossinae and *Riolama*—rendering Cercosaurinae of Pyron et al. (2013) and Cercosaurini of Pellegrino et al. (2001) paraphyletic—from the remaining gymnophthalmids. Within this large clade, there are four major subclades. The first corresponds to *Rhachisaurus*



To fig. 10–12

Fig. 9. Similarity-alignment + maximum likelihood: optimal solution (log likelihood = -319701.933995) showing relationships among 241 terminals of Teioidea and 58 outgroup taxa scored for 34 296 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + I + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

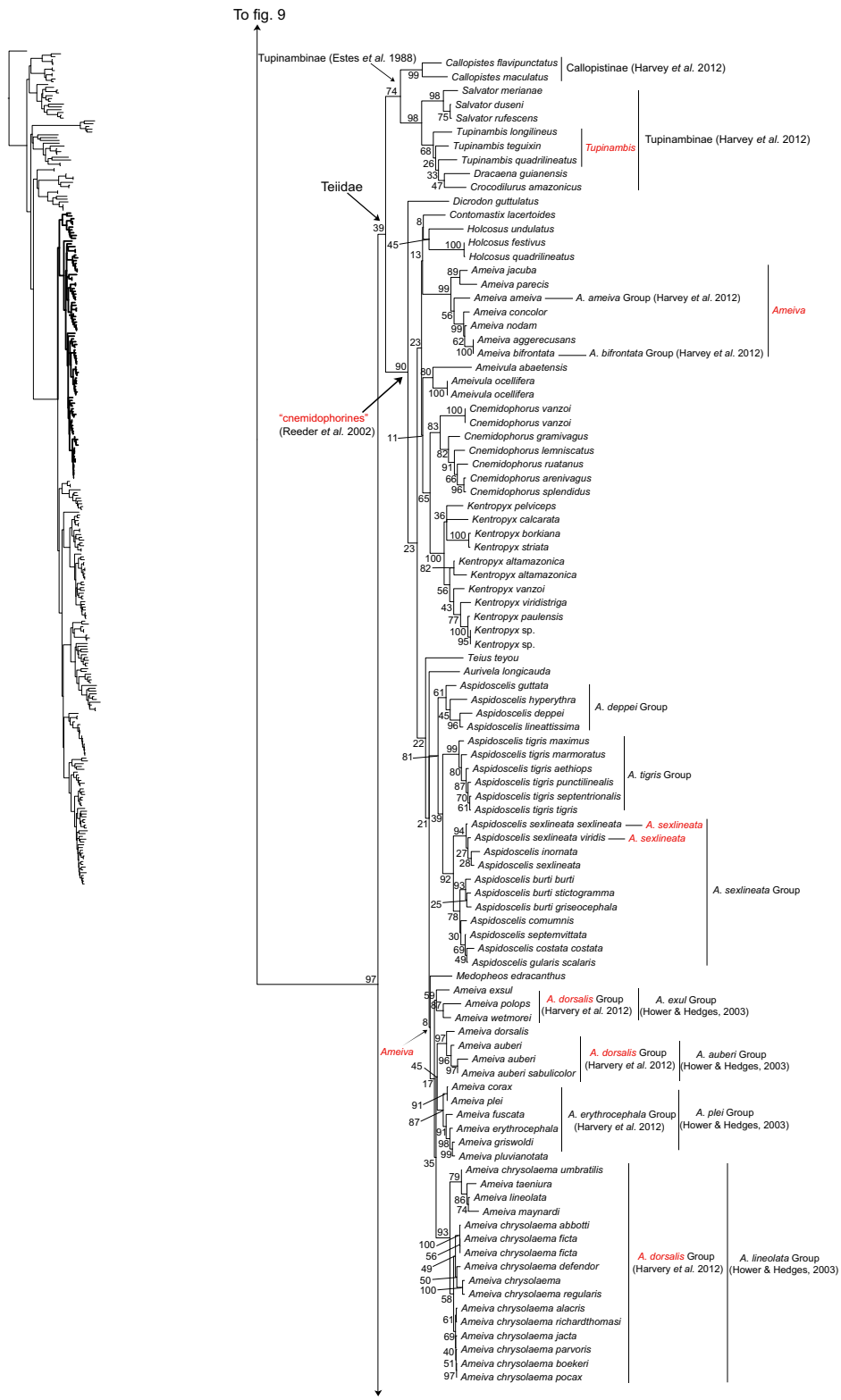


Fig. 10. Similarity-alignment + maximum likelihood: optimal solution (log likelihood = 319701.933995) showing relationships among 241 terminals of Teioidea and 58 outgroup taxa scored for 34 296 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + I + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

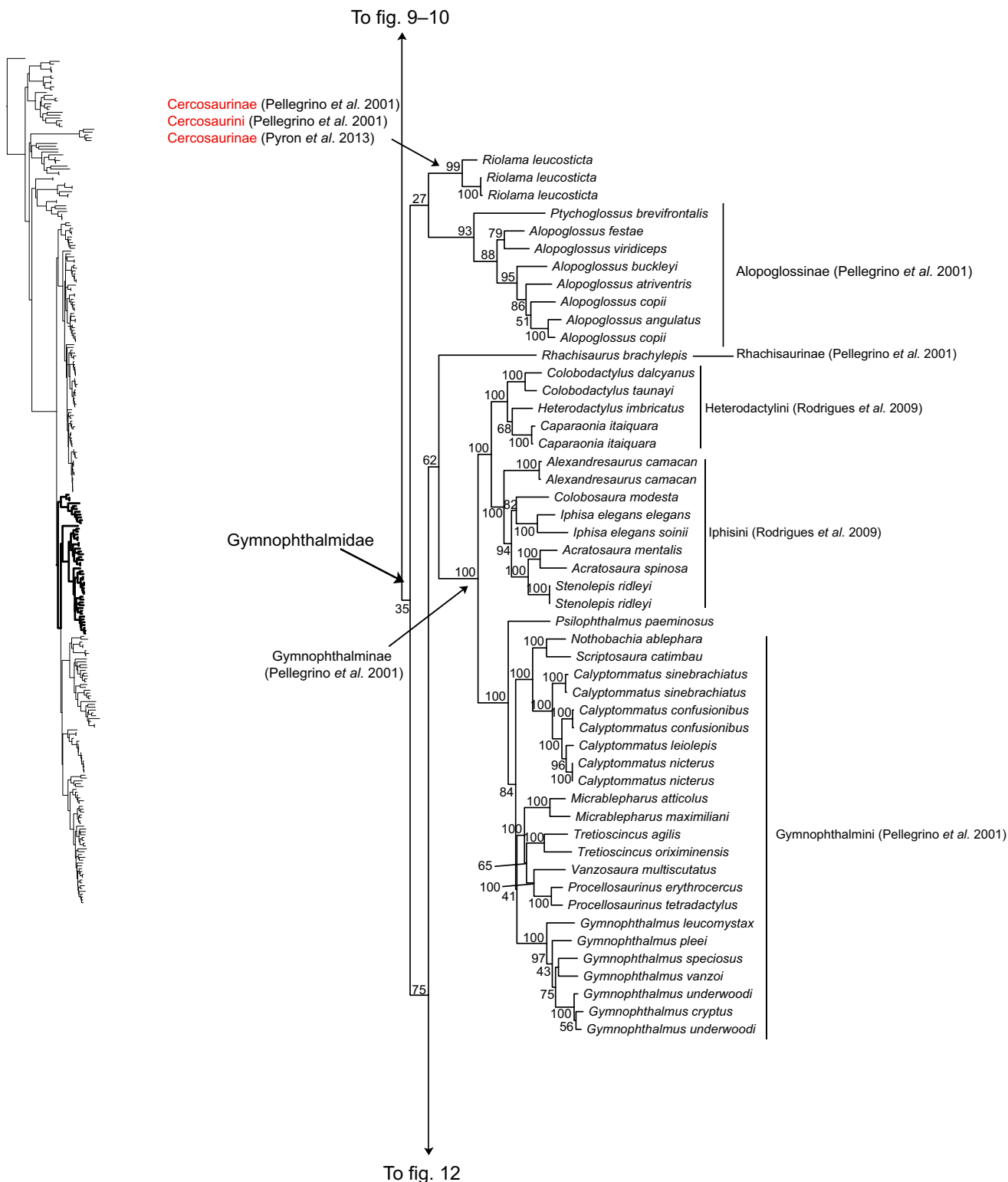


Fig. 11. Similarity-alignment + maximum likelihood: optimal solution (log likelihood = 319701.933995) showing relationships among 241 terminals of Teioidea and 58 outgroup taxa scored for 34 296 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + I + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

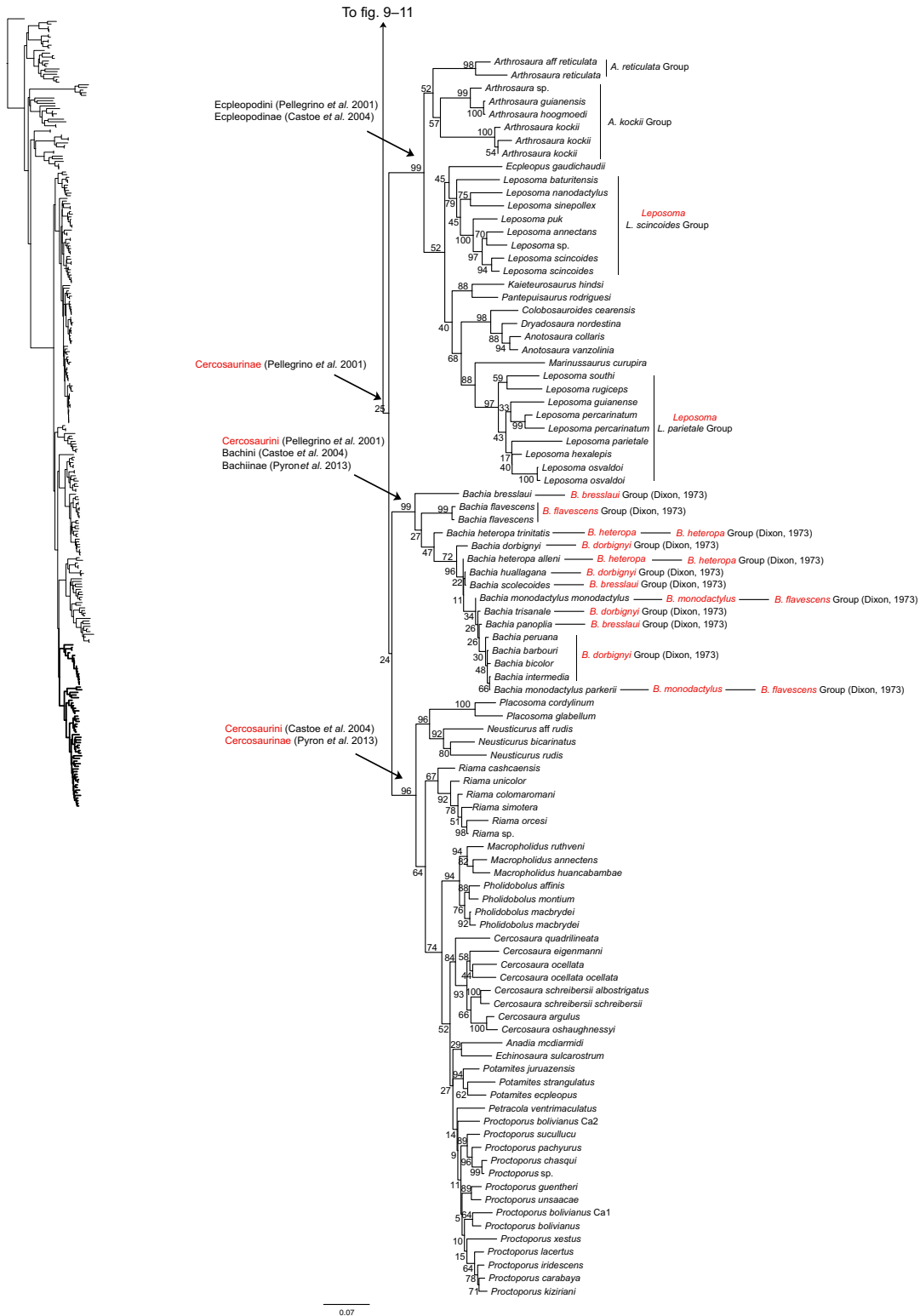


Fig. 12. Similarity-alignment + maximum likelihood: optimal solution (log likelihood = 319701.933995) showing relationships among 241 terminals of Teioidea and 58 outgroup taxa scored for 34 296 aligned sites of mitochondrial and nuclear DNA assuming mitochondrial and nuclear partitions and the GTR + I + G substitution model. Numbers above nodes are bootstrap percentages. Non-monophyletic taxa are highlighted in red (monophyletic taxa within paraphyletic groups remain in black).

Table 5
Cost of all optimal trees (in bold) and reciprocal cost of trees inferred by different methods

	Cost under:			
	TA+PA*	SA+PA	SA+PA _{4th} [†]	SA+ML [‡]
TA+PA tree	67 252	70 181	65 869	–320 543.521654
SA+PA tree	67 629	69 472	65285–300	–320 885.196166
SA+PA _{4th} tree	67 614	69 542–9	65 218	–321 014.126552
SA+ML tree	67 439	69 769	65 457	–319 701.933995

*Cost calculated under IPO.

[†]The lower parsimony cost results from discarding indels as evidence.

[‡]Polytomies in the strict consensus were arbitrarily resolved.

(Rhachisaurinae) as the sister of Gymnophthalminae of Pellegrino et al. (2001), which includes the tribes Heterodactylini and Gymnophthalmini and Iphisini as monophyletic (Fig. 11).

The second clade within Gymnophthalmidae contains Pellegrino et al.'s (2001) Cercosaurinae except *Riolama* (Fig. 12). This topology supports the monophyly of their Ecleopodini but does not support the monophyly of their Cercosaurini. Within Ecleopodini, *Leposoma* is paraphyletic, with the *Leposoma scincoides* and *L. parietale* groups placed in separate clades associated with other nominal genera (Fig. 11). The third clade corresponds to a monophyletic *Bachia* that is sister to part of the Cercosaurini (Fig. 12). Dixon's (1973) species groups for *Bachia* were not corroborated, and the samples of *B. monodactylus* and *B. heteropa* do not form monophyletic units. The fourth clade includes several genera that are part of a paraphyletic Cercosaurini, whereas *Cercosaura* and *Proctoporus* are found to be monophyletic.

Comparison of trees

Comparisons of tree costs among methods indicate that all different strategies of analysis (SA + PA, SA+PA_{4th}, SA + ML) found trees that were overall optimal for each strategy (the costs of all optimal trees and their cost when measured under alternative strategies of character optimization are listed in Table 5). In other words, when trees obtained from a strategy of analysis were measured under the conditions of another strategy (e.g. when the tree from TA + PA was measured under SA + ML), they consistently rendered higher costs. Concerning parsimony solutions, however, TA + PA rendered the overall shortest tree, the one that required the fewest character transforma-

tions to explain evolutionary divergence in sequence length including indels (67 252 steps versus 69 472 of SA + PA). (Of course, the SA+PA_{4th} rendered even shorter solutions because indel transformations were discarded.) Interestingly, the most similar solution to the TA + PA tree in terms of length was the SA + ML tree (only 187 steps longer), followed by the SA + PA_{4th} tree (362 steps longer) and the SA + PA tree (377 steps longer). Still, the SA + PA tree had its length shortened when characters were optimized onto that tree using tree-alignment under the same criterion of optimality and treatment of indels. This was indeed the only case where a topology obtained from one method had a shorter length when measured under the optimization and alignment conditions of a different method. Concerning likelihood scores, the second best score was produced by the TA + PA tree, followed by SA + PA and SA + PA_{4th}.

In terms of alignment, tree-alignment produced a longer matrix (36 267 aligned columns), with double the amount of columns with gaps (4850) than the similarity alignment (34 296 columns, 2180 with gaps). Despite the increment in the number of columns and gaps, TA + PA produced a tree that required fewer steps to explain differences in length among sequences (see above).

The number of nodes and nodes shared among optimal trees are listed in Table 6. The single optimal SA + ML has the highest number of nodes (292), followed by strict consensus of TA + PA (266), SA + PA (252) and SA + PA_{4th} (249). Among these topologies, TA + PA and SA + ML were again the most similar, sharing 195 nodes, while TA + PA and SA + PA shared only 191 nodes despite the same assumptions being applied to both methods. The least similar topologies were SA + PA and SA + PA_{4th},

Table 6
Number of nodes (in parentheses) and nodes shared by parsimony strict consensus trees and the optimal maximum-likelihood tree

	SA + ML (292)	SA + PA _{4th} (249)	SA + PA (252)	TA + PA (266)
TA + PA	195	191	191	–
SA + PA	190	181	–	
SA + PA _{4th}	191	–		

sharing 181 nodes, indicating a clear effect of the treatment of indels on the inferred relationships.

Among the 44 nominal taxa of Teioidea at or above the genus level for which we could test their monophyly, all methods agree in their support or rejection of the monophyly of 34 (77%) of these taxa (Table 4). SA + ML supports the monophyly of 39 taxa (89%), TA + PA supports the monophyly of 35 (80%), and SA + PA and SA + PA_{4th} support the monophyly of 34 (77%) of those taxa (although they differ in which ones they support or reject). All three analyses based on similarity-alignment agree in their support for the monophyly or non-monophyly of 35 taxa (80%), while TA + PA agrees in its support for the monophyly or non-monophyly of 39 taxa (89%) with some or all of the other methods. Although all analyses agree in a majority of clades, they also differ or agree in unique ways. All parsimony analyses agree in the non-monophyly of *Arthrosaura* and Gymnophthalmidae. SA + PA and SA + ML agree in their support for the monophyly of *Cercosaura*; SA + ML and SA + PA_{4th} agree in their support for the monophyly of Gymnophthalminae, Iphisini and *Salvator*; while SA + PA rejects them all. Also, only ML + SA supports the monophyly of *Arthrosaura* and Gymnophthalmidae; only TA + PA and SA + PA_{4th} reject the monophyly of *Cercosaura* and only TA + PA rejects the monophyly of *Ameivula*; only SA + PA rejects the monophyly of Gymnophthalminae and Iphisini; and only SA + PA_{4th} rejects the monophyly of *Proctoporus* and Teiidae.

Considering clade support measures, congruent clades across methods always received moderate to high support by resampling (Table 4), and often also by GB (with the exception of *Aspidoscelis*, GB = 1 in TA + PA). In general, clades that were rejected by one or more analyses received lower support in the analyses that supported them in comparison with clades that were supported by all methods. For example, Gymnophthalmidae, which was rejected by all parsimony analyses, was very poorly supported by SA + ML, with only 35% of support resampling. Similar cases include, for example, *Ameivula*, *Arthrosaura* and *Cercosaura*. However, there are cases in which one or two methods reject a clade that is well supported by others (e.g. “cnemidophorines” is well supported by all analyses that consider gaps as evidence). Jackknife values for clades supported by SA + PA and SA + PA_{4th} were lower when gaps were excluded from analysis (Table 4).

Discussion

The inference of phylogenetic trees from large and heterogeneous datasets is a complex operation. Multiple factors are involved in the identification of optimal solutions, chiefly among them the heuristic shortcuts

that make possible the sampling of a large tree space in reasonable time (e.g. Goloboff, 1999). Diverse artefacts derived from the algorithmic and computational limitations of tree searches further complicate the identification of optimal solutions (Simmons and Goloboff, 2013, 2014; Goloboff, 2014). Other aspects of phylogenetic tree analysis such as alignment (Wheeler, 1994; Morrison and Ellis, 1997; Whiting et al., 2006; Wong et al., 2008; Blackburne and Whelan, 2012), and different treatments of sequence length variation (i.e. indels; Denton and Wheeler, 2012) also affect inferences. As such, multiple aspects need to be considered when comparing and discussing differences among optimal solutions obtained through different strategies (e.g. Padiál et al., 2014; Peloso et al., 2015). In spite of this, the effect of optimality criteria is often the preferred topic when it comes to discussing differences among results of empirical studies (Rindal and Brower, 2011).

We compared four analyses that allow some measure of evaluation of the effects of various methodological approaches to results. The first of these was under direct optimization parsimony (tree-alignment; TA + PA), which treats alignment and tree topology as a single problem (Sankoff, 1975; Wheeler, 1996, 2001; Wheeler et al., 2006; Grant and Kluge, 2009). This necessarily treats indels/length variation as evidence. The second was a more generally applied parsimony approach, where a similarity-alignment was produced using a conventional method (Kato et al., 2005). This preliminary estimate of homology was then treated as an assumption of analysis and subjected to two different analyses, one where length variation was considered as evidence (SA + PA) and a second analysis (SA + PA_{4th}) where it was not (i.e. indels treated as evidence of versus as absence of evidence). This allowed us to evaluate what deviations from the first direct-optimization analysis were caused by (a) the alignment and (b) inclusion or exclusion of length variation. The fourth analysis corresponded to a standard maximum-likelihood analysis (SA + ML). In this analysis we took the similarity-alignment produced previously, excluded indels (i.e. length variation) due to the limitations of the algorithm implemented by the software, and then applied a general model of molecular evolution that assumed a certain transition/transversion rate for each character column within a partition. Our comparisons indicate that it is difficult to predict similarities and differences among optimal solutions obtained from the same or different optimality criteria and that both, similarities and differences, can be attributed to several causes. Below we describe major differences and potential causes among the multiple analyses implemented in our study of teioid relationships. Subsequently, we discuss how our results bear on the phylogenetic relationships and taxonomy of teioid lizards.

Missing data, indels, alignment, and optimality criteria

The analysis of matrices with incomplete terminals can be problematic due to algorithmic artefacts affecting the optimization of missing data (Wilkinson, 1995; Kearney, 2002; Lemmon et al., 2009; De Laet, 2010; Simmons, 2012a,b; Simmons and Goloboff, 2013, 2014; Simmons and Norton, 2013; Padiál et al., 2014; Simmons and Randle, 2014). Several recent studies have found through analyses of empirical data (Siddall, 2010; Simmons and Goloboff, 2013; Padiál et al., 2014) and simulations (Lemmon et al., 2009; Simmons, 2012a; Simmons and Goloboff, 2013) that non-randomly distributed ambiguous data can result in spurious resolutions and clade frequencies. Although the effect is stronger in model-based analyses, parsimony analyses are also affected when tree searches are not exhaustive (e.g. Simmons and Goloboff, 2013). Accordingly, our parsimony analyses implemented several heuristic strategies that have proved useful to mediate the effect of artefacts produced by missing data in parsimony analyses (Simmons and Goloboff, 2013, 2014; Goloboff, 2014). However, despite the large amount and random distribution of missing data in our matrix, parsimony analyses rendered almost completely resolved trees. A few polytomies at shallow nodes indicate some effect of missing data when there is no overlap among terminal taxa (e.g. *Gambelia* or *Lacerta* within the outgroup). However, there are other polytomies where missing data may be a candidate to explain the collapse of branches, whereas it is the treatment of indels as evidence that causes the ambiguous position of taxa. For example, in the strict consensus of SA + PA the relationships of *Bachia* collapse into a polytomy. The collapse is due to *B. bresslaui* behaving as a wildcard despite it being coded for both CMOS and 16S. While CMOS is coded for 14 out of 16 terminals of *Bachia*, 16S is coded for them all and, as such, missing data do not seem to be responsible for the wildcard behaviour of this terminal. Indeed, SA + PA_{4th} fully resolves relationships for *Bachia*, suggesting that the evidence provided by gaps in SA + PA is probably responsible for the ambiguous optimization. Within Tupinambinae the position of *Crocodylurus* and *Dracaena* is also ambiguous in TA + PA and SA + PA, rendering completely unresolved relationships for this clade. Removal of these two taxa simultaneously, but not separately, recovered reciprocally monophyletic *Tupinambis* and *Salvator*. However, the monophyly of *Salvator* is also recovered in TA + PA, and partial resolution of the relationships of other tupinambines is recovered when evidence of indels is discarded. These results point to an important effect of indels in clade resolution and certainly, as discussed below, alignment has an important effect on the inferred relationships of teioids.

All methods of alignment attempt to minimize the number of evolutionary (i.e. historical) events explaining observed differences in sequence length (reviewed by Nicholas et al., 2002). Among the methods used by us, the alignment that required fewer transformations to explain sequence divergence was obtained by TA + PA. As such, the results of TA + PA provided the empirically most explanatory hypothesis of relationships and sequence divergence (Frost et al., 2001; Kluge and Grant, 2006; Grant and Kluge, 2009). Under this method the alignment and the resulting topology was 377 steps shorter than the shortest topology obtained under parsimony with indels treated as evidence (SA + PA). Furthermore, while the SA alignment resulted in 34 296 aligned positions of which 2180 columns contained gaps, TA + PA resulted in 36 267 aligned positions and 4850 columns with gaps. Thus, and although apparently paradoxical in principle, the alignment implying an evolutionary history of sequence divergence with more insertion and deletion events turned into the topology that requires fewer overall character transformations. Indeed, that TA + PA recovers trees with fewer hypothesized transformations is demonstrated by casting topologies obtained from similarity-alignment under the iterative optimization of TA + PA (Table 5). All these topologies (trees from SA + PA, SA + PA_{4th} and SA + ML) were shorter under tree-alignment than under similarity-alignment, which indicates that there are more optimal alignments for those topologies than those found by MAFFT.

Contrary to expectations, the most similar topology to TA + PA was not the one obtained under SA + PA, despite their use of the same criterion of optimality and treatment of indels as absence of evidence; the most similar tree to TA + PA was, instead, the one obtained under SA + ML despite the radically different treatment of evidence implemented by this approach. Concerning costs, the optimal tree inferred from SA + ML has the best parsimony cost after TA + PA, and the TA + PA solution has the best likelihood score after SA + ML. The SA + PA_{4th} tree also rendered a better parsimony score than the SA + PA solution under TA + PA. Furthermore, the two analyses relying on the same optimality criteria and alignment but with indels treated differently (SA + PA_{4th} and SA + PA) share the lowest number of clades, while the two analyses where indels were treated as absence of evidence (SA + PA_{4th} and SA + ML) share more clades despite the differences in optimality criteria. These unexpected findings suggest that similarity-alignments produced in MAFFT, and especially the inferred pattern of indels, drove conventional parsimony analyses away from more optimal solutions. Alternatively, it could be deduced that assumptions of similarity-alignment may be more compatible with

assumptions of maximum-likelihood analyses, which raises the question of whether similarity-alignment is appropriate for parsimony analysis.

Although the different assumptions of optimality criteria can lead to different optimal solutions (e.g. Siddall, 1998; Kolaczkowski and Thornton, 2004), our results indicate that other factors can be as important. Differences in the alignment and especially the pattern of indels can also explain differences among optimal topologies. These results are important insofar as most parsimony analyses of molecular data rely on similarity-alignment, and differences among parsimony and maximum-likelihood solutions are most often discussed in terms of the criterion of optimality only.

Phylogenetic relationships of “Teioidea” (=Gymnophthalmoidea): remedies for various nomenclatural and taxonomic issues uncovered by our study

Prior to discussion of a taxonomy and how our results require some taxonomic novelties, we must first address some nomenclatural issues. Table 7 presents a chronological list of available and unavailable family-group names for the overall teioid group. As can be seen from the table, the state of compliance with the International Code (1999) has been poor, largely driven by the use of fictitious names (e.g. Tupinambinae Daudin, 1802; Teiinae Merrem, 1820; Gymnophthalmidae Merrem, 1820) and substantial misunderstandings of rules of family-group nomenclature (see Table 7 for a detailed account of nomenclatural issues). Going into this study we assumed that the nomenclature was in hand, given the detailed work on the components of the overall group in the 1970s and 1980s and, among other assumptions, that Teiidae was an older name than Gymnophthalmidae. We were mistaken. While the bulk of the nomenclatural issues are noted in Table 7, some bear more detailed discussion here.

Gymnophthalmi Fitzinger (1826) is unambiguously an older family-group name than Teiidae Gray (1827). The problem seems to have originated in Boulenger’s failure (in his treatment of Teiidae *sensu lato*, Boulenger, 1884: 122, 1885: 330) to note that Fitzinger (1826: 11) had named the family-group Gymnophthalmoidea explicitly as a family with the type genus being *Gymnophthalmus* Merrem, 1820. Instead he assigned that family-group name, Gymnophthalmi, to Wiegmann (1834). Presch (1983), however, in error assigned the family-group name Gymnophthalmidae to Merrem (1820), and this designation was followed by Estes et al. (1988), in their influential publication. Unfortunately, Merrem mentioned no such name; he coined only the generic name *Gymnophthalmus*, and, in fact, he mentioned no family-group names whatsoever in that publication. It was Fitzinger (1826) who coined the family-group name Gymnophthalmoidea (an

explicit family-group name with the type genus being *Gymnophthalmus* Merrem, 1820). Presch (1981), while focusing on nomenclatural stabilization of the name Teiidae, in the sense of being a family separate from Gymnophthalmidae, apparently did not notice the over-arching problem in the relative priority of Gymnophthalmidae and Teiidae.

Presch (1981) had noted that both Tupinambidae Gray (1825) and Ameivoidea Fitzinger (1826) apparently had priority over Teiidae Gray (1827, p. 53). He also noted that Tupinambidae (Gray, 1825, p. 199) is invalid due to not being based on a then-valid genus (Tupinambina not being validly named until Bonaparte, 1831, p. 69). Presch (1981) appealed to the International Commission and in Opinion 1300 (Anonymous 1985, pp. 130–133) the ICZN ruled that Teiidae Gray, 1827; should take precedence over Ameivoidea Fitzinger, 1826, whenever *Ameiva* Meyer, 1795, and *Teius* Merrem, 1820, are considered to be in the same family-group. Unfortunately, this still leaves Gymnophthalmidae Fitzinger, 1826, an older name than Teiidae Gray, 1827. See additional comments in Table 7 regarding the ambiguity surrounding the use of the name Tupinambinae, which for the purposes of this study we assign to Bonaparte (1831).

Side-stepping for the moment the issue of Tupinambidae Gray (1825), if we were to place both clades within one nominal family that name would be Gymnophthalmidae Fitzinger, 1826, with at least three subfamilies, one of which would be Teiinae Gray, 1827. So, we are faced with applying either a one-family arrangement (Gymnophthalmidae), a two-family arrangement where the family-group name Alopoglossidae applies to one group (formerly part of Gymnophthalmidae) and the name Gymnophthalmidae applies to the group composed of the remainder of traditional Gymnophthalmidae + traditional Teiidae (as Gymnophthalminae and Teiinae, respectively), or our favored taxonomy, have a three-family arrangement, that recognizes a relatively minor group, Alopoglossidae, and two major groups, Gymnophthalmidae and Teiidae; this arrangement comes closest to existing usage. There are additional nomenclatural issues dealt with in Table 7.

Among the alternative analyses that we implemented, the “tree-alignment under parsimony” option provided the most efficient solution for all observations among all the methods applied (Table 5), so we follow the result of this analysis for our taxonomic interpretations. A detailed taxonomy is provided in Appendix 2 and a summary of the proposed classification is listed in Table 8.

Taxonomy adopted and rationale

The monophyly of Gymnophthalmoidea (as Teioidea) and its subdivision into two families has been

Table 7

Available and unavailable family-group names and their authors for living Alopoglossidae, Gymnophthalmidae and Teiidae in chronological order

-
- “Tupinambinae Daudin, 1802”. Fictitious family-group name provided by Presch (1983: 193)
- “Teiinae Merrem, 1820”. Fictitious family-group name provided by Presch (1983: 193)
- “Gymnophthalmidae Merrem, 1820”. Fictitious family-group name provided by Estes et al. (1988) and Presch (1983: 193)
- Tupinambidae Gray, 1825: 199. Type genus: “Tupinambis, *Lam.*” (= *Tupinambis* Daudin, 1803). *Tupinambis* was given as a synonym of *Uranus* Merrem (= *Varanus* Merrem). Considered by Presch (1981), and Smith et al. (1982: 157–158), as an unavailable family-group name by reason of not being based on a generic name then considered valid (Art. 11.6). However, the treatment of Tupinambina by Bonaparte (1831: 69) as a valid family-group name, based on *Tupinambis* Daudin, 1803, may render this name valid under Art. 11.6.1. But see comments under Tupinambina Bonaparte, 1831
- Gymnophthalmoidea Fitzinger, 1826: 11. Type genus: *Gymnophthalmus* Merrem, 1820. Named explicitly as a family
- Ameivoidea Fitzinger, 1826: 21. Type genus: “*Ameiva* Say” (= *Ameiva* Meyer, 1795). Opinion 1300 of the ICZN (Anonymous 1985: 130–133) ruled that Teiidae Gray, 1827, is to take precedence over Ameivoidea Fitzinger, 1826, whenever *Ameiva* Meyer, 1795, and *Teius* Merrem, 1820, are considered to be in the same family-group
- Teiidae Gray, 1827: 53. Type genus: *Teius* Merrem, 1820. Given precedence by Opinion 1300 (Anonymous 1985: 130–133) over Ameivoidea Fitzinger, 1826, whenever *Teius* Merrem, 1820, and *Ameiva* Meyer, 1795, are placed in the same family-group taxon
- Tupinambina Bonaparte, 1831: 69. Type genus: “*Tupinambis* Fitz.” (1826) (= *Tupinambis* Daudin, 1803). Below subfamily but clearly in the family-group. For purposes of this paper we regard this as the first valid use of the family-group name
- Chirocolidae Gray, 1838: 391. Type genus: *Chirocolis* Wagler, 1830. Name unavailable by reason of being based on a generic name then in synonymy inasmuch as Gray (1838: 391) treated *Chirocolis* Wagler as a junior synonym of *Heterodactylus* Spix. (See Fig. 13 showing Gray’s naming of Chirocolidae and his standard method in this paper of showing that he regarded *Chirocolis* as a junior synonym of *Heterodactylus*.) Although Colli et al. (2015) treated Chirocolidae Gray, 1838, as valid, pretty clearly the name is unavailable.
- Cercosauridae Gray, 1838: 391. Type genus: *Cercosaura* Wagler, 1830. by monotypy
- Crocodyluri Bonaparte, 1840: 95 (p. 5 of separate). Type genus: *Crocodylurus* Spix, 1825. Coined as a subfamily of Ameividae. Junior homonym of Crocodyluri Bonaparte, 1840
- Podinemiae Fitzinger, 1843: 20. Type genus: *Podinema* Wagler, 1830 (= *Tupinambis*)
- Callopiidae Fitzinger, 1843: 20. Type genus: *Callopiastes* Gravenhorst, 1838
- Ecleopoda Fitzinger, 1843: 21. Type species: *Ecleopos* Duméril and Bibron, 1839. See discussion by Colli et al. (2015: 404)
- Thorictidae Fitzinger, 1843: 20. Type genus: *Thorictus* Wagler, 1830 (= *Dracaena*)
- Crocodyluri Fitzinger, 1843: 20. Type genus: *Crocodylurus* Spix, 1825
- Crocodylurina Gray, 1845: 23. Type genus: *Crocodylurus* Spix, 1825. Rank not stated, although clearly in the family-group. Junior homonym of Crocodyluri Bonaparte, 1840
- Emminiina Gray, 1845: 23. Type genus: *Emminia* Gray, 1845 (= *Cercosaura*). Rank not stated, although clearly in the family-group
- Centropygina Gray, 1845: 23. Type genus: “*Centropyx* Spix” (= *Kentropyx* Spix, 1825). Rank not stated, although clearly in the family-group
- Argaliidae Gray, 1846: 67. Type genus: *Argalia* Gray, 1846
- Iphisidae Gray, 1851: 39. Type genus: *Iphisa* Gray, 1851
- Riamidae Gray, 1858: 445. Type genus: *Riama* Gray, 1858
- Teiini Presch, 1974: 26. Type genus: *Teius* Merrem, 1820. Junior homonym of Teiidae Gray, 1827
- Tupinambini Presch, 1974: 26. Type genus: *Tupinambis* Daudin, 1803. Junior homonym of Tupinambina Bonaparte, 1831
- Teioidea Estes et al., 1988: 213. Type genus: *Teius* Merrem, 1820. Junior homonym of Teiidae Gray, 1827, in the family-group category
- Alopoglossinae Pellegrino et al., 2001: 330. Type genus: *Alopoglossus* Boulenger, 1885. Name unavailable (as noted by Colli et al., 2015: 403) due to the original authors not providing characters in words that purport to differentiate this taxon (Art. 13.1.1), leaving it a *nomen nudum*. Colli et al. (2015: 421) recognized the subfamily, but surprisingly, after discussing its unavailability dating from 2001, did not provide a diagnosis for the taxon, continuing it a *nomen nudum*. We provide a diagnosis for this family-group below
- Heterodactylini Pellegrino et al., 2001: 330. Type genus: *Heterodactylus* Spix, 1825. Name unavailable due to the original authors not providing characters in words that purport to differentiate this taxon, leaving it a *nomen nudum*
- Rhachisaurinae Pellegrino et al., 2001: 330. Type genus: *Rhachisaurus* Pellegrino et al., 2001. Colli et al. (2015, pp. 403–404) regarded the reference to the generic description of the monotypic *Rhachisaurus brachylepis* (Dixon, 1974) by Pellegrino et al. (2001), in the form of noting it as the type species, as constituting sufficient evidence that Pellegrino et al. (2001) were referencing (Art. 13.1.2) a “bibliographic reference to such a published statement [i.e. words to distinguish the new taxon, the subfamily Rhachisaurinae of Pellegrino et al. (2001) in this case]”
- Bachini Castoe et al., 2004: 465. Type genus: *Bachia* Gray, 1845. As discussed by Colli et al. (2015), this constitutes an incorrect original spelling of Bachiini. Name unavailable due to the original authors not providing characters in words that purport to differentiate this taxon nor denoting a type genus (Art. 16.3), leaving it a *nomen nudum*. Colli et al. (2015) formally named this taxon Bachiinae
- Iphisiini Rodrigues et al., 2009: 1. Type genus: *Iphisa* Gray, 1851. Incorrect original spelling and primary homonym of Iphisidae Gray, 1851. Name unavailable due to the original authors not providing characters in words that purport to differentiate this taxon, leaving it a *nomen nudum*. See discussion by Colli et al. (2015, pp. 404–405), who noted that this is junior homonym of the available name Iphisidae Gray (1851), itself an incorrect original spelling as discussed by Colli et al., 2015
- Callopiinae Harvey et al., 2012: 77. Type genus: *Callopiastes* Gravenhorst. Junior homonym of Callopiidae Fitzinger, 1843
- Riolaminae Kok, 2015: 513. Type genus: *Riolama* Uzzell, 1973
- Bachiinae Colli et al., 2015: 421. Type genus: *Bachia* Gray, 1845
- Alopoglossidae NEW FAMILY. Type genus: *Alopoglossus* Boulenger, 1885. See Appendix 2 for diagnosis
- Heterodactylini NEW TRIBE. Type genus: *Heterodactylus* Spix, 1825. See Appendix 2 for diagnosis
-

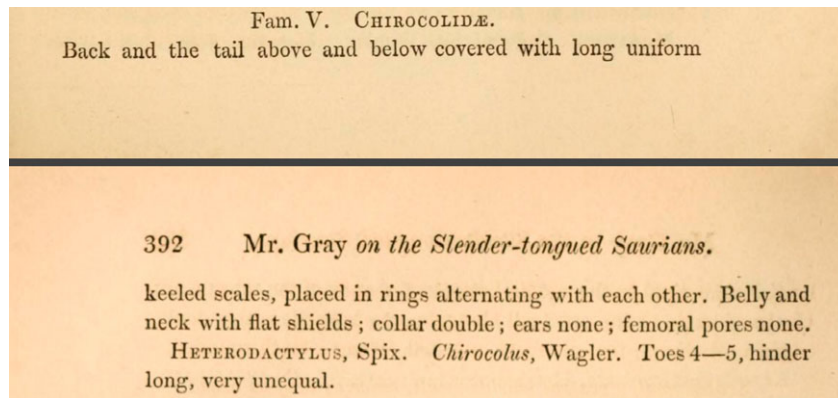


Fig. 13. Relevant section of Gray (1838: 391–392) showing the formulation of the family-group name Chirocolidae and showing his standard method of showing junior synonyms, in this case the synonymy of *Chirocolus* Wagler with *Heterodactylus* Spix, thereby rendering Chirocolidae invalid by reason of not being based on a type genus then recognized.

recognized since Estes et al. (1988), and influenced by the work of MacLean (1974), Presch (1983, 1988) and Estes (1983). Estes et al. (1988) partitioned Boulenger's Teiidae into two families on the basis of several anatomical characters. However, the relationships among species of micro- and macroteids, and hence its subdivision into two families, remained contentious. Harris (1985), based on the study of tongue morphology (of 104 species of 29 genera of gymnophthalmids and 27 species of eight genera of teiids) did not confirm microteiids as a natural group, but provided evidence of monophyly for Boulenger's Teiidae (our Gymnophthalmoidea) based on two synapomorphies: the presence of infralingual plicae and a detached segment of cartilage in the lingual process of the hyoid. Harris also found other features reported in previous literature such as kidney morphology (Cope, 1900), condition of hypohyals (MacLean, 1974), brain anatomy (Northcutt, 1978) and jaw musculature (Rieppel, 1980) that supported the monophyly of Boulenger's Teiidae. Nonetheless, Estes et al. (1988) continued recognizing macro- and microteiids as separate families, seemingly on the basis of Presch's (1983) taxonomy that was consistent with the pattern of synapomorphies in Estes (1983) tree. Subsequent to the efforts by Harris (1985), other studies have not supported Presch and Estes's division of Boulenger's Teiidae. Hoyos (1998), based on 15 osteological and myological characters [some of which previously were used by MacLean (1974), Presch (1980), Estes et al. (1988) and Rieppel (1980)] of 16 gymnophthalmids and three teiid genera (*Ameiva ameiva*, *Cnemidophorus lemmiscatus* and *Kentropyx striatus*), concluded that there were no morphological synapomorphies supporting the monophyly of Gymnophthalmidae. Moro and Abdala (2000) analysed the cranial musculature of several teiids and found that Teiidae was monophyletic only after the inclusion of *Pantodactylus* (*Cercosaura sensu* Doan, 2003). Nonetheless, Lee (1998, 2000) evaluated all osteological and other anatomical characters used in most previous squamate phylogenies (e.g. Northcutt, 1978; Harris, 1985;

Estes et al., 1988; Presch, 1988; Wu et al., 1996; Lee, 1997; Hallermann, 1998; Reynoso, 1998) and, congruent with Estes et al. (1988), found support for the division of Teioidea into Teiidae and Gymnophthalmidae. On the other hand, studies relying on molecular evidence addressed the phylogeny within only one of the two families within Teioidea (Pellegrino et al., 2001; Castoe et al., 2004). More recently, Pyron et al. (2013) found Gymnophthalmidae and Teiidae to be monophyletic in a maximum-likelihood analysis of gene sequences, although Teiidae was poorly supported (bootstrap = 54).

Alopoglossidae and Gymnophthalmidae. As noted, our shortest trees do not support a monophyletic Gymnophthalmidae, instead placing *Alopoglossus* and *Ptychoglossus* in a monophyletic group that forms the sister taxon of Teiidae plus the remaining gymnophthalmids. To preserve the names Gymnophthalmidae and Teiidae as coordinate families, we name Alopoglossidae (see Table 7 and Appendix 2), a *nomen nudum* previously used by several authors, including Colli et al. (2015), for the clade that contains *Alopoglossus* and *Ptychoglossus* [note that Castoe et al. (2004) already transferred *Ptychoglossus* to their Alopoglossinae]. Consistent with previous studies (Pellegrino et al., 2001; Castoe et al., 2004; Pyron et al., 2013) we recovered a close relationship between *Rhachisaurus* (Rhachisaurinae of Pellegrino et al., 2001) and Gymnophthalminae. Our analyses also found *Riolama leucosticta* as the sister of the Rhachisaurinae + Gymnophthalminae clade. Traditionally, *Riolama* was considered on the basis of overall similarity to be a close relative of *Ptychoglossus*, *Alopoglossus* and *Ecleopus* (Uzzell, 1973). Myers et al. (2009) subsequently provided evidence of tongue morphology that placed *Riolama* in Alopoglossinae. However, Pellegrino et al. (2001) placed *Riolama* in their Cercosaurinae. None of these hypotheses is supported by our analyses. But, we do agree with Kok

Table 8

A summary of the supraspecific classification of Gymnophthalmoidea

Taxon
Gymnophthalmoidea Fitzinger, 1826
Alopoglossidae New Family (See Appendix 2 for diagnosis)
<i>Alopoglossus</i> Boulenger, 1885
<i>Ptychoglossus</i> Boulenger, 1890
Gymnophthalmidae Fitzinger, 1826
Cercosaurinae Gray, 1838
Tribe Bachiini Colli, Hoogmoed, Cannatella, Cassimiro, Gomes, Ghellere, Nunes, Pellegrino, Salerno, Souza, and Rodrigues, 2015
<i>Bachia</i> Gray, 1845
Tribe Cercosaurini Gray, 1838
<i>Anadia</i> Gray, 1845
<i>Cercosaura</i> Wagler, 1830
<i>Echinosaura</i> Boulenger, 1890
<i>Euspondylus</i> Tschudi, 1845
<i>Macropholidus</i> Noble, 1921
<i>Neusticurus</i> , Duméril and Bibron, 1839
<i>Pantodactylus</i> , Duméril and Bibron, 1839
<i>Petracola</i> Doan and Castoe, 2005
<i>Pholidobolus</i> Peters, 1862
<i>Placosoma</i> Tschudi, 1847
<i>Potamites</i> Doan and Castoe, 2005
<i>Proctoporus</i> Tschudi, 1845
<i>Riama</i> Gray, 1858
<i>Teuchocercus</i> Fritts and Smith, 1969
Tribe Eclepodini Fitzinger, 1843
<i>Adercosaurus</i> Myers and Donnelly, 2001
<i>Amapasaurus</i> Cunha, 1970
<i>Anotosaura</i> Amaral, 1933
<i>Arthrosaura</i> Boulenger, 1885
<i>Colobosauroides</i> Cunha and Lima Verde, 1991
<i>Dryadosaura</i> Rodrigues, Freire, Pellegrino, and Sites, 2005
<i>Kaieteurosaurus</i> Kok, 2009
<i>Leposoma</i> Spix, 1825
<i>Loxopholis</i> Cope, 1869
<i>Marinussaurus</i> Peloso, Pellegrino, Rodrigues, and Ávila-Pires, 2011
<i>Pantepuisaurus</i> Kok, 2009
Gymnophthalminae Fitzinger, 1826
Tribe Gymnophthalmini Fitzinger, 1826
<i>Calyptommatius</i> Rodrigues, 1991
<i>Gymnophthalmus</i> Merrem, 1820
<i>Micrablepharus</i> Dunn, 1932
<i>Nothobachia</i> Rodrigues, 1984
<i>Procellosaurinus</i> Rodrigues, 1991
<i>Psilophthalmus</i> Rodrigues, 1991
<i>Scriptosaura</i> Rodrigues and Santos, 2008
<i>Tretioscincus</i> Cope, 1862
<i>Vanzosaura</i> Rodrigues, 1991
Tribe Heterodactylini New tribe (See Appendix 2 for diagnosis.)
<i>Caparaonia</i> Rodrigues, Cassimiro, Pavan, Curcio, Verdade, and Pellegrino, 2009
<i>Colobodactylus</i> Amaral, 1933
<i>Heterodactylus</i> Spix, 1825
Tribe Iphisini Gray, 1851
<i>Acratosaura</i> Rodrigues, Pellegrino, Dixo, Verdade, Pavan, Argolo and Sites, 2007

Table 8

(Continued)

Taxon
<i>Alexandresaurus</i> Rodrigues, Pellegrino, Dixo, Verdade, Pavan, Argolo, and Sites, 2007
<i>Colobosaura</i> Boulenger, 1887
<i>Iphisa</i> Gray, 1851
<i>Rondonops</i> Colli, Hoogmoed, Cannatella, Cassimiro, Gomes, Ghellere, Nunes, Pellegrino, Salerno, Souza, and Rodrigues, 2015
<i>Stenolepis</i> Boulenger, 1888
<i>Iphisa</i> Gray, 1851
Rhachisaurinae Pellegrino, Rodrigues, Yonenaga-Yassuda, and Sites, 2001
<i>Rhachisaurus</i> Pellegrino, Rodrigues, Yonenaga-Yassuda, and Sites, 2001
Riolaminae Kok, 2015
<i>Riolama</i> Uzzell, 1993
Teiidae Gray, 1827
Callopietinae Fitzinger, 1843
<i>Callopietes</i> Gravenhorst, 1838
Teiinae Gray, 1827
<i>Ameiva</i> Meyer, 1795
<i>Ameivula</i> Harvey, Ugueto, Gutberlet, 2012
<i>Aspidoscelis</i> Fitzinger, 1843
<i>Aurivela</i> Harvey, Ugueto, Gutberlet, 2012
<i>Cnemidophorus</i> Wagler, 1830
<i>Contomastix</i> Harvey, Ugueto, Gutberlet, 2012
<i>Dicrodon</i> Duméril and Bibron, 1839
<i>Glaucomastix</i> new genus (see Appendix 2 for diagnosis)
<i>Holcosus</i> Cope, 1862
<i>Kentropyx</i> Spix, 1825
<i>Medopheos</i> Harvey, Ugueto, Gutberlet, 2012
<i>Pholidoscelis</i> Fitzinger, 1843
<i>Teius</i> Merren, 1820
Tupinambinae Bonaparte, 1831
<i>Crocodylurus</i> Spix, 1825
<i>Dracaena</i> Daudin, 1802
<i>Salvator</i> Duméril and Bibron, 1839
“ <i>Tupinambis</i> ” Daudin, 1802

Taxon names in bold denote taxa missing in our study.

(2015) that *Riolama* is sister to a clade composed of *Rhachisaurus* and Gymnophthalminae in the sense of Pellegrino et al. (2001). Our earliest inclination was to keep the taxonomy simple and include *Rhachisaurus* and *Riolama* in Gymnophthalminae, but unassigned to previously delimited tribes. But, inasmuch as *Riolama* and *Rhachisaurus* have both been placed in monotypic subfamilies by people actively working on the group and this taxonomy is consistent with the recovered phylogeny, we retain *Rhachisaurus* in Rhachisaurinae and *Riolama* in Riolaminae as outgroups to Gymnophthalminae and consider this overall group of three subfamilies to form the sister taxon of Cercosaurinae.

Gymnophthalminae. Within this subfamily we recognize three tribes in the topology Gymnophthalmini + (Heterodactylini + Iphisini). As

mentioned above, Pellegrino et al.'s (2001) and Castoe et al.'s (2004) classifications differ with respect to the monophyly of Heterodactylini and Gymnophthalmini. Our analysis supports the monophyly of the tribes Heterodactylini and Gymnophthalmini within the subfamily Gymnophthalminae, a result congruent with Pellegrino et al.'s (2001) classification, but substantially different from that of Pyron et al. (2013) and Colli et al. (2015), presumably due to one or more of their less dense taxon sampling, less dense evidence, and less efficient alignment and tree-building methods. Additionally, the condition of the nasals (wide, divergent and in contact at midline in Heterodactylini, separated by contact between frontal and premaxillary in Gymnophthalmini) along with the shape of the interclavicle also support the monophyly of Heterodactylini and Gymnophthalmini as proposed by Pellegrino et al. (2001) (see also Rodrigues et al., 2005; and Colli et al., 2015). Contrarily, Castoe et al. (2004) found the tribe Heterodactylini to be paraphyletic with respect to Gymnophthalmini, and transferred all genera of this clade to the subfamily Gymnophthalminae, without tribal division. Similarly, Pyron et al. (2013) also found the tribe Heterodactylini to be paraphyletic. To resolve conflict among studies, Rodrigues et al. (2009) restricted Heterodactylini to *Heterodactylus*, *Colobodactylus* and *Caparaonia*, and used the tribe Iphisini to accommodate the genera *Alexandresaurus*, *Iphisia*, *Colobosaura*, *Acratosaura* and *Stenolepis*. This tribal division was also recovered by Castoe et al. (2004) and Pyron et al. (2013), and is also supported by our analysis.

Bachiini and Cercosaurinae. Another conflict between our analyses and previous studies is the position of Bachiini (*sensu* Castoe et al., 2004) and Bachiinae of Colli et al. (2015). Our analyses recovered *Bachia* as the sister of a clade formed by the ecleopodines and the cercosaurines. As such, our analyses do not support the tribe Cercosaurini of Pellegrino et al. (2001) or Cercosaurinae of Castoe et al. (2004). Pyron et al. (2013), found a well-supported relationship between the Bachiini and the clade Rhachisaurinae + Gymnophthalminae and accordingly restricted Cercosaurinae to the tribe Cercosaurini (*sensu* Castoe et al., 2004), and elevated Castoe et al.'s (2004) tribe Bachiini to the subfamily level. We here consider *Bachia* as part of the Cercosaurinae (as did Pellegrino et al., 2001), but as a tribe, Bachiini, making for three tribes within Cercosaurinae: Bachiini (for *Bachia*), Ecleopodini (largely congruent with the Ecleopodini of Pellegrino et al., 2001) and Cercosaurini (largely congruent with the Cercosaurini of Pellegrino et al., 2001). In agreement with other studies (Kohlsdorf and Wagner, 2006; Kohlsdorf et al., 2010; Galis et al., 2010), our

molecular evidence rejects the earlier classification of *Bachia* in four species groups (*bresslaui*, *dorbignyi*, *heteropa* and *flavescens*) as proposed by Dixon (1973). The distant placement of *Bachia heteropa alleni* and *B. h. trinitatis*, and *B. monodactylus monodactylus* and *B. m. parkerii* supports the existence of several species of *Bachia* that are currently considered parts of polytypic species. We therefore agree with Kohlsdorf and Wagner (2006) and consider these subspecies to be species under the names *Bachia monodactylus* and *B. parkerii* (but see Galis et al., 2010). Because our dataset lacks samples of *Bachia heteropa* subspecies other than *Bachia heteropa heteropa* we do not take taxonomic action on *B. h. alleni* and *B. h. trinitatis*.

Our results also differ in part with respect to the relationships recovered by Pellegrino et al. (2001), Castoe et al. (2004), Pyron et al. (2013) and Colli et al. (2015) for the ecleopodines [Ecleopodini of Pellegrino et al. (2001) and Ecleopodinae of Castoe et al. (2004) and Colli et al. (2015)]. These differences are expected as we sampled species of the *Leposoma scincoides* and *L. parietale* groups not included in the studies of Pellegrino et al. (2001) and Castoe et al. (2004), as well as the monotypic genera *Pantepuisaurus*, *Kaiteurosaurus* and *Marinussaurus*, lacking in the studies of Pellegrino et al. (2001), Castoe et al. (2004), Pyron et al. (2013) and Colli et al. (2015). Our analysis recovered Ecleopodinae as a monophyletic group closely related to the Cercosaurini (*sensu* Castoe et al., 2004), in agreement with Pyron et al. (2013), and in contrast to the results of Pellegrino et al. (2001), who found the ecleopodines sister to a clade containing the Cercosaurinae (*sensu* Castoe et al., 2004). Rodrigues et al. (2005, 2007b) and Colli et al. (2015) recovered the ecleopodines as a monophyletic group unrelated to the Cercosaurini based on morphological and molecular characters. Nevertheless, because of their limited taxon sampling and because of the shape of the postorbital and its contact with the post-frontal, the shape of the interclavicle and the condition of the nasals suggest a close relationship between the Ecleopodini and the Cercosaurini (*sensu* Pellegrino et al., 2001), they did not adopt the classification of Castoe et al. (2004). Our results are consistent with the recognition of Ecleopodini as a tribe within the Cercosaurinae.

Within the Ecleopodini our results differed to some extent from those inferred in previous studies (Pellegrino et al., 2001; Castoe et al., 2004; Rodrigues et al., 2005; Peloso et al., 2011; Colli et al., 2015). This was not surprising as our data set includes species lacking in previous studies. Missing in Pellegrino et al. (2001), Castoe et al. (2004) and Pyron et al. (2013) but included in our analyses are species of the genera *Marinussaurus*, *Kaiteurosaurus* and *Pantepuisaurus*, and additional species of *Leposoma* and *Arthrosaura*. We

recovered a paraphyletic *Leposoma* because species of the *L. scincoides* and the *L. parietale* groups were not recovered as sister groups. Our results, and several previous studies based on morphological (Ruibal, 1952), karyotypic (Pellegrino et al., 1999, 2003; Laguna et al., 2010) and molecular data (Pellegrino et al., 2011; Pyron et al., 2013) agree in the non-monophyly of *Leposoma*. The type species of *Leposoma* is *L. scincoides* Spix, 1825, which means that the group that retains the generic name *Leposoma* is the taxon composed of the *L. scincoides* group of Ruibal (1952), forming the sister-taxon of a group composed of *Eupleopus*, *Kaieteurosaurus*, *Pantepuisaurus*, *Colobosauroides*, *Dryadosaurus*, *Anotosaura*, *Marinussaurus* and other species incorrectly assigned to *Leposoma* and *Arthrosaura*, for which we resurrect the name *Loxopholis* Cope, 1869 “1868”. Those species formerly within *Leposoma* and now within *Loxopholis* represent the former *Leposoma parietale* group. MacCulloch and Lathrop (2001) postulated the existence of two species groups of *Arthrosaura*, one group containing the species having four supraoculars and a short body with relatively long legs [which contains *Arthrosaura guianensis*, *Arthrosaura hoogmoedi*, *Arthrosaura kockii* and *Arthrosaura testiguensis* and which Kok (2008) formally named *A. kockii* group] and the other group containing species with three supraoculars, gracile body and relatively short legs [which contains *Arthrosaura reticulata*, *A. synaptolepis*, *A. tyleri* and *A. versteegii* which Kok (2008) formally named *A. reticulata* group]. Our results do not support the *A. kockii* and *A. reticulata* species groups. To remedy this, but considering that our analyses only included four of the eight species of *Arthrosaura*, we tentatively place *A. guianensis* and *A. hoogmoedi* into *Loxopholis* and retain the remaining species of this genus in *Arthrosaura*.

Cercosaura. *Cercosaura quadrilineata* is the sister of a clade containing *Anadia mediarmidi*, *Potamites*, *Proctoporus* and the remaining *Cercosaura* species. This topology renders a paraphyletic *Cercosaura* (*sensu* Torres-Carvajal et al., 2015), in contrast to the molecular analyses of Pellegrino et al. (2001), Castoe et al. (2004) and Pyron et al. (2013) and morphological analyses of Doan (2003). *Cercosaura quadrilineata* in our TA + PA tree falls distant from the cluster of *Cercosaura* species containing the type species (*Cercosaura ocellata* Wagler, 1830). The generic name *Pantodactylus* Duméril and Bibron, 1839 is available, but the type species of this genus, *Pantodactylus d'Orbigny* Duméril and Bibron, 1839 (= *Cercosaura schreibersi*), is in a monophyletic group containing the type species of *Cercosaura*. It is possible that the name *Prionodactylus* O'Shaughnessy (1881) is available but the type species of that genus, *Cercosaura manicata* O'Shaughnessy, 1881, was not

included in our analysis. We suspect that “*Cercosaura*” *quadrilineata* will ultimately be placed in its own genus, but at present we cannot exclude the possibility that *Prionodactylus* is the appropriate assignment for this species and *Cercosaura manicata*. Until more data are available, we tentatively resurrect *Pantodactylus* to allocate *C. quadrilineata* and *C. schreibersi*.

Within Cercosaurini our analyses included the genera *Anadia*, *Echinosaura*, *Macropholidus* and *Riolama*, missing in Pellegrino et al. (2001), Castoe et al. (2004), Pyron et al. (2013) and Colli et al. (2015). These genera were placed within Cercosaurinae by Pellegrino et al. (2001) on the basis of the proposed relationships with other genera included in their analysis. As mentioned above, *Riolama* was found to be sister to the *Rhachisaurus brachylepis* + *Gymnophthalminae* clade. *Anadia* was found sister to *Potamites*, whereas *Echinosaura* was found sister to *Macropholidus*.

We recovered a paraphyletic *Cercosaura*, with all sampled species except *C. quadrilineata* forming the sister group of *Proctoporus*. *Petracola* was found to be the sister of a clade containing the genera *Potamites*, *Cercosaura*, *Anadia* and *Proctoporus*. These results differ from those of Castoe et al. (2004), who recovered the genus *Petracola* as the sister of *Proctoporus*, and from Goicoechea et al. (2012), who recovered the genus *Potamites* as the sister of *Proctoporus*.

Teiidae. The monophyly of the teiid subfamily Tupinambinae (in the sense of containing *Callopiestes*, *Crocodylurus*, *Dracaena* and *Tupinambis*) is not supported by our analyses due to the position of *Callopiestes* as the sister taxon of Tupinambinae + *Teiinae* in the sense of Harvey et al. (2012). This result is in disagreement with many previous studies (Gorman, 1970; Presch, 1974, 1983; Rieppel, 1980; Vanzolini and Valencia, 1965; Veronese and Krause, 1997; Giugliano et al., 2007; Pyron et al., 2013). Teixeira (2003), however, using a combined analysis of different morphological and ultrastructural characters, also found a paraphyletic Tupinambinae with *Callopiestes* closely related to *Teiinae*. Harvey et al. (2012) named Callopiestinae as a new subfamily for *Callopiestes* (unaware that it was previously named by Fitzinger, 1843). They also argued that the paraphyly of Tupinambinae was supported by the 12S gene analyses of Giugliano et al. (2007), despite the combined analysis of 16S and 12S sequences in that study supported the monophyly of Tupinambinae *sensu lato*. Unfortunately, Harvey et al. (2012) used *Callopiestes maculatus* to root their tree of *Teiidae*, hindering a test of the monophyly of Tupinambinae. Regardless, our analyses reveal that available sequence data support this reallocation and we therefore recognize the subfamily Callopiestinae.

Within Tupinambinae, our results did not support the novel classification of Harvey et al. (2012) for *Tupinambis*, as *Tupinambis* (in the sense of excluding

Salvator) collapsed into a polytomy with *Dracaena* and *Crocodylurus* (Fig. 2). The first revision of *Tupinambis* based on morphological data was provided by Presch (1973), who recognized only two species of the four recognized by Peters and Donoso-Barros (1970): *Tupinambis rufescens*, which includes *T. duseni* (following Burt and Burt, 1931), and *T. teguixin*, which includes *T. nigropunctatus*. This arrangement was not followed by subsequent authors (e.g. Hoogmoed, 1973; Cei, 1986). Ávila-Pires (1995) reviewed type material and available names for *T. teguixin* and rejected Presch's (1973) changes for this genus, retained the name *T. teguixin* for the populations of South America and Amazonia, and resurrected *T. merianae* to allocate the southern populations of *T. teguixin sensu* Boulenger (1885). Fitzgerald et al. (1999) first studied the phylogenetic relationships within the *Tupinambis* species using molecular data. These authors found two well-differentiated groups within this genus: the southern clade, consisting of *T. duseni*, *T. merianae* and *T. rufescens*, and the northern/Amazonian clade, formed by *T. longilineus*, *T. quadrilineatus* and *T. teguixin*. Nonetheless, Fitzgerald et al. (1999) did not test the monophyly of *Tupinambis*, as neither *Dracaena* nor *Crocodylurus* was included in their analysis.

Harvey et al. (2012), using morphological data, found the southern clade of *Tupinambis* (Fitzgerald et al., 1999) closely related to *Dracaena*, and the northern/Amazonian clade closely related to *Crocodylurus*. Accordingly, Harvey et al. (2012) resurrected *Salvator* for species of the southern clade, and retained northern/Amazonian species within *Tupinambis*. Previous phylogenetic and phenetic studies based on morphology had suggested discordant relationships between *Dracaena*, *Crocodylurus* and *Tupinambis*. Presch (1974), based on osteological data of nine macroteiid genera (including *Crocodylurus amazonicus*, *Dracaena guianensis*, *D. paraguayensis*, *Tupinambis rufescens* and *T. teguixin*), found *Dracaena* to be the sister taxon of a clade including *Crocodylurus* and *Tupinambis*. More recently, analyses by Teixeira (2003), based on sperm ultrastructural data, cranial myology, osteology, external morphology, and tongue and hemipenial characters, favoured the monophyly of *Tupinambis* (data were scored from *Tupinambis merianae*, *T. nigropunctata*, *T. rufescens* and *T. teguixin* in her analyses) and a close relationship between *Dracaena* and *Crocodylurus*. Pyron et al. (2013) molecular reconstruction recovered *Tupinambis* as paraphyletic, with one clade containing *T. duseni*, *T. merianae* and *T. rufescens* (*Salvator sensu* Harvey et al., 2012), and another clade containing *T. longilineus*, *T. quadrilineatus* and *T. teguixin* nested with *Crocodylurus amazonicus* and *Dracaena guianensis*, thus rendering a paraphyletic *Tupinambis* as outlined by Harvey et al. (2012). Our analyses also revealed that available sequence data are insufficient to fully resolve

the phylogenetic relationships between *Dracaena*, *Crocodylurus* and *Tupinambis*. Therefore, for the time being we retain the current taxonomy although we suggest that a detailed study of this group would come to interesting conclusions.

Teiinae. Within Teiinae our results further support the monophyly of cnemidophorines. In contrast, Pyron et al. (2013) rejected the monophyly of this group, as *Dicrodon guttulatus* was found in a clade with *Ameiva fuscata*. The position of *Kentropyx* in our analysis differs from Harvey et al. (2012), who found *Kentropyx* to be the sister group of the rest of Teiinae, and corroborates the results of previous molecular studies whereas *Kentropyx* is the sister group of *Cnemidophorus* (Reeder et al., 2002; Giugliano et al., 2007; Pyron et al., 2013).

Cnemidophorus. Our analyses support some changes to the classification of Harvey et al. (2012) for the polyphyletic genus *Cnemidophorus*. Previous to the resurrection of the name *Aspidoscelis* the taxonomy of this diverse group of lizards was deeply unsatisfactory and until partitioned by Reeder et al. (2002), species of *Cnemidophorus* were allocated to five species groups based on external morphology and karyology (Lowe et al., 1970). Five of these groups (*C. cozumela*, *C. deppei*, *C. sexlineatus*, *C. tessellatus* and *C. tigris* groups) include North and Central American species, whereas South American species were grouped into the *C. lemniscatus* species group. Reeder et al. (2002) employed mitochondrial DNA, allozymes and morphological data to infer the phylogenetic relationships among *Cnemidophorus* and other teiids. They concluded that *Ameiva*, *Cnemidophorus* and *Kentropyx* formed a monophyletic group, the “cnemidophorines”, and that *Cnemidophorus* was not monophyletic, with species in the *C. lemniscatus* group being more closely related to *Ameiva* and *Kentropyx* than to a North and Central American clade of *Cnemidophorus*, for which the name *Aspidoscelis* was resurrected. Reeder et al. (2002) also concluded that the *C. lemniscatus* group was paraphyletic, and identified four unrelated lineages within this clade: the *Cnemidophorus lemniscatus* complex (represented by *C. arenivagus*, *C. gramivagus*, *C. l. lemniscatus*, *C. l. splendidus* and *C. murinus* in their analysis), *C. lacertoides*, *C. longicauda* and *C. ocellifer*. More recently, Giugliano et al. (2006) used allozymes to infer the relationships between *Cnemidophorus parecis* (placed within the *ocellifer* complex by Colli et al., 2003) and other teiids. Their results fully agree with those of Reeder et al. (2002). They also found *C. parecis* closely related to *Ameiva ameiva*, a result that was also supported by the presence of a lingual sheet in *C. parecis*, a trait presumably unique to the genus

Ameiva (Presch, 1971; Giugliano et al., 2006; Arias et al., 2011a; Harvey et al., 2012). Based on these results, and on additional morphological data, Harvey et al. (2012) transferred the various species of the former *Cnemidophorus longicauda* complex (*C. longicaudus* and *C. tergoaevigatus*) to the novel genus *Aurivela*, whereas species of the *Cnemidophorus lacertoides* complex (*C. charrua*, *C. lacertoides*, *C. serranus*, *C. vacariensis*, *C. vittatus*) were placed in the novel genus *Contomastix*. Species of the *Cnemidophorus ocellifer* complex (*C. abaetensis*, *C. confusonibus*, *C. cyanurus*, *C. japalensis*, *C. littoralis*, *C. mumbuca*, *C. nativo*, *C. nigrigula*, *C. ocellifer* and *C. venetacaudus*) were also placed into the novel genus *Ameivula*, except *Cnemidophorus parecis*, which was transferred to the genus *Ameiva*. Species of the *lemniscatus* complex along with Caribbean species were retained in *Cnemidophorus*, which was split into four species groups: the *Cnemidophorus lemniscatus* group (*C. arenivagus*, *C. arubensis*, *C. cryptus*, *C. flavissimus*, *C. gramivagus*, *C. lemniscatus speuti*, *C. l. gagei*, *C. l. lemniscatus*, *C. l. splendidus*, *C. pseudoanomalus* and *C. senectus*), the *Cnemidophorus murinus* group (*C. marinus* and *C. ruthveni*), the *Cnemidophorus nigricolor* group (*C. leucopsammus*, *C. nigricolor* and *C. rostralis*) and the *Cnemidophorus vanzoi* group (with *C. vanzoi* as the only member of the group). Our analysis placed *Aurivela*, *Cnemidophorus* and *Contomastix* in different clades, supporting Harvey et al. (2012) arrangement for these genera. Nonetheless, several key taxa have not been included in our analyses (members of the *C. murinus* and *C. nigricolor* groups); thus, the monophyly of Harvey et al. (2012) *Cnemidophorus* species groups could not be assessed.

Our analyses recovered *Ameivula* as non-monophyletic as *A. abaetensis* is sister to *Cnemidophorus* + *Kentropyx*. Harvey et al. (2012) considered that the *Ameivula littoralis* subgroup of Arias et al. (2011a,b) (including *Ameivula abaetensis*, *Ameivula cyanura*, *Ameivula littoralis* and *Ameivula venetacauda*) could be related to *Ameiva* but that the phylogenetic position of this taxon should be re-assessed to test whether they should be retained in *Ameivula*, transferred to *Ameiva* or placed in a new genus. Our results do not support a relationship of the *Ameivula littoralis* subgroup (i.e. *A. abataensis*) with either *Ameiva* or *Ameivula*. To resolve the non-monophyly of *Ameivula* we erect the new genus *Glaucomastix* for the *A. littoralis* group, and propose the new combinations *Glaucomastix abaetensis*, *G. cyanura*, *G. littoralis* and *G. venetacauda* (see Appendix 2 for content and diagnosis of this new genus).

Ameiva. Our analysis supports the recognition of *Holcosus* but rejects a monophyletic *Ameiva* (*sensu*

Harvey et al., 2012). Harvey et al. (2012) found that cis-Andean (*Ameiva ameiva* and *A. bifrontata* groups) and West Indian *Ameiva* formed a monophyletic group and retained this clade within the genus *Ameiva*. They nonetheless resurrected *Holcosus* to accommodate Western and Central American species (*Holcosus anomalus*, *H. bridgesii*, *H. chaitzami*, *H. festivus*, *H. leptophrys*, *H. niceforoi*, *H. orcesi*, *H. quadrilineatus*, *H. septemlineatus* and *H. undulatus*). Pyron et al. (2013) recovered the monophyly of *Holcosus* but found *Ameiva* to be paraphyletic, as the cis-Andean *Ameiva* clade was found widely separated from the West Indian *Ameiva* clade, which was also found paraphyletic inasmuch as *Cnemidophorus lacertoides*, *C. longicaudus* and *Dicrodon guttulatus* were in an inclusive group with *Ameiva fuscata*. Our analyses recovered the monophyly of two groups within *Ameiva*, one containing cis-Andean *Ameiva* and the other containing West Indies *Ameiva* (Fig. 2). Given these results, and because *A. ameiva* (the type species of this genus) is nested with the cis-Andean *Ameiva* clade, it seems clear that the name *Ameiva* should be retained for that lineage. For the West Indies *Ameiva*, the generic name *Pholidoscelis* Fitzinger is available. Accordingly, we assign West Indies *Ameiva* to *Pholidoscelis* and propose the new combinations *Pholidoscelis atrata*, *P. auberi*, *P. cineracea*, *P. corvina*, *P. chrysolaeama*, *P. corax*, *P. dorsalis*, *P. erythrocephala*, *P. exul*, *P. fuscatus*, *P. griswoldi*, *P. lineolatus*, *P. major*, *P. maynardi*, *P. plei*, *P. polops*, *P. pluvianotatus*, *P. taenura* and *P. wetmorei*. One worrisome problem, however, is that *Pholidoscelis* was erected for *Ameiva major* (Fitzinger, 1843), a taxon that has not been included in our study, and is presumed to be extinct (Schwartz and Henderson, 1991; Hower and Hedges, 2003). Thus, the name *Pholidoscelis* is applied provisionally to this clade based on the assumed close relationship to *Pholidoscelis major* and the remaining West Indies *Ameiva* species (Hower and Hedges, 2003). Besides *P. major*, two other species of West Indies *Ameiva* were not included in our study (*P. cineracea* and *P. corvina*), and are here tentatively transferred to *Pholidoscelis* based on previous evidence. *Pholidoscelis cineracea* and *P. major* were considered to be closely related by Baskin and Williams (1966), and were placed into the Lesser Antillean clade by Hower and Hedges (2003) because of their geographical location. *Pholidoscelis corvina* seems to be indistinguishable from *P. corax* (Censky and Paulson, 1992; Hower and Hedges, 2003).

Within *Ameiva*, Harvey et al. (2012) also proposed the *A. ameiva* group (containing *A. ameiva*, *A. atrigularis*, *A. pantherina* and *A. praesignis*) and the *A. bifrontata* group (containing *A. bifrontata* and *A. provitaae*). Because of our limited taxon sampling (only *A. ameiva* and *A. bifrontata* were represented in our study), the monophyly of these groups was not

assessed. Nevertheless, this division presents some weakness. First, our knowledge of the phylogenetic relationships among species of *Ameiva* is incomplete. On the other hand, the morphological variation within these groups has not been adequately studied, as the *Pholidoscelis* species that Harvey et al. (2012) considered to be part of *Ameiva* were included in their analysis of such groups. In addition, *A. provittae* is a possible synonym of *A. bifrontata* as the characters thought to be unique to diagnose this species (such as a red snout) are present in different populations of *A. bifrontata* (Rivas et al., 2012). Therefore, it is possible that the *A. bifrontata* group is a monotypic group. Because of our limited knowledge and uncertainty regarding the morphological limits of these species and because the phylogenetic relationships within *Ameiva* are not sufficiently clarified, we do not recognize species groups within this genus.

Pholidoscelis. Within *Pholidoscelis*, our analyses do not support the species groups proposed by Harvey et al. (2012). Hower and Hedges (2003) first named four species groups for West Indies species based on their phylogenetic results: the *P. auberi* group (*P. auberi* and *P. dorsalis*); the *P. exsul* group (*P. exsul*, *P. polops* and *P. wetmorei*); the *P. lineolata* group (*P. chrysolaema*, *P. lineolata*, *P. maynardi* and *P. taeniura*); and the *P. plei* group (*P. atrata*, *P. cineracea*, *P. corax*, *P. corvina*, *P. erythrocephala*, *P. fuscata*, *P. griswoldi*, *P. major*, *P. plei* and *P. pluvianotata*). Based on the convention that the oldest species name must be chosen as the group or series name, Harvey et al. (2012) renamed Hower and Hedges's *P. plei* group as the *P. erythrocephala* group. They also placed the *P. auberi*, *P. exul* and *P. lineolata* groups in the *P. dorsalis* group based on purported synapomorphies, and *A. lineolata*, *A. maynardi* and *A. wetmorei* were included into the new *Ameiva lineolata* series based on “unequivocal synapomorphies”. Nonetheless, the *P. dorsalis* group and the *P. lineolata* series are clearly non-monophyletic (Hower and Hedges, 2003; Pyron et al., 2013; this study). Thus, we do not recognize these species groups within *Pholidoscelis*, and follow the classification proposed by Hower and Hedges (2003).

Pholidoscelis chrysolaema is a polytypic taxon composed of 16 subspecies (Uetz and Hošek, 2015) distributed throughout the island of Hispaniola in the West Indies (Gifford et al., 2004). Some authors (Schwartz and Henderson, 1991; Harvey et al., 2012) have noted that there is considerable variation among populations of *P. chrysolaema* and that it probably contains more than one species (Harvey et al., 2012). Schwartz and Klinikowski (1966) noted that the coloration and pattern of *P. chrysolaema chrysolaema* and *P. c. umbratilis* were strikingly different. Among other

differences, these authors found that *P. c. umbratilis* was smaller than *P. c. chrysolaema*, and it tends to have 10 versus 12 transverse rows of ventrals. Also, *P. c. chrysolaema* and *P. c. umbratilis* differ in the number of femoral pores, with a mean of 43.7 mm in *P. chrysolaema* and 35.6 mm in *P. umbratilis*. As our analyses do not recover the monophyly of *P. chrysolaema* and *P. c. umbratilis* is nested with *P. taeniura*, *P. lineolata* and *P. maynardi*, we consider *P. c. umbratilis* to be a distinct species.

Aspidoscelis. Congruent with Reeder et al. (2002) our analysis supported the monophyly of the *A. deppii*, *A. sexlineata* and *A. tigris* groups. Our analysis recovered the *A. sexlineata* group as the sister of the *A. tigris* group, although Reeder et al. (2002) recovered the *A. deppii* group as sister to the *A. tigris* group. A close relationship between the *A. sexlineata* and *A. tigris* groups was also recovered by Lowe et al. (1970) based on karyotype analysis and by Moritz et al.'s (1992) mitochondrial restriction site analysis, so at this juncture we think that denser taxon sampling might change our results to theirs. Within the *A. sexlineata* group, our analysis did not recover the monophyly of the samples of *A. sexlineata*, as *A. inornata* is nested within those of *A. sexlineata*. Reeder et al. (2002) also found a close relationship between *A. inornata* and *A. sexlineata*, but with *A. inornata* as the sister of *A. s. sexlineata* + *A. s. viridis*. We provisionally retain the older taxonomy, noting that both *A. sexlineata* and *A. inornata* as currently understood probably involve more than one lineage.

Conclusions

Previous attempts to resolve phylogenetic relationships of the gymnophthalmoid lizards were hampered by limited taxonomic sampling, limited data sets and use of apomorphic morphological characters. The result was a poorly resolved picture of their relationships. This study, relying on molecular data, represents the first comprehensive test of previous hypotheses of relationships within Gymnophthalmoidea based on a global analysis of the group, and provides a general framework for the study of its evolution. Our analyses also shed light on the effect that optimality criteria, strategies of alignment and treatments of evidence have on tree topology. Despite much ongoing discussion on the relative merit of methods and the effect of missing data on them, our parsimony and maximum-likelihood analyses under different strategies of alignment and treatments of evidence (indels) produced almost completely resolved trees of gymnophthalmoid lizards despite 86% of missing data. All analyses agree in a majority of

clades, although they differ from each other in unique ways, suggesting that neither the tree optimality measures, alignment methods nor treatment of indels alone can explain all the differences. Interestingly, tree-alignment under parsimony produced the shortest trees and the most similar to the maximum-likelihood tree, in terms of both number of clades shared, parsimony cost and likelihood scores. Based on these results we propose a new classification for Gymnophthalmoidea that better reflects hypothesized relationships: Alopoglossidae + (Gymnophthalmidae + Teiidae). Nonetheless, in spite of this advance in gymnophthalmoid systematics, many inner details of their relationships remain contentious. Among the greatest deficiencies in our understanding of the phylogenetic relationships of parts of the gymnophthalmoids are those of several species-rich genera, such as *Alopoglossus*, *Ameiva*, *Anadia*, *Cnemidophorus*, *Euspondylus* and *Pholidobolus*, as well as some monotypic genera (e.g. *Amapasaurus*, *Macropholidus*, *Medopheos*, *Scriptosaura*, *Teuchocercus*). Inclusion of unrepresented groups, such as the large but extinct gymnophthalmoid Polyglyphanodontidae, and broader taxon sampling of poorly represented groups will be a key task for the future. Also, an extensive, well-researched non-molecular data set is a major void in gymnophthalmoid systematics. A combined analysis of molecular and morphological data, including all relevant fossils, will help to understand how morphological characters evolved in this group of lizards, and would contribute to improve the current classification of Gymnophthalmoidea.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1 Similarity-alignment + parsimony excluding length variation as evidence: strict consensus of 129 most parsimonious trees of 65 218 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa.

Fig. S2 Similarity-alignment + parsimony excluding length variation as evidence: strict consensus of 129 most parsimonious trees of 65 218 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa.

Fig. S3 Similarity-alignment + parsimony excluding length variation as evidence: strict consensus of 129 most parsimonious trees of 65 218 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa.

Fig. S4 Similarity-alignment + parsimony excluding length variation as evidence: strict consensus of 129 most parsimonious trees of 65 218 steps for a dataset of 34 296 aligned sites of mitochondrial and nuclear DNA showing relationships among 241 terminals of Teioidea and 58 outgroup taxa.

Table S1 GenBank accession numbers for loci and terminals of Gymnophthalmoidea and outgroups sampled in this study.

Appendix 1

GenBank sequence re-identification and updating of generic names for sequences used in this study

Terminal name	Original name and rationale for re-identification
<i>Acratosaura mentalis</i>	<i>Colobosaura mentalis</i> (MRT 906448) from Pellegrino et al. (2001) is <i>Acratosaura mentalis</i> according to Rodrigues et al. (2007b).
<i>Alexandresaurus camacan</i>	<i>Colobosaura</i> spn. (MD 1106), from Pellegrino et al. (2001) is <i>Alexandresaurus camacan</i> according to Rodrigues et al. (2009).
<i>Ameiva chrysolema</i>	<i>Ameiva leberi</i> (SBH 194764) is now a junior synonym of <i>Ameiva chrysolema</i> according to Hower and Hedges (2003)
<i>Aspidoscelis burti burti</i>	<i>Aspidoscelis burti burti</i> (AMNH R-131433) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus burti burti</i>
<i>Aspidoscelis burti griseocephala</i>	<i>Aspidoscelis burti griseocephala</i> (AMNH R-131442) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus burti griseocephalus</i>
<i>Aspidoscelis burti strictogramma</i>	<i>Aspidoscelis burti strictogramma</i> (AMNH R-126768) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus strictogrammus</i>
<i>Aspidoscelis costata costata</i>	<i>Aspidoscelis costata costata</i> (MZFC 811) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus costatus costatus</i> .
<i>Aspidoscelis deppii</i>	<i>Aspidoscelis deppii</i> (MZFC 7046) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus deppii</i>
<i>Aspidoscelis gularis gularis</i>	<i>Aspidoscelis gularis gularis</i> (TNHC 5322) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus gularis gularis</i>
<i>Aspidoscelis gularis scalaris</i>	<i>Aspidoscelis gularis scalaris</i> (AMNH R-129175) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus gularis scalaris</i>
<i>Aspidoscelis gularis septemvittata</i>	<i>Aspidoscelis gularis septemvittata</i> (TNHC 53902) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus gularis septemvittatus</i>
<i>Aspidoscelis guttata</i>	<i>Aspidoscelis guttata</i> (MZFC 7044) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus guttatus</i>
<i>Aspidoscelis hyperythra</i>	<i>Aspidoscelis hyperythra</i> (RWM 1025) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus hyperythrus</i> .
<i>Aspidoscelis inornata</i>	<i>Aspidoscelis inornata</i> (AMNH R-126861) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus inornatus</i>
<i>Aspidoscelis sexlineata sexlineata</i>	<i>Aspidoscelis sexlineata sexlineata</i> (LSUMZ 749566) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus sexlineatus sexlineatus</i>
<i>Aspidoscelis sexlineata viridis</i>	<i>Aspidoscelis sexlineata viridis</i> (AMNH R-126901) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus sexlineatus viridis</i>
<i>Aspidoscelis tigris aethiops</i>	<i>Aspidoscelis tigris aethiops</i> (AMNH R-131432) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus tigris aethiops</i>
<i>Aspidoscelis tigris marmorata</i>	<i>Aspidoscelis tigris marmorata</i> (AMNH R-127072) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus tigris marmoratus</i>
<i>Aspidoscelis tigris maxima</i>	<i>Aspidoscelis tigris maxima</i> (LACM 128251) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus tigris maximus</i>
<i>Aspidoscelis tigris punctilinealis</i>	<i>Aspidoscelis tigris punctilinealis</i> (AMNH R-127052) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus tigris punctilinealis</i>
<i>Aspidoscelis tigris septentrionalis</i>	<i>Aspidoscelis tigris septentrionalis</i> (AMNH R-136792) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus tigris septentrionalis</i>
<i>Aspidoscelis tigris tigris</i>	<i>Aspidoscelis tigris tigris</i> (LVT 00007) generated by Reeder et al. (2002) is labelled in GenBank as <i>Cnemidophorus tigris tigris</i> .
<i>Caparaonia itaiquara</i>	<i>Caparaonia itaiquara</i> (MTR 10852) from Rodrigues et al. (2009) and Nunes et al. (2012) is labelled as <i>Gymnophthalmidae</i> sp. in GenBank
<i>Cercosaura argulus</i>	<i>Prionodactylus argulus</i> (LSUMZ H12591) from Pellegrino et al. (2001) correspond to <i>Cercosaura argulus</i> according to Doan (2003). This species and <i>C. oshaughnessyi</i> are recognized as different by Torres-Carvajal et al. (2015)
<i>Cercosaura eigenmanni</i>	<i>Prionodactylus eigenmanni</i> (MFE 976979) from Pellegrino et al. (2001) corresponds to <i>Cercosaura eigenmanni</i> according to Doan (2003)
<i>Cercosaura oshaughnessyi</i>	<i>Prionodactylus oshaughnessyi</i> (LSUMZ H13584) from Pellegrino et al. (2001) is <i>Cercosaura oshaughnessyi</i> according to Doan (2003)
<i>Cercosaura quadrilineata</i>	<i>Pantodactylus quadrilineatus</i> (LG 936) from Pellegrino et al. (2001) corresponds to <i>Cercosaura quadrilineata</i> according to Doan (2003)
<i>Cercosaura schreibersii albostrigatus</i>	<i>Pantodactylus schreibersii albostrigatus</i> (LG 1168) from Pellegrino et al. (2001) correspond to <i>Cercosaura schreibersii albostrigatus</i> according to Doan (2003)
<i>Cercosaura schreibersii schreibersii</i>	<i>Pantodactylus schreibersii schreibersii</i> (LG 927) from Pellegrino et al. (2001) corresponds to <i>Cercosaura schreibersii schreibersii</i> according to Doan (2003)

Appendix 1

(Continued)

Terminal name	Original name and rationale for re-identification
<i>Cnemidophorus splendidus</i>	<i>Cnemidophorus lemniscatus splendidus</i> (AMNH R-142592) of Reeder et al. (2002) is now recognized as a distinct species, <i>Cnemidophorus splendidus</i> , according to McCranie and Hedges (2013)
<i>Dryadosaura nordestina</i>	<i>Anotosaura</i> spn. (MRT 05060) from Pellegrino et al. (2001) is <i>Dryadosaura nordestina</i> according to Rodrigues et al. (2005).
<i>Echinosaura sulcarostrum</i>	<i>Neusticurus</i> sp. (ROM 22892) from Fu (2000) is <i>Echinosaura sulcarostrum</i> according to Donnelly et al. (2006) and Kok et al. (2012)
<i>Eutropis macularia</i>	<i>Eutropis macularia</i> (ZMK 77753) from Mausfeld et al. (2000) is labelled in GenBank as <i>Mabuya macularia</i> due to a generic shift
<i>Macropholidus annectens</i>	<i>Macropholidus annectens</i> (QCAZ 11120) generated by Torres-Carvajal and Mafla-Endara (2013) is labelled in GenBank as <i>Pholidobolus annectens</i>
<i>Macropholidus huancabambae</i>	<i>Macropholidus huancabambae</i> (CORBIDI 10492) generated by Torres-Carvajal and Mafla-Endara (2013) is labelled in GenBank as <i>Pholidobolus huancabambae</i>
<i>Namazonurus namaquensis</i>	<i>Cordylus namaquensis</i> (CAS 223964 and EU116507) from Whiting et al. (2003) and J. Pramuk et al. (unpubl. data) is now <i>Namazonurus namaquensis</i> (<i>sensu</i> Stanley et al., 2011)
<i>Petracola ventrimaculatus</i>	<i>Proctoporus ventrimaculatus</i> (KU 219838) of Castoe et al. (2004) is <i>Petracola ventrimaculatus</i> according to Doan and Castoe (2005)
<i>Potamites ecleopus</i>	<i>Neusticurus ecleopus</i> (MRT 0472) of Pellegrino et al. (2001) is <i>Potamites ecleopus</i> according to Doan and Castoe (2005)
<i>Potamites strangulatus</i>	<i>Neusticurus strangulatus</i> (KU 21677) of Castoe et al. (2004) is <i>Potamites strangulatus</i> according to Doan and Castoe (2005)
<i>Proctoporus bolivianus</i> Ca1	<i>Proctoporus</i> sp. (UTA R-52945) from Doan et al. (2005) is a unnamed species referred to as <i>Proctoporus bolivianus</i> Ca1 by Goicoechea et al. (2012)
<i>Proctoporus bolivianus</i> Ca2	<i>Proctoporus bolivianus</i> (AMNH R-150695) from Doan et al. (2005) is a unnamed species referred to as <i>Proctoporus bolivianus</i> Ca2 by Goicoechea et al. (2012)
<i>Proctoporus carabaya</i>	<i>Proctoporus bolivianus</i> Ca4 (MHNC 5429) from Goicoechea et al. (2012) is <i>Proctoporus carabaya</i> according to Goicoechea et al. (2013).
<i>Proctoporus iridescens</i>	<i>Proctoporus bolivianus</i> Ca3 (MHNC 5417) from Goicoechea et al. (2012) is <i>Proctoporus iridescens</i> according to Goicoechea et al. (2013)
<i>Proctoporus kiziriani</i>	<i>Proctoporus bolivianus</i> Ca5 (MHNC 4751) from Goicoechea et al. (2012) is <i>Proctoporus kiziriani</i> according to Goicoechea et al. (2013)
<i>Proctoporus lacertus</i>	<i>Proctoporus bolivianus</i> (UTA R-51487) of Doan and Castoe (2003) is <i>Proctoporus lacertus</i> according to Goicoechea et al. (2013).
<i>Riama cashcaensis</i>	<i>Proctoporus cashcaensis</i> (KU 217205) of Castoe et al. (2004) is <i>Riama cashcaensis</i> according to Doan and Castoe (2005).
<i>Riama colomaromani</i>	<i>Proctoporus colomaromani</i> (KU 217209) of Castoe et al. (2004) is <i>Riama colomaromani</i> according to Doan and Castoe (2005)
<i>Riama orcesi</i>	<i>Proctoporus orcesi</i> (KU 221772) of Castoe et al. (2004) is <i>Riama orcesi</i> according to Doan and Castoe (2005)
<i>Riama simotera</i>	<i>Proctoporus simotera</i> (KU 217207) of Castoe et al. (2004) is <i>Riama simotera</i> according to Doan and Castoe (2005)
<i>Riama unicolor</i>	<i>Proctoporus unicolor</i> (KU 217211) of Castoe et al. (2004) is <i>Riama unicolor</i> according to Doan and Castoe (2005)
<i>Smaug warreni</i>	<i>Cordylus warreni</i> (NC_005962) from Kumazawa and Endo (2004) is now <i>Smaug warreni</i> according to Stanley et al. (2011)
<i>Smaug warreni depressus</i>	<i>Cordylus warreni depressus</i> (DQ24903) from Daniels et al. (2006) is now <i>Smaug warreni depressus</i> according to Stanley et al. (2011)
<i>Trachylepis quinquetaeniata</i>	<i>Mabuya quinquetaeniata</i> (EU108028) from J. Pramuk et al. (unpublished) is now <i>Trachylepis quinquetaeniata</i> (<i>sensu</i> Bauer, 2003). <i>Trachylepis quinquetaeniata</i> from Wiens et al. (2012) is labelled in GenBank as <i>Mabuya quinquetaeniata</i> , although Wiens' generic usage is correct

Appendix 2

Taxonomy of Gymnophthalmoidea

SUPERFAMILY: Gymnophthalmoidea Fitzinger, 1826. Content: 3 families, 65 genera, 405 species.

FAMILY: Alopoglossidae New Family.¹

Type genus: *Alopoglossus* Boulenger, 1885.

Diagnosis: from other gymnophthalmoids (from Presch, 1980), alopoglossids can be distinguished by having: (i) an open Meckel's groove (closed in other genera except for *Gymnophthalmus* and *Heterodactylus*); (ii) have a tubular frontal bone (flanged in *Gymnophthalmus* and *Heterodactylus*).

***Alopoglossus* Boulenger, 1885.** Content: *A. angulatus* (Linnaeus, 1758); *A. atriventris* Duellman, 1973; *A. buckleyi* (O'Shaughnessy, 1881); *A. copii* Boulenger, 1885; *A. festae* Peracca, 1904; *A. lehmanni* Ayala and Harris, 1984; *A. viridiceps* Torres-Carvajal, 2014.

***Ptychoglossus* Boulenger, 1890.** Content: *P. bicolor* (Werner, 1916); *P. bilineatus* (Boulenger, 1890); *P. brevifrontalis* Boulenger, 1912; *P. danieli* Harris, 1994; *P. eurylepis* Harris and Rueda, 1985; *P. festae* (Peracca, 1896); *P. gorgonae* Harris, 1994; *P. grandisquamatus* Rueda, 1985; *P. kugleri* Roux, 1927; *P. myersi* Harris, 1994; *P. nicefori* (Loveridge, 1929); *P. plicatus* (Taylor, 1949); *P. romaleos* Harris, 1994; *P. stenolepis* (Boulenger, 1908); *P. vallisensis* Harris, 1994.

FAMILY: Gymnophthalmidae Fitzinger, 1826.

SUBFAMILY: Cercosaurinae Gray, 1838

TRIBE: Bachiini Colli et al., 2015.

***Bachia* Gray, 1845.** Content: *B. barboursi* Burt and Burt, 1931; *B. bicolor* (Cope, 1896); *B. bresslaui* (Amaral, 1935); *B. cacerensis* Castrillon and Strussman, 1998; *B. didactyla* Freitas, Strüssmann, Carvalho, Kawashita-Ribeiro, and Mott, 2011; *B. dorbignyi* (Duméril and Bibron, 1839); *B. flavescens* (Bonnaterre, 1789); *B. geraldista* Teixeira Jr., Recoder, Camacho, Sena, Navas, and Rodrigues, 2013; *B. guianensis* Hoogmoed and Dixon, 1977; *B. heteropa* (Wiegmann, 1856); *B. huallagana* Dixon, 1973; *B. intermedia* Noble, 1921; *B. micromela* Rodrigues, Pavan, and Curcio, 2007; *B. monodactylus* (Daudin, 1802); *B. oxyrhina* Rodrigues, Camacho, Nunes, Recoder, Teixeira Jr., Valdujo, Ghellere, Mott, and Nogueira, 2008; *B. pallidiceps* (Cope, 1862); *B. panoplia* Thomas, 1965; *B. parkeri* Donoso-Barros, 1968; *B. peruana* (Werner, 1901); *B. psammophila* Rodrigues, Pavan, and Curcio, 2007; *B. pyburni* Kizirian and McDiarmid, 1998; *B. scaea* Teixeira Jr., Dal Vecchio, Nunes, Mollo-Neto, Lobo, Storti, Gaiga, Dias and Rodrigues, 2013; *B. scolecoides* Vanzolini, 1961; *B. talpa* Ruthven, 1925; *B. trisanale* (Cope, 1868).

TRIBE: Cercosaurini Gray, 1838.

***Anadia* Gray, 1845.** Content: *A. altaserria* Harris and Ayala, 1987; *A. antioquensis* Arredondo, 2013; *A. bitaeniata* Boulenger, 1903; *A. blakei* Schmith, 1932; *A. bogotensis* (Peters, 1863); *A. brevifrontalis* (Boulenger, 1903); *A. bumanguesa* Rueda-Almonacid and Caicedo, 2004; *A. escalerae* Myers, Rivas and Jadin, 2009; *A. hobarti* La Marca and García-Pérez, 1990; *A. marmorata* (Gray, 1846); *A. mcDiarmidi* Kok and Rivas, 2011; *A. ocellata* Gray, 1845; *A. pampilonensis* Dunn, 1944; *A. pariaensis* Rivas, La Marca and Oliveros, 1999; *A. petersi* Oftedal, 1974; *A. pulchella* Ruthven, 1926; *A. rhombifera* (Günther, 1859); *A. steyeri* Nieden, 1914; *A. vittata* Boulenger, 1913.

***Cercosaura* Wagler, 1830.** Content: *C. argulus* Peters, 1863; *C. bassleri*, Ruibal, 1952; *C. eigenmanni* (Griffin, 1917); *C. hypnoides* Doan and Lamar, 2012; *C. manicata* O'Shaughnessy, 1881; *C. nigroventris* (Gorzula and Senaris, 1999); *C. ocellata* Wagler, 1830;

C. oshaughnessyi (Boulenger, 1885); *C. parkeri* (Ruibal, 1952); *C. phelpsonum* (Lancini, 1968); *C. steyeri* (Tedesco, 1998).

***Echinosaura* Boulenger, 1890.** Content: *E. brachycephala* Köhler, Böhme, and Schmitz, 2004; *E. horrida* Boulenger, 1890; *E. orcesi* Fritts, Almendáriz, and Samec, 2002; *E. palmeri* Boulenger, 1911; *E. panamensis* Barbour, 1924; *E. sulcarostrum* Donnelly et al., 2006.

Genus *Euspondylus* Tschudi, 1845. Content: *E. acutirostris* (Peters, 1863); *E. auyanensis* Myers, Rivas and Jadin, 2009; *E. caideni* Köhler, 2003; *E. guentheri* (O'Shaughnessy, 1881); *E. josyi* Köhler, 2003; *E. maculatus* Tschudi, 1845; *E. monsumum* Mijares-Urrutia, Señaris, and Arends, 2001; *E. nellycarrillae* Köhler and Lehr, 2004; *E. oreades* Chávez, Siu-Ting, Duran, and Venegas, 2011; *E. Paxcorpus* Doan and Adams, 2015; *E. rahmi* (De Grijis, 1936); *E. simonsii* Boulenger, 1901; *E. spinalis* (Boulenger, 1911).

***Macropholidus* Noble, 1921.** Content: *M. annectens* (Parker, 1930), *M. ataktolepis* Cadle and Chuna, 1995; *M. huancabambae* (Reeder, 1996); *M. ruthveni* Noble, 1921.

***Neusticurus* Duméril and Bibron, 1839.** Content: *N. bicarinatus* (Linnaeus, 1758); *N. medemi* Dixon and Lamar, 1981; *N. racenisi* Roze, 1958; *N. rudis* Boulenger, 1900; *N. tatei* (Burt and Burt, 1931).

***Pantodactylus* Dumeril and Bibron, 1839.** Content: *P. quadrilineatus* (Boettger, 1876); *P. schreibersii* (Wiegmann, 1834).

***Petracola* Doan and Castoe, 2005.** Content: *P. angustisoma* Echevaría and Venegas, 2015; *P. labioocularis* (Köhler and Lehr, 2004); *P. ventrimaculatus* (Boulenger, 1900); *P. waka* Kizirian, Bayefsky-Anand, Eriksson, Minh, and Donnelly, 2008.

***Pholidobolus* Peters, 1863.** Content: *P. affinis* (Peters, 1863); *P. anomalous* Müller, 1923; *P. dicra* (Uzzell, 1973); *P. hillisi* Torres-Carvajal, Venegas, Lobos, Mafla-Endara, and Nunes, 2014; *P. macbrydei* Montanucci, 1973; *P. montium* (Peters, 1863); *P. prefrontalis* Montanucci, 1973; *P. vertebralis* (O'Shaughnessy, 1879).

***Placosoma* Tschudi, 1847.** Content: *P. cipoense* Cunha, 1966; *P. cordylinum* Fitzinger, 1847; *P. glabellum* (Peters, 1870).

***Potamites* Doan and Castoe, 2005.** Content: *P. apodemus* (Uzzell, 1966); *P. cochraniae* (Burt and Burt, 1931); *P. ecleopus* (Cope, 1876); *P. erythrochalaris* Chavez and Catenazzi, 2014; *P. flavogularis* Altamirano-Benavides, Zaher, Lobo, Grazziotin, Nunes, and Rodrigues, 2013; *P. juruazensis* (Avila-Pires and Vitt, 1998); *P. monticola* Chávez and Vásquez, 2012; *P. ocellatus* (Sinitin, 1930); *P. strangulatus* (Cope, 1868).

***Proctoporus* Tschudi, 1845.** Content: *P. bolivianus* Werner, 1910; *P. carabaya* Goicoechea et al., 2013; *P. cephalolineatus* García-Pérez and Yustiz, 1995; *P. chasqui* (Chávez, Siu-Ting, Durán, and Venegas, 2011); *P. guentheri* (Boettger, 1891); *P. iridescens* Goicoechea et al., 2013; *P. kiziriani* Goicoechea et al., 2013; *P. lacertus* (Stejneger, 1913); *P. machupicchu* Mamani, Goicoechea, and Chaparro, 2015; *P. pachyurus* Tschudi, 1845; *P. succullucu* Doan and Castoe, 2003; *P. unsaaca* Doan and Castoe, 2003; *P. xestus* (Uzzell, 1969).

***Riama* Gray, 1858.** Content: *R. achlyens* (Uzzell, 1958); *R. afrania* (Arredondo and Sánchez-Pacheco, 2010); *R. anatoloros* (Kizirian, 1996); *R. aurea* Sánchez-Pacheco, Aguirre-Penafiel, and Torres-Carvajal, 2012; *R. balneator* (Kizirian, 1996); *R. cashcaensis* (Kizirian and Coloma, 1991); *R. colomaromani* (Kizirian, 1996); *R. columbiana* (Andersson, 1914); *R. crypta* Sánchez-Pacheco, Kizirian, and Nunes, 2011; *R. hyposticta* (Boulenger, 1902); *R. inanis* (Doan and Schargel, 2003); *R. kiziriani* (Sánchez-Pacheco, Aguirre-Penafiel, and Torres-Carvajal, 2012); *R. labionis* (Kizirian, 1996); *R. laevis* (Boulenger, 1908); *R. laudahnae* (Köhler and Lehr, 2004); *R. luctuosa* (Peters, 1863); *R. meleagris* (Boulenger, 1885); *R. oculata* (O'Shaughnessy, 1879); *R. orcesi* (Kizirian, 1995); *R. petrorum* (Kizirian, 1996); *R. raneyi* (Kizirian, 1996); *R. rhodogaster* (Rivas, Schargel, and Meik, 2005); *R. shrevei* (Parker, 1935); *R. simotera* (O'Shaughnessy, 1879); *R. stellae* (Sánchez-Pacheco, 2010); *R. stigmatoral* (Kizirian, 1996); *R. striata* (Peters, 1863); *R. unicolor* Gray, 1858; *R. vespertina*

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(Kizirian, 1996); *R. vieta* (Kizirian, 1996); *R. yumborum* Aguirre-Penafiel, Torres-Carvajal, Sales Nunes, Peck, and Maccocock, 2014.

Teuchocercus Fritts and Smith, 1969. Content: *T. keyi* Fritts and Smith, 1969.

TRIBE: Ecleopodini Fitzinger, 1843.

Adercosaurus Myers and Donnelly, 2001. Content: *A. vixadnexus* Myers and Donnelly, 2001.

Amapasaurus Cunha, 1970. Content: *A. tetradactylus* Cunha, 1970.

Anotosaura Amaral, 1933. Content: *A. collaris* Amaral, 1933; *A. vanzolinia* Dixon, 1974.

Arthrosaura Boulenger, 1885. Content: *A. kockii* (van Lidth de Jeude, 1904); *A. montigena* Myers and Donnelly, 2008; *A. reticulata* (O'Shaughnessy, 1881); *A. synaptolepis* Donnelly, McDiarmid and Myers, 1992; *A. testigenis* Gorzula and Señaris, 1999; *A. tyleri* (Burt and Burt, 1931); *A. versteegii* van Lidth de Jeude, 1904.

Colobosauroides Cunha and Lima Verde, 1991. Content: *C. carvalhoi* Soares and Caramaschi, 1998; *C. cearensis* Cunha and Lima Verde, 1991.

Dryadosaura Rodrigues, Xavier Freire, Pellegrino and Sites, 2005. Content: *D. nordestina* Rodrigues, Xavier Freire, Pellegrino and Sites, 2005.

Ecleopos Duméril and Bibron, 1839. Content: *Ecleopos gaudicau-dii* Duméril and Bibron, 1839.

Kaiteurosaurus Kok, 2005. Content: *K. hindsii* Kok, 2005.

Leposoma Spix, 1825. Content: *L. annectans* Ruibal, 1952; *L. baturitensis* Rodrigues and Borges, 1997; *L. nanodactylus* Rodrigues, 1997; *L. puk* Rodrigues, Dixo, Pavan and Verdade, 2002; *L. sinopollex* Rodrigues, Teixeira Jr., Recoder, Dal Vechio, Damasceno and Pellegrino, 2013; *L. scincoides* Spix, 1825.

Loxopholis Cope, 1869 “1868”.² Content: *L. caparensis* (Esqueda, 2005), **comb. nov.**; *L. ferreirai* (Rodrigues and Avila-Pires, 2005), **comb. nov.**; *L. guianense* (Ruibal, 1952), **comb. nov.**; *L. guianensis* (MacCulloch, 2001), **comb. nov.**; *L. hexalepis* **comb. nov.** (Ayala and Harris, 1982); *L. ioanna* (Uzzell and Barry, 1971), **comb. nov.**; *L. hoogmoedi* (Kok, 2008) **comb. nov.**; *L. osvaldoi* (Ávila-Pires, 1995), **comb. nov.**; *L. parietalis* (Cope, 1885), **comb. nov.**; *L. percarinatum* (Müller, 1923), **comb. nov.**; *L. rugiceps* (Cope, 1869), **comb. nov.**; *L. snethlageae* (Ávila-Pires, 1995), **comb. nov.**; *L. southi* (Ruthven and Gaige, 1924), **comb. nov.**

Marinussaurus Peloso et al., 2011. Content: *M. curupira* Peloso et al., 2011.

Pantepuisaurus Kok, 2009. Content: *P. rodriguessi* Kok, 2009.

SUBFAMILY: Gymnophthalminae Fitzinger, 1826.

TRIBE: Gymnophthalmini Fitzinger, 1826.

Calyptommatius Rodrigues, 1991. Content: *C. confusionibus* Rodrigues, Zaher, and Curcio, 2001; *C. leirolepis* Rodrigues, 1991; *C. nicterus* Rodrigues, 1991; *C. sinebrachiatus* Rodrigues, 1991.

Gymnophthalmus Merrem, 1820. Content: *G. cryptus* Hoogmoed, Cole, and Ayarzagüena, 1992; *G. leucomystax* Vanzolini and Carvalho, 1991; *G. lineatus* (Linnaeus, 1758); *G. pleei* Bocourt, 1881; *G. speciosus* (Hallowell, 1861); *G. underwoodi* Grant, 1958; *G. vanzoi* Carvalho, 1999.

Micrablepharus Dunn, 1932. Content: *M. atticolus* Rodrigues, 1996; *M. maximiliani* (Reinhardt and Lütken, 1862).

Nothobachia Rodrigues, 1984. Content: *N. ablephara* Rodrigues, 1984.

Procellosaurinus Rodrigues, 1991. Content: *P. erythrocerus* Rodrigues, 1991; *P. tetradactylus* Rodrigues, 1991.

Psilophthalmus Rodrigues, 1991. Content: *P. paeminosus* Rodrigues, 1991.

Scriptosaura Rodrigues and Santos, 2008. Content: *S. catimbau* Rodrigues and Santos, 2008.

Tretioscincus Cope, 1862. Content: *T. agilis* (Ruthven, 1916); *T. bifasciatus* (Duméril, 1851); *T. oriximinensis* Ávila-Pires, 1995.

Vanzosaura Rodrigues, 1991. Content: *V. multiscutatus* (Amaral, 1933); *V. rubricauda* (Boulenger, 1902); *V. savanicola* Recoder, Werneck, Texeira, Colli, Sites, and Rodrigues, 2014.

TRIBE: Heterodactylini NEW TRIBE.

Type genus: *Heterodactylus* Spix, 1825.

Diagnosis: Defined by the presence of opened supratemporal fenestra, a narrow postorbital covering the postfrontal, and the absence of lateral expansion on parietal bones (from Rodrigues et al., 2009).

Caparaonia Rodrigues et al., 2009. Content: *C. itaiquara* Rodrigues et al., 2009.

Colobodactylus Amaral, 1933. Content: *C. dalcyanus* (Vanzolini and Ramos, 1977); *C. taunayi* Amaral, 1933.

Heterodactylus Spix, 1825. Content: *H. imbricatus* Spix, 1825; *H. hundi* Reinhardt and Lütken, 1862; *H. septentrionalis* Rodrigues, Freitas, and Silva, 2009.

TRIBE: Iphisini Gray, 1851.

Acratosaura Rodrigues, Pellegrino, Dixo, Verdade, Pavan, Argolo and Sites, 2007. Content: *A. mentalis* (Amaral, 1933); *A. spinosa* Rodrigues, Cassimiro, Freitas and Silva, 2009.

Alexandresaurus Rodrigues, Pellegrino, Dixo, Verdade, Pavan, Argolo and Sites, 2007. Content: *A. camacan* Rodrigues, Pellegrino, Dixo, Verdade, Pavan, Argolo and Sites, 2007.

Colobosaura Boulenger, 1887. Content: *C. modesta* (Reinhardt and Lütken, 1862).

Iphisa Gray, 1851. Content: *I. elegans* Gray, 1851.

Rondonops Colli et al., 2015. Content: *R. biscutatus* Colli et al., 2015; *R. xanthomystax* Colli et al., 2015.

Stenolepis Boulenger, 1888. Content: *S. ridleyi* Boulenger, 1888.

SUBFAMILY: Rhachisaurinae Pellegrino et al., 2001

Rhachisaurus Pellegrino et al., 2001. Content: *R. brachylepis* (Dixon, 1974).

SUBFAMILY: Riolaminae Kok, 2015.

Riolama Uzzell, 1973. Content: *R. inopinata* Kok, 2015; *R. leucosticta* (Boulenger, 1900); *R. luridiventris* Esqueda, La Marca and Praderio, 2004; *R. uzzelli* Molina and Señaris, 2003.

FAMILY: Teiidae Gray, 1827.

SUBFAMILY: Callopietinae Fitzinger, 1843.

Callopietes Gravenhorst, 1837. Content: *C. flavipunctatus* (Duméril and Bibron, 1839); *C. maculatus* Gravenhorst, 1837.

SUBFAMILY: Tupinambinae Bonaparte, 1831.

Crocodylurus Spix, 1825. Content: *C. amazonicus* Spix, 1825.

Dracaena Daudin, 1802. Content: *D. guianensis* Daudin, 1802; *D. paraguayensis* Amaral, 1950.

Salvator Duméril and Bibron, 1839. Content: *S. duseni* (Lönnberg, 1910); *S. merianae* (Duméril and Bibron, 1839); *S. rufescens* (Günther, 1871).

Tupinambis Daudin, 1802. Content: *T. longilineus* Ávila-Pires, 1995; *T. palustris* Manzani and Abe, 2002) *T. quadrilineatus* Manzani and Abe, 1997; *T. teguixin* (Linnaeus, 1758).

SUBFAMILY: Teiinae Gray, 1827.

Ameiva Meyer, 1795. Content: *A. aggerescans* Koch, Venegas, Rödder, Flecks and Böhme, 2013; *A. ameiva* (Linnaeus, 1758); *A. atrigularis* Garman, 1887; *A. bifrontata* Cope, 1862; *A. concolor* Ruthven, 1924; *A. fuliginosa* (Cope, 1892); *A. jacuba* Giugliano, Nogueira, Valdujo, Collevatti, and Colli, 2013; *A. nodam* Koch, Venegas, Rödder, Flecks and Böhme, 2013; *A. pantherina* Ugueto and Harvey, 2011; *A. parecis* (Colli, Costa, Garda, Kopp, Mesquita, Péres, Valdujo, Vieira, and Wiederhecker, 2003); *A. praesignis* (Baird

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and Girard, 1852); *A. provitae* (García-Perez, 1995); *A. reticulata* Landauro, Gracia-Bravo, and Venegas, 2015.

Ameivula Harvey et al., 2012. Content: *A. abalosi* (Cabrera, 2012); *A. cipoensis* Arias, Carvalho, Zaher, and Rodrigues, 2014; *A. confusioniba* (Arias, Carvalho, Rodrigues, and Zaher, 2011); *A. jalapensis* (Colli, Giugliano, Mesquita, and Franca, 2009); *A. mumbuca* (Colli, Caldwell, Costa, Gainsbury, and Garda, 2003); *A. nativo* (Rocha, Bergallo, and Peccinni-Seale, 1997); *A. nigrigula* (Arias, Carvalho, Rodrigues, and Zaher, 2011); *A. ocellifera* (Spix, 1825); *A. pyrrhogularis* (Silva and Ávila-Pires, 2013); *A. xacriaba* Arias, Teixeira Jr., Recoder, Carvalho, Zaher and Rodrigues, 2014.

Aspidoscelis Fitzinger, 1843. Content: four species groups, including the polyphyletic hybrid-origin classes, the *A. cozumela* group and the *A. neomexicana* group:

A. cozumela group (a class of hybrid-origin members): *A. cozumela* (Gadow, 1906); *A. maslini* (Fritts, 1969); *A. rodecki* (McCoy and Maslin, 1962).

A. deppei group: *A. ceralbensis* (Van Denburgh and Slevin, 1921); *A. danheimae* (Burt, 1929); *A. deppei* (Wiegmann, 1834); *A. guttata* (Wiegmann, 1834); *A. hyperythra* (Cope, 1864); *A. lineatissima* (Cope, 1878); *A. picta* (Van Denburgh and Slevin, 1921);

A. neomexicana group (a class of hybrid-origin members): *A. dixoni* (Squidday, 1973); *A. neomexicana* (Lowe and Zweifel, 1952); *A. neoteselata* (Walker, Cordes, and Taylor, 1997); *A. tessellata* (Say, 1823).

A. sexlineata group: *A. angusticeps* (Cope, 1878); *A. burti* (Taylor, 1938); *A. calidipes* (Duellman, 1955); *A. communis* (Cope, 1878); *A. costata* (Cope, 1878); *A. exsanguis* (Lowe, 1956); *A. flagellicauda* (Lowe and Wright, 1964); *A. gularis* (Baird and Girard, 1852); *A. inornata* (Baird, 1859); *A. labialis* (Stejneger, 1890); *A. laredoensis* (McKinney, Kay, and Anderson, 1973); *A. mexicana* (Peters, 1869); *A. motaguae* (Sackett, 1941); *A. neavesi* Cole, Taylor, Baumann, and Baumann, 2014; *A. opatae* (Wright, 1967); *A. parvisocia* (Zweifel, 1960); *A. pai* (Wright and Lowe, 1993); *A. sackii* (Wiegmann, 1834); *A. scalaris* (Cope, 1892); *A. sexlineata* (Linnaeus, 1766); *A. sonora* (Lowe and Wright, 1964); *A. stictogramma* (Burger, 1950); *A. uniparens* (Wright and Lowe, 1965); *A. velox* (Springer, 1928); *A. xanthonota* (Duellman and Lowe, 1953).

A. tigris group: *A. marmorata* (Baird and Girard, 1852); *A. maxima* (Cope, 1864); *A. tigris* (Baird and Girard, 1852).

Aurivela Harvey et al., 2012. Content: *A. longicauda* (Bell, 1843); *A. tergolaevigata* (Cabrera, 2004).

Cnemidophorus Wagler, 1830. Content: four species groups:

C. lemniscatus group: *C. arenivagus* Markezich, Cole and Dessauer, 1997; *C. arubensis* van Lidth de Jeude, 1887; *C. cryptus* Cole and Dessauer, 1993; *C. duellmani* McCranie and Hedges, 2013; *C. gaigei* Ruthven, 1915; *C. flavissimus* Ugueto, Arvey and Rivas, 2010; *C. gramivagus* McCrystal and Dixon, 1987; *C. lemniscatus* (Linnaeus, 1758); *C. pseudolemniscatus* Cole and Dessauer, 1993; *C. ruatanus* Barbour, 1928; *C. senectus* Ugueto, Harvey, and Rivas, 2010; *C. splendidus* (Markezich, Cole and Dessauer, 1997).

C. murinus group: *C. murinus* (Laurenti, 1768); *C. ruthveni* Burt, 1935.

C. nigricolor group: *C. leucopsammus* Ugueto and Harvey, 2010; *C. nigricolor* Peters, 1873; *C. rostralis* Ugueto and Harvey, 2010.

C. vanzoi group: *C. vanzoi* (Baskin and Williams, 1966).

Contomastix Harvey et al., 2012. Content: *C. lacertoides* (Duméril and Bibron, 1839); *C. leachei* (Peracca, 1897); *C. serrana* (Cei and

Martori, 1991); *C. vacariensis* (Feltrim and Lema, 2000); *C. vittata* (Boulenger, 1902).

Dicrodon Duméril and Bibron, 1839. Content: *D. guttulatus* Duméril and Bibron, 1839.

Glaucomastix gen. nov.

Type species: *Glaucomastix littoralis* (Rocha, Araújo and Vrcibradic, 2000).

Diagnosis: species of *Glaucomastix* are characterized by the absence of preanal spurs, presence of granules in the supraorbital semicircles, less than 40 femoral pores, first superciliary divided, absence of an opercular projection of skin in the anterodorsal margin of ear-opening, a light vertebral stripe, and a bright bluish-green tail and divided first superciliary (Arias et al., 2011b). *Glaucomastix* can be distinguished from *Ameivula* in having a light vertebral stripe, a bright bluish-green tail and divided first superciliary (Arias et al., 2011; Harvey et al., 2012). Etymology: *Glaucomastix* is a composite name derived from the Greek adjectives “glaukós”, meaning blue-green, and “mastix”, meaning whip. The name alludes to the bluish-green tail that characterizes this group of lizards.

Content: *G. abaetensis* (Dias, Rocha, and Vrcibradic, 2002) **comb. nov.**; *G. cyanura* (Arias, Carvalho, Rodrigues, and Zaher, 2011) **comb. nov.**; *G. littoralis* (Rocha, Araújo, and Vrcibradic, 2000) **comb. nov.**; *G. venetacauda* (Arias, Carvalho, Rodrigues, and Zaher, 2011) **comb. nov.**

Holcosus Cope, 1862. Content: *H. anomalus* (Echternacht, 1977); *H. bridgesii* (Cope, 1869); *H. chaitzami* (Stuart, 1942); *H. festivus* (Lichtenstein and Von Martens, 1856); *H. leptophrys* (Cope 1893); *H. niceforoi* (Dunn, 1943); *H. orcesi* (Peters, 1964); *H. quadrilineatus* (Hallowell, 1851); *H. septemlineatus* (Duméril and Duméril, 1851); *H. undulatus* (Wiegmann, 1834).

Kentropyx Spix, 1825. Content: *K. altamazonica* (Cope, 1876); *K. borckiana* (Peters, 1869); *K. calcarata* Spix, 1825; *K. lagartija* Gallardo, 1862; *K. paulensis* (Boettger, 1893); *K. pelviceps* (Cope, 1868); *K. striata* (Daudin, 1802); *K. vanzoi* Gallagher and Dixon, 1980; *K. viridistriga* (Boulenger, 1894).

Medopheos Harvey et al., 2012. Content: *M. edracanthus* (Bocourt, 1874).

Pholidoscelis Fitzinger, 1843.³ Content: four species groups:

P. auberi group: *P. auberi* (Cocteau, 1838), **comb. nov.**; *P. dorsalis* (Gray, 1838), **comb. nov.**

P. exul group: *P. wetmorei* (Stejneger, 1913), **comb. nov.**; *P. exsul* (Cope, 1862), **comb. nov.**; *P. polops* (Cope, 1862), **comb. nov.**

P. lineolata group: *P. chrysolaeama* (Cope, 1868), **comb. nov.**; *P. lineolata* (Duméril and Bibron, 1839), **comb. nov.**; *P. maynardi* (Garman, 1888), **comb. nov.**; *P. taeniura* (Cope, 1862), **comb. nov.**; *P. umbratilis* (Schwartz and Klinikowski, 1966), **comb. nov.**

P. plei group: *P. atrata* (Garman, 1887), **comb. nov.**; *P. cineracea* (Barbour and Noble, 1915), **comb. nov.**; *P. corvina* (Cope, 1861), **comb. nov.**; *P. corax* (Censky and Paulson, 1992), **comb. nov.**; *P. erythrocephala* (Daudin, 1802), **comb. nov.**; *P. fuscata* (Garman, 1887), **comb. nov.**; *P. griswoldi* (Barbour, 1916), **comb. nov.**; *P. major* (Duméril and Bibron, 1839), **comb. nov.**; *P. plei* (Duméril and Bibron, 1839), **comb. nov.**; *P. pluvianotata* (Garman, 1887), **comb. nov.**

Teius Merrem, 1820. Content: *T. oculus* (d’Orbigny and Bibron, 1837); *T. suquiensis* Ávila and Martori, 1991; *T. teyou* (Daudin, 1802).

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