The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2012, **165**, 163–189. With 4 figures

The phylogenetic systematics of blue-tailed skinks (*Plestiodon*) and the family Scincidae

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Received 22 September 2011; accepted for publication 2 November 2011

Blue-tailed skinks (genus *Plestiodon*) are a common component of the terrestrial herpetofauna throughout their range in eastern Eurasia and North and Middle America. *Plestiodon* species are also frequent subjects of ecological and evolutionary research, yet a comprehensive, well-supported phylogenetic framework does not yet exist for this genus. We construct a comprehensive molecular phylogeny of *Plestiodon* using Bayesian phylogenetic analyses of a nine-locus data set comprising 8308 base pairs of DNA, sampled from 38 of the 43 species in the genus. We evaluate potential gene tree/species tree discordance by conducting phylogenetic analyses of the concatenated and individual locus data sets, as well as employing coalescent-based methods. Specifically, we address the placement of *Plestiodon* within the evolutionary tree of Scincidae, as well as the phylogenetic relationships between *Plestiodon* species, and their taxonomy. Given our sampling of major Scincidae lineages, we also re-evaluate 'deep' relationships within the family, with the goal of resolving relationships that have been ambiguous in recent molecular phylogenetic analyses. We infer strong support for several scincid relationships, including a major clade of 'scincines' and the inter-relationships of major Mediterranean and southern African genera. Although we could not estimate the precise phylogenetic affinities of *Plestiodon* with statistically significant support, we nonetheless infer significant support for its inclusion in a large 'scincine' clade exclusive of Acontinae, Lygosominae, *Brachymeles*, and *Ophiomorus*. *Plestiodon* comprises three major geographically cohesive clades. One of these clades is composed of mostly large-bodied species inhabiting northern Indochina, south-eastern China (including Taiwan), and the southern Ryukyu Islands of Japan. The second clade comprises species inhabiting central China (including Taiwan) and the entire Japanese archipelago. The third clade exclusively inhabits North and Middle America and the island of Bermuda. A vast majority of interspecific relationships are strongly supported in the concatenated data analysis, but there is nonetheless significant conflict amongst the individual gene trees. Coalescent-based gene tree/species tree analyses indicate that incongruence amongst the nuclear loci may severely obscure the phylogenetic inter-relationships of the primarily small-bodied *Plestiodon* species that inhabit the central Mexican highlands. These same analyses do support the sister relationship between *Plestiodon marginatus* Hallowell, 1861 and *Plestiodon stimpsonii* (Thompson, 1912), and differ with the mitochondrial DNA analysis that supports *Plestiodon elegans* (Boulenger, 1887) + *P. stimpsonii*. Finally, because the existing *Plestiodon* taxonomy is a poor representation of evolutionary relationships, we replace the existing supraspecific taxonomy with one congruent with our phylogenetic results.

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doi: 10.1111/j.1096-3642.2011.00801.x

ADDITIONAL KEYWORDS: Americas – Bayesian – Eurasia – gene tree – multilocus – phylogenetics – Squamata – taxonomy.

INTRODUCTION

Lizards of the genus *Plestiodon* (Scincidae) are a common component of the terrestrial herpetofauna throughout their range in eastern Eurasia, including Japan, China (including Taiwan), North and Middle America, and Bermuda (Fig. 1). They use a variety of habitat types, including deciduous forests, high plateaus, and subtropical islands, and possess body forms ranging from the 'typical' stocky, robustly limbed lizard morphology to elongate, miniaturized, and limb reduced (Griffith, 1991). Given this ecological and evolutionary diversity, *Plestiodon* species have frequently been used to address ecological (e.g. Hikida, 1981; Vitt & Cooper, 1986; Hasegawa, 1994), physiological (e.g. Cooper, Mendonca & Vitt, 1986; Thompson & Stewart, 1997; Lin, Qu & Ji, 2006), behavioural (e.g. Cooper & Vitt, 1986; Cooper, 1999), developmental (e.g. Hikida, 1978a; Stewart & Florian, 2000; Masson & Guillette, 2005), and evolutionary (e.g. Vitt & Cooper, 1985; Griffith, 1990, 1991; Richmond & Jockusch, 2007) biology questions. However, previous studies were conducted in the absence of a comprehensive phylogenetic framework, thereby severely limiting the power of comparative analyses across the genus.

Until recently, much of our understanding of *Plestiodon* systematic relationships was derived from Edward Taylor's (1935) seminal monograph. Besides providing the first phylogenetic hypothesis of *Plestiodon* (then included within the genus *Eumeces*) based primarily on scale pattern and number of dorsal stripes, Taylor's (1935) study remains the only study that has attempted to determine the systematics of the entire genus, although this taxonomic framework of selected species groups has since undergone major modification (Dixon, 1969; Robinson, 1979; Lieb, 1985; Hikida, 1993; Table 1).

Recent molecular phylogenetic examinations of *Plestiodon* have done much to improve upon this taxonomic framework. Recently, Brandley *et al*. (2011) used *Plestiodon* as a model system to assess the efficacy of divergence dating methods with multilocus data. Although that study inferred a species phylogeny of the group, it was examined only in the context of divergence date estimation and biogeography, rather than a detailed systematic analysis of the genus. Previous molecular studies included no more than half of the described species (e.g. Schmitz, Mausfeld & Embert, 2004; Brandley, Schmitz & Reeder, 2005), and have usually focused on regional subsets of the genus' range in the USA (Murphy, Cooper & Richardson, 1983; Richmond & Reeder, 2002; Macey *et al*., 2006; Richmond, 2006) and Asia (Kato, Ota & Hikida, 1994; Hikida & Motokawa, 1999; Motokawa & Hikida, 2003; Okamoto *et al*., 2006; Honda *et al*., 2008; Okamoto & Hikida, 2009). Moreover, multiple studies have inferred conflicting or poorly supported placements of *Plestiodon* within the scincid tree of life (Whiting, Bauer & Sites, 2003; Brandley *et al*., 2005; Austin & Arnold, 2006). The general lack of osteological variation among the *Plestiodon* species constrains the phylogenetic value of these kinds of data for this group; indeed, Griffith, Ngo & Murphy (2000) found no osteological synapomorphic characters that supported the monophyly of *Plestiodon*.

For much of its taxonomic history, *Plestiodon* was considered to be a member of the genus *Eumeces* Wiegmann, 1834 that also included other North African, Central Asian, and Central American species. Subsequent morphological (Griffith *et al*., 2000) and molecular analyses (Schmitz *et al*., 2004; Brandley *et al*., 2005, 2011) recognized that *Eumeces s.l.* was not monophyletic, and is instead composed of four genera: the North African and Central Asian *Eumeces s.s.*, Central and South Asian *Eurylepis*, Central American *Mesoscincus*, and East Asian and North American *Plestiodon* (see also Smith, 2005). The morphological analysis of Griffith *et al*. (2000) implied that *Plestiodon* is the sister taxon to all other skinks. The multilocus molecular phylogenies of Whiting *et al*. (2003), Siler & Brown (2011), and Siler *et al*. (2011) concluded that *Plestiodon* was nested within the subfamily Lygosominae; this result is puzzling as lygosomines are one of the few major clades of skinks with multiple putative morphological synapomorphies (Greer, 1970a, 1986). In addition, the molecular phylogenies of Brandley *et al*. (2005), Austin & Arnold (2006), and Skinner, Hugall & Hutchinson (2011) strongly supported lygosomine monophyly. In the absence of a phylogeny, Greer (1970a) assumed that *Eumeces s.l.* represented the most 'primitive' group of skinks (thereby implying it is an early diverging lineage), and some subsequent studies later used the morphology of the genus as an estimate of the 'primitive' scincid body form from which to interpret morphological evolution in other scincid lizards (e.g. Greer & Broadley, 2000; Andreone & Greer, 2002). Indeed, the analysis of Brandley *et al*. (2005) suggested that *Plestiodon* was the sister taxon

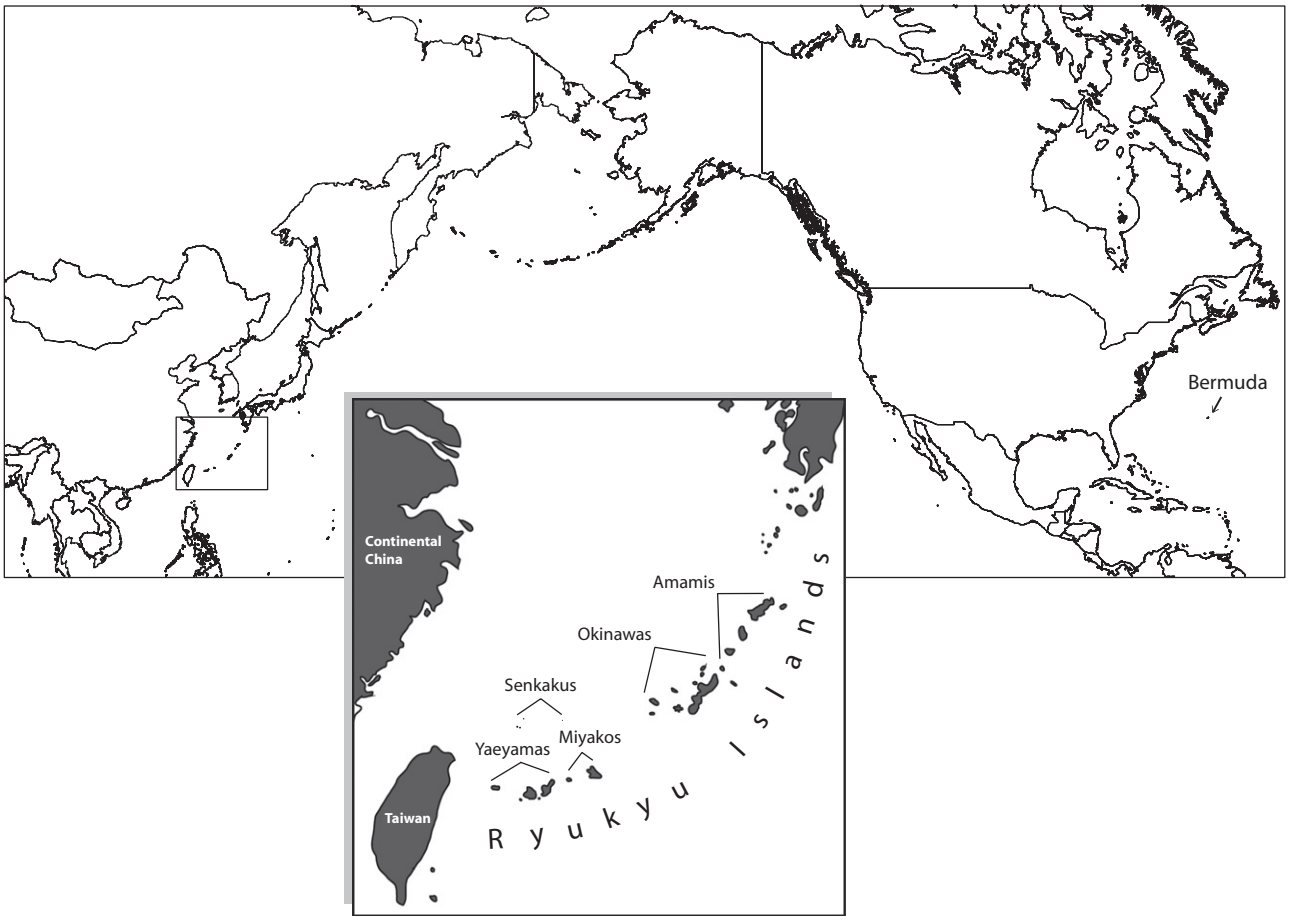

Figure 1. The geographical distribution of *Plestiodon*, with an inset showing the Ryukyu Islands.

of all other skinks, but this relationship had low posterior probability (PP = 0.82), as did the relationships of the other genera formerly assigned to *Eumeces s.l.*

In summary, there has been no synthetic study of the phylogenetic systematics of *Plestiodon* species since Taylor (1935). Therefore, a robustly estimated *Plestiodon* phylogeny would be useful in its own right. Perhaps more importantly, the lack of phylogenetic framework impedes the explanatory power of all comparative biological research of the genus. Here, we provide this phylogenetic framework and conduct a comprehensive examination of the evolutionary relationships among *Plestiodon* species. We apply partitioned Bayesian phylogenetic analyses to a nine-locus data set, representing nearly all described species from all major species groups from throughout the range of the genus, to address two fundamental questions of *Plestiodon* evolutionary history: (1) where does *Plestiodon* belong in the evolutionary tree of Scincidae; and (2) what is the phylogenetic history of *Plestiodon* species, and does the current taxonomy reflect the estimated phylogeny?

Furthermore, we sample 18 other scincid lineages, representing a broad phyletic diversity of skinks, to re-evaluate 'deep' skink phylogenetic relationships from a multilocus perspective. This is important because skinks represent one of the most diverse families of squamate reptiles in terms of species number (~1200 sp.; Pough *et al.*, 2004) and geographic distribution (all continents excepting Antarctica, and most continental and oceanic islands located from temperate to tropical zones; Vitt & Caldwell, 2008). Furthermore, limb reduction (Greer, 1991; Wiens, Brandley & Reeder, 2006; Brandley, Huelsenbeck & Wiens, 2008) and viviparity (Blackburn, 2006) have evolved more times in skinks than in any other lizard family. The few comprehensive molecular phylogenetic studies of skinks have resolved several 'deep' relationships, such as the clade composed of primarily African, Malagasy, and Seychellois taxa, and the nesting of the enigmatic *Feylinia* (see Rieppel, 1981) deep within this clade (Whiting *et al.*, 2003; Brandley *et al.*, 2005). However, the relationships among the major lineages of skinks remain largely unresolved, and there exist

Table 1. *Plestiodon* species, their primary geographic distribution, and traditional taxonomy *sensu* Dixon (1969), Hikida (1993), and Lieb (1985). See the Discussion and Figure 3 for a revised taxonomy

Species	Primary distribution	Previous species group taxonomy	Included in this study?
P. anthracinus	USA	*anthracinus* group	Yes
P. barbouri	Japan	*latiscutatus* group	Yes
P. brevirostris bilineatus	Mexico	*brevirostris* group	Yes
P. brevirostris brevirostris	Mexico	*brevirostris* group	Yes
P. brevirostris dicei	Mexico	*brevirostris* group	Yes
P. brevirostris indubitus	Mexico	*brevirostris* group	Yes
P. brevirostris pineus	Mexico	*brevirostris* group	No
P. capito	Continental China	*capito* group	Yes
P. chinensis	China (including Taiwan)	*chinensis* group	Yes
P. colimensis	Mexico	*brevirostris* group	No
P. coreensis	Korea	*chinensis* group	No
P. copei	Mexico	*brevirostris* group	Yes
P. dugesii	Mexico	*brevirostris* group	Yes
P. egregius	USA	*egregius* group	Yes
P. elegans	China (including Taiwan)	*latiscutatus* group	Yes
P. fasciatus	Canada, USA	*fasciatus* group	Yes
P. gilberti	USA	*skiltonianus* group	Yes
P. inexpectatus	USA	*fasciatus* group	Yes
P. japonicus	Japan	*latiscutatus* group	Yes
P. kishinouyei	Japan	*chinensis* group	Yes
P. lagunensis	Mexico	*skiltonianus* group	Yes
P. laticeps	USA	*fasciatus* group	Yes
P. latiscutatus	Japan	*latiscutatus* group	Yes
P. liui	Continental China	*capito* group	No
P. longirostris	Bermuda	*longirostris* group	Yes
P. lynxe	Mexico	*lynxe* group	Yes
P. marginatus marginatus	Japan	*latiscutatus* group	Yes
P. marginatus oshimensis	Japan	*latiscutatus* group	Yes
P. multilineatus	Mexico and USA	*multivirgatus* group	No
P. multivirgatus	USA	*multivirgatus* group	Yes
P. obsoletus	USA	*obsoletus* group	Yes
P. ochoteranae	Mexico	*brevirostris* group	Yes
P. parviauriculatus	Mexico	*multivirgatus* group	Yes
P. parvulus	Mexico	*multivirgatus* group	Yes
P. popei	Continental China	*capito* group	No
P. quadrilineatus	Northern Indochina and southern China	*quadrilineatus* group	Yes
P. reynoldsi	USA	*Incertae sedis*	Yes
P. septentrionalis	USA	*anthracinus* group	Yes
P. skiltonianus	Canada, USA	*skiltonianus* group	Yes
P. stimpsonii	Japan	*latiscutatus* group	Yes
P. sumichrasti	Mexico and northern Central America	*sumichrasti* group	Yes
P. tamdaoensis	Northern Indochina and southern China	*tamdaoensis* group	Yes
P. tetragrammus	Mexico and USA	*anthracinus* group	Yes
P. tunganus	Continental China	*capito* group	Yes

conflicting hypotheses of Lygosominae monophyly and the placement of the limbless Southern African Acontinae (see Greer, 1986; Whiting *et al*., 2003; Brandley *et al*., 2005; Siler & Brown, 2011; Siler *et al*., 2011; Skinner *et al*., 2011).

MATERIAL AND METHODS

TAXON AND CHARACTER SAMPLING

Our sampling strategy was to include as many species of *Plestiodon* as possible throughout their geographic

range (Appendix; Table 1). We collected nucleotide data for 38 of the 43 described species of *Plestiodon*. To capture both the genetic diversity among and within the species we sampled multiple individuals per species when possible, frequently from different parts of the range of the species, for a total of 71 *Plestiodon* individuals. This sampling does not include *Plestiodon liui* (Hikida & Zhao, 1989) and *Plestiodon popei* (Hikida, 1989), two species known only from holotypes (Hikida, 1989, 1993; Hikida & Zhao, 1989); or *Plestiodon colimensis* (Taylor, 1935) (*brevirostris* group), *Plestiodon coreensis* (Doi & Kamita, 1937) (*chinensis* group), and *Plestiodon multilineatus* (Tanner, 1957) (*multivirgatus* group), three species we could not capture in the field. Given the phylogenetic and taxonomic uncertainty in the *Plestiodon gilberti* (Van Denburgh, 1896) + *Plestiodon lagunensis* (Van Denburgh, 1895) + *Plestiodon skiltonianus* Baird & Girard, 1852 complex (Richmond & Reeder, 2002), we sampled five lineages previously identified by Richmond & Reeder (2002). Previous studies could not infer the placement of *Plestiodon* within the scincid phylogeny with statistical support (see above). Therefore, we sampled 18 representatives of the major scincid lineages, including acontines, lygosomines, and 'scincines' (Greer, 1970a, b; Whiting *et al*., 2003; Brandley *et al*., 2005) as out-groups. In addition, this is the first molecular study to include all four genera that comprised *Eumeces s.l.* (*Eumeces s.s.*, *Eurylepis*, *Mesoscincus*, and *Plestiodon*). To permit the possibility that *Plestiodon* could be the sister taxon to all other skinks, we also included representatives of the families Xantusiidae and Gerrhosauridae, two close relatives of Scincidae (Townsend *et al*., 2004; Vidal & Hedges, 2005; Hugall, Foster & Lee, 2007), for a total of 91 taxa (Appendix).

We used the data for 62 individuals for eight independently evolving loci from Brandley *et al*. (2011), including: mitochondrial (mt)DNA [*ND1*, $tRNA^{LEU}$, $tRNA^{ILE}$, and $tRNA^{GLN}$; 1227 total base pairs (bp)] *BDNF* (653 bp); *MKL1* (903 bp); *PRLR* (570 bp); *PTGER4* (468 bp); *R35* (682 bp); *RAG1* (2728 bp), and *SNCAIP* (483 bp) (Table 1). To these data, we added 29 individuals as well as data for the *UBN1* gene (684 bp) for most taxa, for a data set totalling 91 taxa and 8398 bp [see Townsend *et al*. (2008) and Brandley *et al*. (2011) for PCR conditions and primer information]. Nucleotide sequences were examined and aligned by eye; this process was relatively straightforward for the protein-coding genes (*BDNF*, *MKL1*, mtDNA *ND1*, *PRLR*, *PTGER4*, *R35*, *RAG1*, *SNCAIP*, and *UBN1*) because of their codon reading frames. mtDNA tRNAs were aligned according to their secondary structure, and regions in which homology was uncertain because of multiple insertions and deletions were excluded from subsequent analysis. Although the visual determination of uncertain homology in aligned sequences is admittedly subjective, the value of removing potentially misleading data outweighs our concerns that informative data might also be lost. The size of the final concatenated data set for phylogenetic analysis was 8308 bp.

Partitioning and model testing

We conducted Bayesian phylogenetic analyses of each locus assuming both partitioned and unpartitioned (i.e. single model for the entire data set) models. We then used TRACER 1.5 (Rambaut & Drummond, 2007) to calculate the 2ln Bayes factor between the two partitioning schemes (see Brandley *et al*., 2005). We interpret 2ln Bayes factors ≥ 10 as evidence that the partitioned model best explains the data (Kass & Raftery, 1995); in other words, if the 2ln Bayes factor comparing a partitioned and unpartitioned model is < 10, we use the unpartitioned model.

We estimated the appropriate model of nucleotide substitution for each partition using Akaike's information criterion (AIC; Akaike, 1974), implemented in MRMODELTEST (Nylander, 2004). Like all model-testing strategies, the goal of the AIC is to strike a balance between selecting a model that adequately describes the data and assuming too many parameters (which can introduce random error). The models used in subsequent Bayesian phylogenetic analysis (see below), as well as the characteristics of each data set, are provided in Table 2.

Bayesian phylogenetic analyses

We conducted a comprehensive Bayesian phylogenetic analyses of *Plestiodon* including separate analyses of each of the nine independently evolving loci and concatenated nine locus data sets. In doing so we identified two subclades of *Plestiodon* for which there is notable gene tree discordance – the *latiscutatus* and *brevirostris* groups (taxonomy *sensu* this study, see Discussion) – and conducted Bayesian species tree analyses using a multispecies coalescent in *BEAST.

We performed Bayesian analyses of each data set using parallel MRBAYES 3.1.2 (Altekar *et al*., 2004), employing the optimal partitioning strategies and models calculated above. Bayes factors indicated that the *BDNF*, *PRLR*, and *SNCAIP* genes were best modelled assuming a single partition for each locus. Each analysis of the concatenated data was run for 75 000 000 generations, sampled every $10\,000^{th}$ generation. We assumed the default MRBAYES priors, with the exception that the mean of the exponential prior on branch lengths was changed to 100 (following Marshall, Simon & Buckley, 2006), and the number of Markov chain Monte Carlo (MCMC) chains was

Table 2. Characteristics of each data gene and data partition, as well as models used in the Bayesian phylogenetic analyses

		Out-group + in-group taxa				In-group taxa only*	
		No. of characters	No. of variable	No. parsimony informative	Model	No. of variables	No. parsimony informative
BDNF	Full data set	645	124	61	GTR + I + G	29	16
	1st codon position	215	22	9	–	7	6
	2nd codon position	215	4	1	–	0	0
	3rd codon position	215	98	51	–	22	10
MKL1	Full data set	903	408	233	–	119	70
	1st codon position	301	116	57	GTR + G	25	14
	2nd codon position	301	69	34	GTR + I	14	9
	3rd codon position	301	223	142	K80 + G	80	47
mtDNA	Full data set	1168	671	595	–	553	514
	ND1 1st codon position	320	162	138	GTR c+ I + G	120	100
	ND1 2nd codon position	320	75	57	GTR + I + G	47	39
	ND1 3rd codon position	320	319	316	GTR + I + G	317	310
	tRNAs	208	115	84	GTR + G	69	65
PRLR	Full data set	567	396	253	GTR + G	396	253
	1st codon position	189	115	69	–	115	69
	2nd codon position	189	121	78	–	121	78
	3rd codon position	189	160	106	–	160	106
PTGER4	Full data set	468	128	85	–	46	31
	1st codon position	156	16	8	GTR + I + G	3	2
	2nd codon position	156	12	5	F81 + I	3	1
	3rd codon position	156	100	72	GTR + G	40	28
R35	Full data set	663	349	230	–	112	77
	1st codon position	221	97	50	GTR + G	24	12
	2nd codon position	221	75	43	GTR + G	23	16
	3rd codon position	221	177	137	HKY + G	65	49
RAG1	Full data set	2724	1199	745	–	396	250
	1st codon position	908	269	142	GTR + I + G	89	49
	2nd codon position	908	216	113	GTR + I + G	61	40
	3rd codon position	908	714	490	GTR + G	246	161
SNCAIP	Full data set	483	197	113	HKY + G	65	44
	1st codon position	161	37	21	–	9	5
	2nd codon position	161	34	14	–	12	6
	3rd codon position	161	126	78	–	44	33
UBN1	Full data set	735	349	169	–	103	62
	1st codon position	245	103	35	GTR + G	20	10
	2nd codon position	245	58	22	HKY + G	13	6
	3rd codon position	245	188	112	GTR + G	70	46

*Provided for descriptive purposes. In-group-only phylogenetic analyses were not performed.

increased from four to eight. To decrease the chance of not adequately sampling the posterior distribution of trees, we ran a total of 16 analyses of the concatenated data. For eight of the analyses, we used a maximum-likelihood starting tree. We estimated this tree using ten replicate maximum likelihood searches using RAxML 7.0.4 (Stamatakis, 2006), assuming a separate GTR+CAT model for each of the data partitions used in the subsequent Bayesian analyses. We used the default random tree in the remaining eight analyses. The individual gene analyses were run for 50 000 000 generations using the same parameters as the concatenated analyses, with the exceptions that we ran each analysis four times and used the default four MCMC chains and random starting tree.

To determine apparent stationarity, we constructed cumulative posterior probability plots for each analysis using the 'cumulative' function in 'Are we there yet?' (AWTY; Nylander *et al*., 2008). To ensure that each analysis of each data set was sampled from the same posterior distribution, we analysed the results using the 'compare' function in AWTY. If each of the analyses for each data set converged on the same posterior distribution, posterior probabilities of each clade were calculated from the concatenated results using the sumt command in MRBAYES. Posterior probabilities (PPs) ≥ 0.95 are considered to be strongly supported (Huelsenbeck & Rannala, 2004).

When comparing the results of the individual gene trees, we interpret any incongruent relationships with statistically significant clade support (i.e. PP ≥ 0.95) as evidence of gene tree discordance. The results of the separate gene tree analyses demonstrate gene tree discordance in both the eastern Eurasian *latiscutatus* group [*Plestiodon barbouri* (Van Denburgh, 1912), *Plestiodon elegans* (Boulenger, 1887), *Plestiodon japonicus* (Peters, 1864), *Plestiodon latiscutatus* Hallowell, 1861, *Plestiodon marginatus* Hallowell, 1861, and *Plestiodon stimpsonii* (Thompson, 1912)] and the primarily Middle American *brevirostris* group [*Plestiodon brevirostris brevirostris* (Günther, 1860), *Plestiodon brevirostris bilineatus* (Cope, 1880) , *Plestiodon brevirostris dicei* (Ruthven & Gaige, 1933), *Plestiodon brevirostris indubitus* (Taylor, 1933), *Plestiodon colimensis* (Taylor, 1935), *Plestiodon copei* (Taylor, 1933), *Plestiodon dugesii* (Thominot, 1883), *Plestiodon ochoteranae* (Taylor, 1933), *Plestiodon parvulus* (Taylor, 1933), *Plestiodon parviauriculatus* (Taylor, 1933), and *Plestiodon sumichrasti* (Cope, 1867)]. We therefore conducted additional analyses simultaneously estimating gene trees and a species tree using *BEAST (Heled & Drummond, 2010). Because the taxon sampling differs from the previous Bayesian analyses, we recalculated the model of sequence evolution for each gene using the AIC (see above). Each *BEAST analysis consisted of 100 000 000 generations (sampled every 5000 generations), a lognormal prior distribution of rates (i.e. an uncalibrated molecular clock), and an inverse gamma distributed population size prior with a mean = 3 and standard deviation = 0.1 (as recommended by Leaché, 2009). For the analysis of the *latiscutatus* group, we excluded the *UBN1* data because we could not sequence this gene for *P. stimpsonii*. For the analysis of the *brevirostris* group, we considered each subspecies of *P. brevirostris*, and the two populations of *P. b. indubitus*, as separate species in accordance with a recent comprehensive analysis of *P. brevirostris* species limits (Fería-Ortíz, Manríquez-Morán & Nieto-Montes de Oca, 2011). An additional subspecies, *Plestiodon brevirostris pineus* (Axtell, 1960) is not included in this study (but see Fería-Ortíz, Manríquez-Morán & Nieto-Montes de Oca, 2011). Because analyses including the mtDNA failed to converge, we excluded this locus from all *BEAST analyses, and because molecular clocks simultaneously estimate rooting, we did not include out-groups.

RESULTS

The concatenated enalyses and individual locus analyses achieved stationarity by 15 000 000 and 10 000 000 generations, respectively. These post-burn-in trees were discarded, and the remaining trees and associated parameter estimates were saved, with the frequency of inferred relationships representing estimated posterior probabilities. For clarity, we first limit our discussion to higher level scincid relationships (Fig. 2), and follow with presentation of the inter-relationships of the sampled *Plestiodon* species (Figs 3 & 4). Given the very strong support for most clades throughout the phylogeny. We focus on the concatenated data results (Figs 2 & 3), but discuss individual gene trees (Figs S1–S10) if they differ significantly from those of the concatenated analysis, and present Bayesian gene tree/species tree analyses for the appropriate species groups.

SCINCID PHYLOGENY AND THE PLACEMENT OF *PLESTIODON*

Support for the monophyly of Scincidae is strong, and there is equally strong support for the subfamily Acontinae (represented here by *Typhlosaurus* sp.) as the sister taxon to all remaining skinks (Fig. 2). The basal relationships among the non-acontines are generally weak. There is no significant support for the placement of *Ophiomorus* and *Brachymeles*, although *RAG1* supports the placement of both genera in a clade containing all other 'scincines' (Fig. S1). However, there is strong support for Lygosominae monophyly and a clade containing the remaining

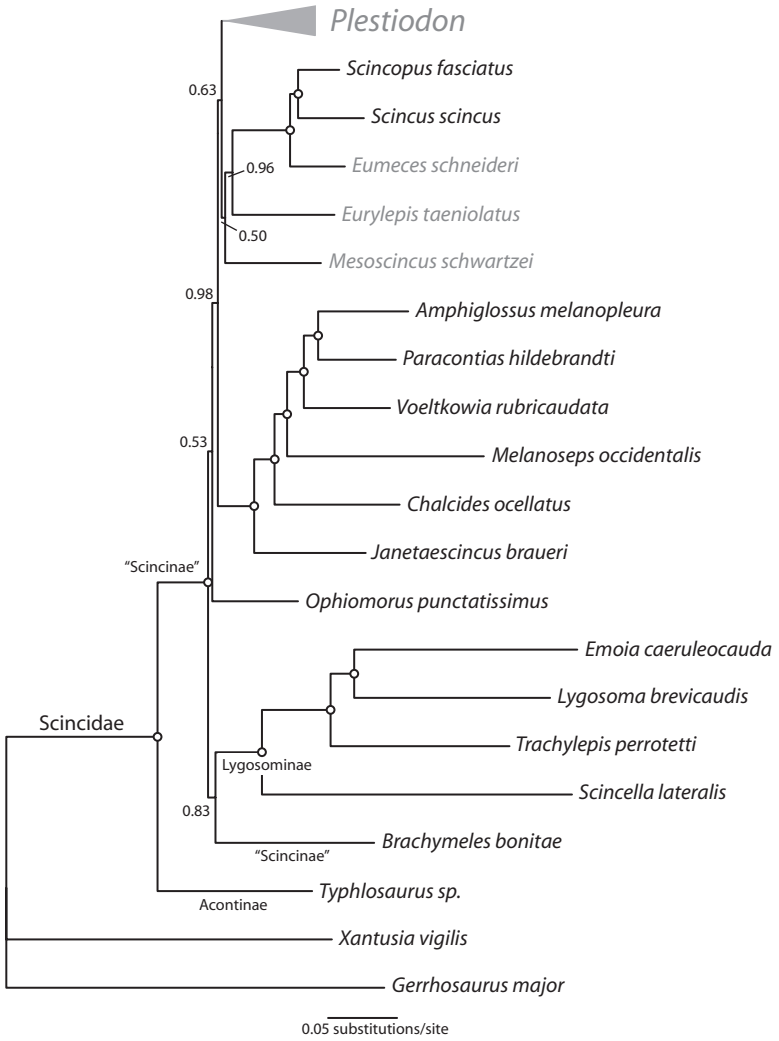

Figure 2. The inter-relationships of the major lineages of Scincidae, including the placement of *Plestiodon*, inferred by partitioned Bayesian analysis of the entire concatenated multilocus DNA data set. Nodes with open circles are supported with a posterior probability of 1.0. Nodes with a posterior probability < 1.0 are indicated with numbers above or below the node. Branch lengths represent means of the posterior distribution. Taxa once considered part of the genus *Eumeces s.l.* are shaded in grey.

'scincines'. We did not sample the monotypic Feylinae, but previous studies have strongly supported its placement in a clade with *Melanoseps* (included in this study) and *Typhlacontias* (not included in this study) (Whiting *et al*., 2003; Brandley *et al*., 2005). The 'scincine' clade splits into a strongly supported clade of African, Malagasy, and Seychellois taxa and a weakly supported clade (PP = 0.63), containing primarily northern hemisphere species, including all genera of *Eumeces s.l.* (*Eumeces s.s.*, *Eurylepis*, *Mesoscincus*, and *Plestiodon*), *Scincopus*, and *Scincus*. The placement of *Mesoscincus* is weakly supported (PP = 0.50), but the primarily Northern African and Central Asian genera of *Eurylepis*, *Eumeces s.s.*, *Scincus*, and *Scincopus* form a well-supported clade. The precise placement of *Plestiodon* is not strongly supported (PP = 0.63), but there is a strong support for its inclusion in the larger 'scincine' clade, to the exclusion of the Africa + Madagascar + Seychelles clade.

Although numerous scincid relationships differ between the nine loci and concatenated analyses, only one of these differences is strongly supported (Fig. S1); most loci and the concatenated data infer strong support for *Scincella* (*Sphenomorphus* group) as the sister taxon to the remaining lygosomines, but the mtDNA infers strong support for the sister relationship between *Scincella* and *Trachylepis* (*Mabuya* group). There are three cases where the concatenated data and analyses of eight of the nine loci cannot estimate the phylogenetic placement of a taxon with

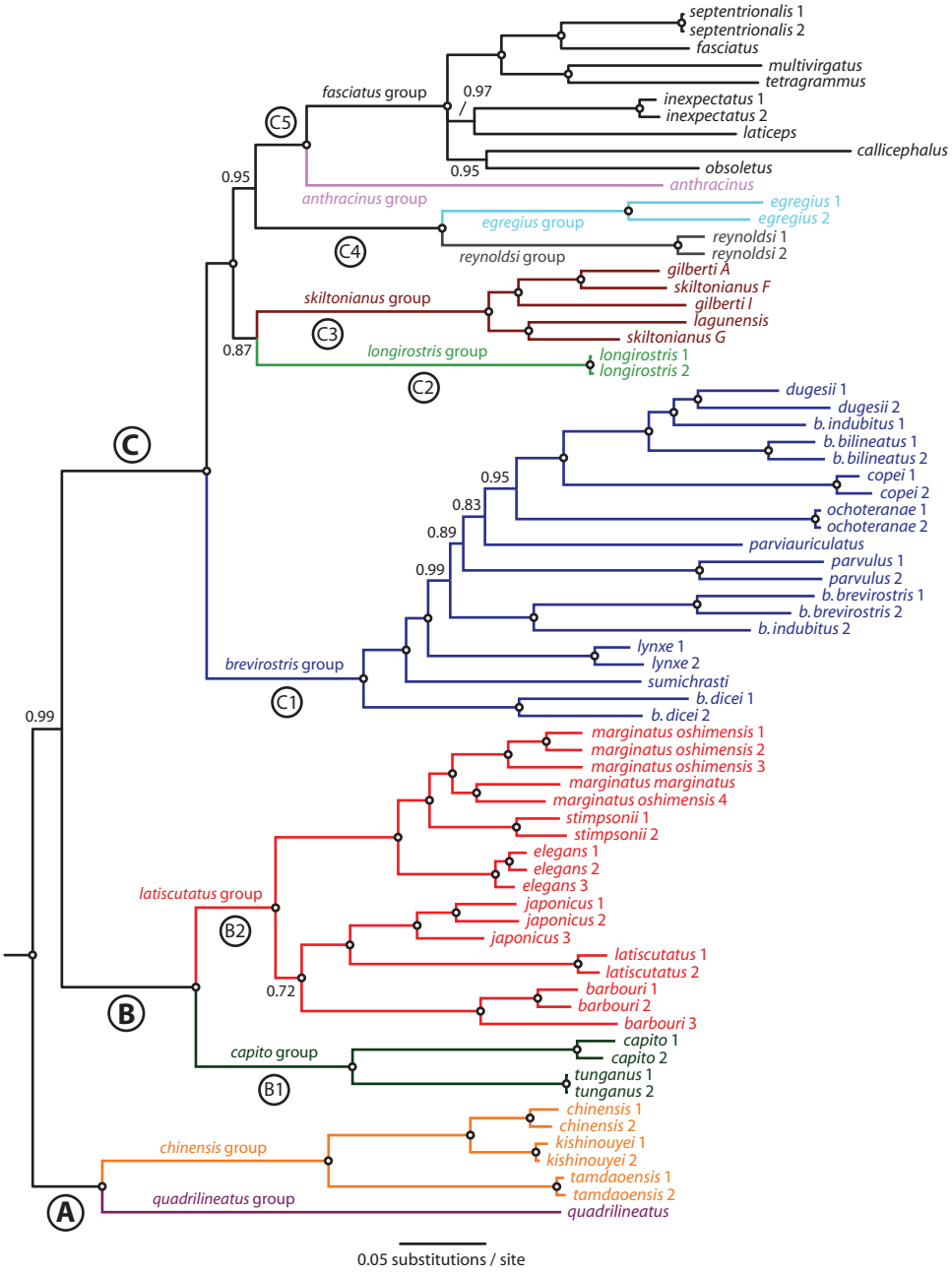

Figure 3. A continuation of Figure 2 showing the inter-relationships of *Plestiodon* species. Nodes with open circles are supported with a posterior probability of 1.0. Nodes with a posterior probability < 1.0 are indicated with numbers above or below the node. Nodes with a posterior probability of < 0.50 are collapsed. Branch lengths represent means of the posterior distribution. Clades A, B1, B2, and C1–C5 refer to the clades discussed in the text.

strong support, yet this relationship is strongly supported in one locus. In the first case, *RAG1* data support a basal split of the non-acontine skinks into lygosomines and all sampled 'scincines' (Fig. S1). In addition, these data strongly support the inclusion of *Mesoscincus* in a clade including *Eumeces s.s.*, *Eurylepis*, *Scincus*, and *Scincopus*. The *SNCAIP* data strongly support the inclusion of *Brachymeles* in a clade containing lygosomines, but given the poor support within this clade, we cannot distinguish whether *Brachymeles* represents the sister lineage to lygosomines or disrupts lygosomine phylogeny (Fig. S1). We note that none of these relationships strongly conflicts with the concatenated data analysis (Fig. 2).

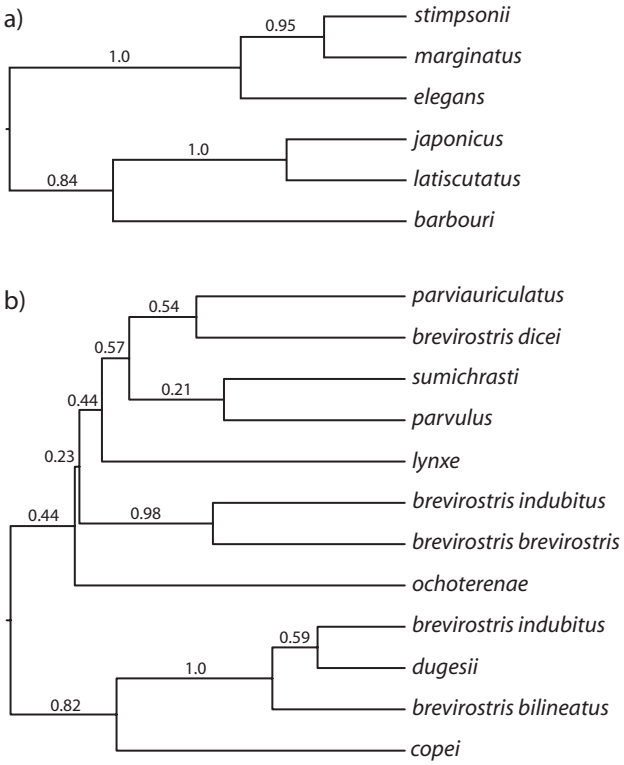

Figure 4. The inter-relationships of (A) *Plestidon latiscutatus* group (*sensu* this study) and (b) the *brevirostris* group species (*sensu* this study) inferred by simultaneous gene tree and species tree analysis of the nuclear loci assuming a multi-species coalescent with *BEAST.

Interspecific relationships of *Plestiodon*

Support for the monophyly of the genus *Plestiodon* is strong in all analyses (Figs 3, S2–S10). There are three strongly supported major clades, and we refer to them as clades A, B, and C in the text and Figure 3. We refer to subclades within these larger clades using numerals (e.g. C1, C2, etc.). We present the results for clades A, B, and C below.

Clade A

This clade contains large-bodied species from northern Indochina and south-eastern continental China [*Plestiodon quadrilineatus* Blyth, 1853 and *Plestiodon tamdaoensis* (Bourret, 1937)], south-eastern and eastern continental China and Taiwan [*Plestiodon chinensis* (Gray, 1838)], and the southern Ryukyu Islands (Yaeyama and Miyako) of Japan [*Plestiodon kishinouyei* (Stejneger, 1901)]. Support for the interrelationships of these species is strong in the concatenated data analysis, and none of the nine gene trees strongly contradict the concatenated data tree; however, both the mtDNA (Fig. S2) and *UBN1* (Fig. S10) trees infer *P. quadrilineatus* as the sister lineage to all other *Plestiodon* species, but with poor support (PP = 0.65 and 0.82, respectively).

Clade B

All of the species of this clade inhabit eastern Eurasia. The continental Chinese species *Plestiodon capito* (Bocourt, 1879) (formerly *Plestiodon xanthi* [Günther, 1889]; Smith, Smith & Guibe, 1975) and *Plestiodon tunganus* (Stejneger, 1924) are sister taxa (clade B1 in Fig. 3), and represent one of the two basal divergences in clade B. Species in clade B2 mostly (*P. japonicus*; Hikida, 1993) or exclusively (the others) inhabit the Japanese archipelago. One exception is *P. elegans* that broadly inhabits China (including Taiwan) and a few continental shelf islands of Japan (Ota *et al*., 1993). The placement of the Ryukyu Islands *P. barbouri* in a clade containing primarily mainland *P. japonicus* (formerly *P. latiscutatus*; Motokawa & Hikida, 2003) and *P. latiscutatus* [formerly *Plestiodon okadae* (Stejneger, 1907); Motokawa & Hikida, 2003] is only weakly supported in the concatenated data analyses (PP = 0.72) and simultaneous nuclear gene tree/species tree *BEAST analysis (PP = 0.84; Fig. 4a). There is strong support for the sister relationship of *P. japonicus* and *P. latiscutatus* in the analyses of the concatenated, *MKL1*, *R35*, and *RAG1* analyses. However, the mtDNA tree strongly supports the exclusion of *P. latiscutatus* from both the *P. barbouri* + *P. japonicus* clade and the rest of clade B2 (Fig. S2).

The sister relationship between the primarily continental Chinese and Taiwanese *P. elegans* and a clade composed of the Ryukyu Islands *P. marginatus* + *P. stimpsonii* is strongly supported in the concatenated data analysis, but none of the individual nuclear gene analyses strongly support or reject this arrangement. However, the analysis of mtDNA strongly supports the sister relationship of *P. elegans* and *P. stimpsonii* (Fig. S2), a result that is congruent with Honda *et al*. (2008)'s analysis of mitochondrial *12S* and *16S* ribosomal RNA but incongruent with the concatenated data. The *BEAST analyses of seven of the eight nuclear loci strongly support the sister relationship of *P. marginatus* and *P. stimpsonii* (PP = 0.95), thus rejecting the mtDNA results (Fig. 4a). The current subspecific classification of *P. marginatus* (see Nakamura & Uéno, 1963; Toyama, 1989) is statistically rejected as the sampled representative of *Plestiodon marginatus marginatus* Hallowell, 1861 from Okinawa is nested within *Plestiodon marginatus oshimensis* (Thompson, 1912) and sister to the geographically proximate Yoronjima population of *P. m. oshimensis*.

Clade C

Members of clade C exclusively inhabit North and Middle America (including Bermuda; see also

Brandley *et al*., 2010a). For clarity, we identify five separate subclades for individual discussion (labelled C1–C5 in Fig. 3).

Clade C1 is essentially Robinson's (1979) *brevirostris* group, but with the addition of *P. sumichrasti* and *Plestiodon lynxe* (Wiegmann, 1834). *Plestiodon brevirostris*, as currently recognized, is polyphyletic (see also Fería-Ortíz *et al*., 2011). The sampled populations of *P. b. brevirostris*, *P. b. bilineatus*, and *P. b. dicei* form their respective clades, but they are not each other's closest relatives. More importantly, the two sampled *P. b. indubitus* populations reside in completely separate subclades within clade C1, with one the sister lineage to *P. dugesii* and the other the sister to *P. b. brevirostris*. Although support throughout most of this clade is high, inspection of the individual gene trees reveals two cases of significant incongruence or ambiguous phylogenetic relationships. In contrast to the concatenated data tree, and the mtDNA (Fig. S2) and *RAG1* (Fig. S8) trees, the *R35* tree (Fig. S7) strongly excludes *P. copei* from the clade containing *P. b. bilineatus*, *P. b. indubitus*, and *P. dugesii*. In addition, the *UBN1* analysis strongly supports the sister relationship between *P. b. dicei* and *P. parviauriculatus*. More notable is the overall lack of resolution among the species lineages across the gene trees. This is especially evident in the *BEAST analysis of the nuclear loci that infers strong support only for the sister relationship between *P. b. brevirostris* and one population of *P. b. indubitus*, as well as a clade containing *P. dugesii*, *P. b. indubitus*, and *P. b. bilineatus* (Fig. 4b).

Clade C2 consists solely of the Bermudian endemic, *Plestiodon longirostris* Cope, 1861. Although the data most strongly suggest it has a sister relationship with clade C3, this hypothesis is not significantly strongly supported (PP = 0.87; see also Brandley *et al*., 2010a).

Clade C3 includes species inhabiting western Canada and the USA, and the Mexican Baja California peninsula. Previous analyses have indicated that the current species designations (*P. gilberti*, *P. lagunensis*, and *P. skiltonianus*) underestimate the species diversity (Richmond & Reeder, 2002), and that these 'species' are in fact part of a large species complex. The sampling in the current study includes members of four clades of the *skiltonianus/gilberti* species complex (labelled A, F, G, and I in Figures 3 and S2–S10 of this paper; these labels correspond to the clade labels in Richmond & Reeder 2002: fig. 4). There is no strong support for the monophyly of *P. gilberti* or *P. skiltonianus*, and *P. lagunensis* is supported as sister to a clade of *P. skiltonianus* inhabiting southern California and Utah (clade G in Richmond & Reeder 2002). The individual gene trees either strongly support this relationship or do not strongly conflict with it, with one exception: the *PRLR* tree that supports the sister relationship of the two sampled populations of *P. gilberti* (Fig. S5). The *R35* analysis (Fig. S7) also infers *P. gilberti* monophyly, but this relationship is only moderately supported (PP = 0.88).

Clade C4 comprises a well-supported clade of two small, attenuate, endemic Florida species: *Plestiodon egregius* Baird, 1859 and the severely limb-reduced *Plestiodon reynoldsi* (Stejneger, 1910) (formerly *Neoseps*; Brandley *et al*., 2005). This relationship is consistent across all gene trees, mostly with very high support (e.g. PP > 0.90).

Clade C5 contains eight species of relatively large-bodied skinks that inhabit wide regions of Southern Canada, the USA, and northern Mexico. The concatenated data analysis infers a basal split between *Plestiodon anthracinus* Baird, 1849 and the remaining species in clade C5. Whereas most of the gene trees infer ambiguous support for the placement of *P. anthracinus*, the mtDNA infers strong support for the alternative sister relationship of this species and the *P. egregius* Baird, 1859 + *P. reynoldsi* (C4) clade. The three phenotypically similar species, *Plestiodon fasciatus* (Linnaeus, 1758), *Plestiodon inexpectatus* (Taylor, 1932), and *Plestiodon laticeps* (Schneider, 1801) do not form an exclusive clade. Instead *P. fasciatus* is the sister species to *Plestiodon septentrionalis* Baird, 1858, whereas *P. inexpectatus* and *P. laticeps* are sister taxa. However, there exist three strongly supported incongruities among gene trees for these four (including *P. septentrionalis*) taxa. The mtDNA tree excludes *P. laticeps* from a clade containing all three other species; although this relationship is not strongly supported, the posterior probability (0.94) is high. The *R35* analysis (Fig. S7) infers the sister relationship between *P. septentrionalis* and *Plestiodon multivirgatus* Hallowell, 1857. Finally, the *MKL1* gene (Fig. S4) supports the sister relationship between *P. inexpectatus* and *Plestiodon tetragrammus* Baird, 1859 (PP = 0.97). With the exception of the relationships inferred by the *MKL1*, *R35*, and *PRLR* genes, the concatenated data and the remaining gene trees infer a sister relationship of *P. multivirgatus* and *P. tetragrammus* with varied statistical support.

DISCUSSION

Skink phylogeny and the placement of *Plestiodon*

Although they constitute the largest lizard family in terms of species, skinks have only recently been the subject of molecular phylogenetic analysis. These studies (Whiting *et al*., 2003; Brandley *et al*., 2005, 2011; Austin & Arnold, 2006; Siler & Brown, 2011;

Siler *et al*., 2011; Skinner *et al*., 2011) have both supported and refuted many of the relationships proposed by previous morphological analyses (Taylor, 1935; Greer, 1970a, b). However, many relationships, especially 'deep' relationships among the major skink lineages, have remained poorly supported, or in at least one case (the monophyly of Lygosominae), completely conflicting (Greer, 1986; Whiting *et al*., 2003; Brandley *et al*., 2005, 2011; Siler & Brown, 2011; Siler *et al*., 2011; Skinner *et al*., 2011). In his pioneering evolutionary taxonomy of skinks, Greer (1970a, b) identified four scincid subfamilies: Acontinae, Feylinae, Lygosominae, and Scincinae, and assumed that Scincinae was a group from which the three other subfamilies were derived (thereby rendering it paraphyletic). Subsequent studies have demonstrated conclusively that the enigmatic Feylinae (not included in this study) is closely related to the southern African 'scincines' *Melanoseps* and *Typhlacontias* (Whiting *et al*., 2003; Brandley *et al*., 2005). However, a well-supported phylogenetic placement of the lygosomines with major 'scincine' lineages has remained elusive. Our study does much to revise the existing phylogenetic framework of skinks resolving several additional 'deep' relationships, including the placement of Acontinae, Lygosominae, and 'Scincinae'.

Our results strongly support a basal split within Scincidae between the limbless acontines (represented by *Typhlosaurus* sp. in Figs 2 and S1) and all other skinks, thereby corroborating the results of Whiting *et al*. (2003) and Skinner *et al*. (2011). This phylogenetic relationship has bearing on the evolution of limb reduction in skinks. Complete limblessness has evolved independently ~25 times among squamate reptiles, with the majority of these derivations ocurring within Scincidae (Greer, 1991; Wiens *et al*., 2006; Brandley *et al*., 2008; Siler *et al*., 2011). Although we lack sufficient phylogenetic evidence to evaluate the ancestral body plan of scincid lizards, that acontines represent one of the two earliest lineages of crown Scincidae suggests that limb reduction may have been a feature of scincid evolution for a very long time (79–114 Mya; Brandley *et al*., 2008, 2011).

Lygosomines represent the bulk of species diversity in skinks. Although our sampling of lygosomines is low, we sampled four of its five major lineages: the *Eugongylus* group [represented by *Emoia caeruleocauda* (De Vis, 1892)], the *Lygosoma* group [*Lygosoma brevicaudis* Greer, Grandison, & Barbault, 1985], the *Mabuya* group [*Trachylepis perrotetii* (Duméril & Bibron, 1839)], and the *Sphenomorphus* group [*Scincella lateralis* (Say, 1823)]; but not the *Egernia* group. This therefore allows us to make a cursory evaluation of competing hypotheses of 'deep' lygosomine relationships. Molecular studies that have focused specifically on lygosomine relationships have supported the *Sphenomorphus* group as the sister lineage to all other lygosomine skinks (Honda *et al*., 2000, 2003; Reeder, 2003; Austin & Arnold, 2006; Linkem, Diesmos & Brown, 2011; Skinner *et al*., 2011), a result congruent with our analysis of the concatenated data (Fig. 2). However, the relationships of the remaining groups differ among these studies. With the caveat that we did not sample the *Egernia* group, our results support Reeder (2003) and Skinner *et al*. (2011) who inferred strong support for a clade composed of (*Mabuya* (*Lygosoma* + *Eugongylus*)) groups. That Austin & Arnold (2006) did not sample the *Lygosoma* group makes comparison with our study uninformative. With the exception of the placement of the *Sphenomorphus* group, our results are completely incongruent with Honda *et al*. (2000, 2003), but we note that these relationships were not strongly supported in those studies.

With one exception, the individual gene tree analyses either support the same relationships as the concatenated data or are not strongly incongruent; the mtDNA gene tree (Fig. S2) supports a sister relationship between the *Mabuya* and *Sphenomorphus* group. We speculate that this relationship is explained by homoplasy resulting from a combination of the relatively rapid evolution of mtDNA and the relatively old age of lygosomines (see Brandley *et al*., 2011; Skinner *et al*., 2011): a problem that is probably exacerbated by our low level of taxon sampling. Even with explicit model-based methods (e.g. maximum likelihood and Bayesian), extreme homoplasy can nonetheless lead to high support for incorrect relationships (Felsenstein, 1978, 1985; Brandley *et al*., 2006, 2009).

When compared with previous molecular phylogenetic studies of scincid relationships, perhaps the most notable result in the current study is an increased resolution among the 'scincine' genera. Our multilocus phylogenetic analysis reveals multiple, well-supported novel 'scincine' relationships. Although previous studies have inferred a close phylogenetic affinity of the 'scincine' genera inhabiting Africa, Madagascar, and the Seychelles, ours is the first to infer very strong support for the interrelationships of many of these lineages. We find the Seychellois *Janetaescincus*, North African and Mediterranean *Chalcides* (and presumably *Sphenops*; Brandley *et al*., 2005; Carranza *et al*., 2008), Southern African *Melanoseps*, and Malagasy *Voeltzkowia* and *Amphiglossus* + *Paracontias* form progressively more exclusive clades. Only the mtDNA gene tree (Fig. S2) supports a strongly incongruent relationship by supporting a clade that is exclusive of *Melanoseps*. The geographical distribution of these genera suggests that the break-up of Gondwana played a major role in

the phylogenetic history of the clade; however, inclusion of the Indian and Sri Lankan genera in future analyses will be critical for testing this hypothesis. We note that we did not fully sample other African, Malagasy, and Mauritian 'scincine' genera, but we can infer from other studies that they too are members of this larger clade (Whiting *et al*., 2003; Brandley *et al*., 2005; Schmitz *et al*., 2005). We also infer strong support for the sister relationship of this putatively Gondwanan clade with the primarily Laurasian-distributed *Eumeces s.l.*, *Scincus*, and *Scincopus*.

The phylogenetic affinities of *Ophiomorus* and *Brachymeles* are complex. Although our concatenated data analysis did not infer strong support for the placement of either genus, inspection of the 95% credible set of unique topologies reveals that 837 of 2816 trees are compatible with 'scincine' monophyly (not shown). In other words, although we cannot strongly support the placement of these genera, we also cannot statistically reject their placement in a monophyletic Scincinae. The *RAG1* gene tree (Fig. S1g) also strongly supports 'scincine' monophyly. However, the SNCAIP tree strongly supports *Brachymeles* in a clade containing the four lygosomine genera (Fig. S1h). Brandley *et al*.'s (2011) time-calibrated analysis of a smaller data set (see Brandley *et al*., 2011: appendix IV) infers strong support for the sister relationship of *Brachymeles* and Lygosominae (PP = 1.0), and the sister relationship of *Ophiomorus* and all other 'scincines' (PP = 0.96).

Different taxon and gene sampling may explain the discrepancies between Brandley *et al*. (2011) and the current study. An alternative explanation is that, unlike the current study, Brandley *et al*. (2011) used a relaxed molecular clock model of evolution that attempts to correct for rate heterogeneity amongst lineages for the purposes of divergence date estimation. Regardless, because the relationships of these two genera are strongly supported in Brandley *et al*. (2011), and our present phylogenetic results do not strongly conflict with that study, we argue that the Brandley *et al*. (2011) tree may be a better estimate of the relationships of *Brachymeles* and *Ophiomorus* in the absence of more phylogenetic evidence.

We infer strong support for the hypothesis that *Plestiodon* and other *Eumeces s.l.* genera do not represent the earliest diverging lineage of skinks. These results therefore refute Greer's (1970a) hypothesis that 'Morphologically, *Eumeces* [*s.l.*] is very possible the most primitive living skink taxon and may, in fact, be quite similar to the ancestor of all skinks'. Although the genus '*Eumeces*' was long considered to be monophyletic, numerous recent studies have rejected this hypothesis (Griffith *et al*., 2000; Schmitz *et al*., 2004; Brandley *et al*., 2005). These studies are also in concordance with karyotypic studies that have demonstrated that three of the four genera possess unique shared, derived karyotypes, $2N = 32$ in *Eumeces s.s.* (Gorman, 1973; Caputo *et al*., 1993; Caputo, Odierna & Aprea, 1994), $2N = 28$ in *Eurylepis* (Ivanov & Bogdanov, 1975; Kupriyanova, 1986; Eremchenko, Panfilov & Tsarinenko, 1992), and $2N = 26$ in *Plestiodon* (e.g. Deweese & Wright, 1970; McDiarmid & Wright, 1976; Kato *et al*., 1998). The karyotype of *Mesoscincus* is unknown. However, these molecular and karyotype studies are only able to reject monophyly, and are unable to elucidate with strong support the phylogenetic affinities of the four genera that were once part of *Eumeces s.l.* (*Eumeces s.s.*, *Eurylepis*, *Mesoscincus*, and *Plestiodon*). The concatenated data tree, and all nine gene trees, support a clade composed of *Eumeces s.s.*, *Scincopus*, and *Scincus*, to the exclusion of all other skink genera. Moreover, the concatenated data also support *Eurylepis* as the sister lineage to this clade. The precise phylogenetic affinities of *Mesoscincus* and *Plestiodon* remain elusive, although we note that our concatenated data tree at least excludes them from lygosomines, acontines, *Ophiomorus*, and *Brachymeles*.

The phylogeny of *Plestiodon*

The phylogenetic analyses in this study strongly support the existence of three biogeographically cohesive clades of *Plestiodon* with clades A and B inhabiting East Asia, and clade C inhabiting North and Middle America. This result is consistent with the biogeographical analysis of Brandley *et al*. (2011), who inferred that crown *Plestiodon* originated in Asia and subsequently dispersed to North America via Beringia 18–30 Mya. Our phylogenetic results strongly conflict with the previous taxonomic arrangement and morphological phylogenetic analyses (Taylor, 1935; Lieb, 1985; Hikida, 1993), which relied mostly on scale counts and shapes. Given the potentially high convergence exhibited by scale count and shape characters in lizards (e.g. Brandley & de Queiroz, 2004), it is likely that these phylogenies were misled by excessive morphological convergence Moreover, the relationships inferred by these previous studies, if an accurate representation of *Plestiodon* evolutionary history, would also imply highly improbable biogeographic relationships.

For organizational purposes, we will discuss how these results compare with previous phylogenetic hypotheses for each clade separately. We discuss the relationships within *Plestiodon* clade by clade, with reference to Figures 3 and S2–S10.

Clade A

These four species inhabit northern Indochina, southeastern China (including Taiwan), and the southern

Ryukyu Islands (Yaeyama and Miyako) of Japan, and represent the sister group to all remaining *Plestiodon* (Fig. 3). No previous phylogenetic or taxonomic study inferred a close relationship between these four species. However, simply re-rooting the morphological phylogeny of Hikida (1993) results in a tree that matches our concatenated phylogenetic analysis [if *Plestiodon obsoletus* Baird & Girard, 1852 is removed].

The sister relationship between *P. chinensis* and *P. kishinouyei* confirms the hypothesis of Taylor (1935) and Honda *et al*. (2008): that these species are closely related. This relationship and the close proximity of the southern Ryukyu Islands to south-eastern China (including Taiwan; Fig. 1) are congruent with the hypothesis that these landmasses were previously connected (Hikida & Ota, 1997; Hikida & Motokawa, 1999), and that *P. kishinouyei* represents a population that was isolated when the connection between these landmasses was severed. Taylor (1935) placed these two taxa in the *obsoletus* group, with the nominal species based on numerous shared character states, including the dark coloration of juveniles and overall coloration of adults. Indeed, the three species bear a striking resemblance, and their close relationship is supported by the phylogenetic examination of scalation and colour (Hikida, 1993). However, the results of the current multilocus phylogenetic analysis strongly reject a close relationship between these three taxa, and thus suggest that these similarities evolved convergently.

The phylogenetic placement of *P. tamdaoensis* within *Plestiodon* has varied since its original description (Bourret, 1937). Two authors placed this species in the *fasciatus* group *s.l.*, but did so without direct examination of specimens (Fitch, 1958; Lieb, 1985). An examination of additional specimens led Hikida & Darevsky (1987) to conclude, on the basis of body size and scalation characters, that *P. tamdaoensis* was most closely related to *P. chinensis* and *P. kishinouyei*. However, subsequent morphological phylogenetic analysis of the species suggested that *P. tamdaoensis* was isolated from any previously described species group (Hikida, 1993). The results of the current phylogenetic analysis support Hikida & Darevsky's (1987) hypothesis of a close relationship between these three species.

Based on the exclusively shared body coloration characterized by the lack of mid-dorsal stripe, both Taylor (1935) and Lieb (1985) assumed a close relationship between *P. quadrilineatus* and the North American *P. skiltonianus* group, despite that this relationship would imply a remarkable biogeographic distribution for sister species lineages (the western coast of North America and south-eastern Eurasia). This assumed relationship has been used as evidence that the distribution of these two clades is the result of dispersal to or from Asia, independent of any other dispersal events in the genus (Lazell & Ota, 2000; Lazell, 2004). However, this phylogenetic relationship, and indeed, this biogeographic scenario, is strongly rejected, as these species are not sister taxa, and the closest relatives of both of these species reside in their respective geographically proximate regions. From the perspective of morphology, the inclusion of *P. quadrilineatus* in clade A is also a surprising finding. All other species in clade A possess five yellow dorsal stripes (at least as juveniles), instead of the four stripes found in *P. quadrilineatus*. Additionally, *P. chinensis*, *P. kishinouyei*, and *P. tamdaoensis* are some of the largest known *Plestiodon* (~120, ~170, and ~130 mm snout–vent lengths, respectively; Taylor, 1935; Hikida & Darevsky, 1987; Hikida, Lau & Ota, 2001), and yet *P. quadrilineatus* attains a maximum snout–vent length of only ~77 mm (Taylor, 1935; Lazell & Ota, 2000). From a biogeographical perspective, however, this phylogenetic relationship is expected given the distribution of the species in the south-eastern part of continental China and northern Indochina.

Clade B

All of the taxa in this clade (Fig. 3) have been the subject of previous morphological or molecular phylogenetic analyses, but never in the context of a larger, genus-wide phylogeny. Our phylogenetic analysis (that does not include *P. liui* and *P. popei*) supports Hikida's (1993) hypothesis that the *capito* and *latiscutatus* groups are both monophyletic and sister clades. Additionally, a sister relationship between *P. capito* and *P. tunganus* is strongly supported (Taylor, 1935, as *P. xanthi*; Hikida, 1993). Although this relationship is unremarkable from a biogeographical perspective (both species inhabit central China), the two species bear little phenotypic resemblance to each other in either juvenile or adult coloration (M.C. Brandley, unpubl. data).

The present results are also concordant with numerous previous molecular analyses supporting the sister relationship of *P. japonicus* (formerly *P. latiscutatus*) and *P. latiscutatus* (formerly *P. okadae*)(Kato *et al*., 1994; Hikida & Motokawa, 1999; Motokawa & Hikida, 2003; Okamoto *et al*., 2006). However, there is a strong disagreement between the present study and previous analyses concerning the inter-relationships of the species that inhabit the Ryukyu Islands of Japan (*P. barbouri*, *P. marginatus*, and *P. stimpsonii*), and *P. elegans* that inhabits China (including Taiwan) and a few continental shelf islands of Japan. Analyses of the *R35* and RAG1 data strongly place *P. barbouri* in a clade with *P. japonicus* and *P. latiscutatus* (Figs S7, S8), but the

mtDNA strongly supports the sister relationship of *P. barbouri* and *P. japonicus*, and the position of *P. latiscutatus* sister to *P. capito* and *P. tunganus* (Fig. S2). The relationships inferred by mtDNA are almost certainly erroneous in this case, as they strongly conflict with the multiple independently evolving nuclear loci. The conflict between the mtDNA and nuclear data sets may be responsible for the weak support for *P. barbouri* in a clade with *P. japonicus* and *P. latiscutatus* in the concatenated data analysis. However, it is surprising that the *BEAST analysis of only the nuclear data does not significantly support the placement of *P. barbouri*, despite none of the nuclear loci strongly supporting conflicting relationships. Although our study does not infer statistically significant support for the phylogenetic affinity of *P. barbouri*, our nuclear and concatenated data analyses nonetheless consistently place it sister to *P. japonicus* + *P. latiscutatus*, as was argued in some previous publications on the basis of a few morphological characters (Taylor, 1935) and geographical distribution patterns of these and other species (Hikida, 1978b; Toyama, 1989).

A recent phylogenetic analysis of mtDNA (*12S* and *16S* mitochondrial rRNA: Honda *et al*., 2008) strongly supports the sister relationship of *P. elegans* and *P. stimpsonii*, to the exclusion of *P. marginatus*. This sister relationship contrasts with the results of previous allozyme (Kato *et al*., 1994) and morphological (Hikida, 1993) analyses that inferred the sister relationship of *P. marginatus* and *P. stimpsonii*. Our phylogenetic analyses of mtDNA (Fig. S2) also support the results of Honda *et al*. (2008), yet our concatenated data analysis (Fig. 3) supports the previous allozyme and morphological studies that instead support the sister relationship of *P. marginatus* and *P. stimpsonii*. Although none of the nuclear gene analyses strongly support any resolution of these three species, the *BEAST analysis of seven of the eight nuclear loci also strongly support the concatenated data results (Fig. 4). It is therefore clear that the discrepancy between the results of the nuclear genes and the mtDNA in the analyses of Honda *et al*. (2008) and herein solely arises from the mtDNA not tracking species history (see Potential sources of gene tree conflict). Finally, the data do not support the current arrangement of the two subspecies of *P. marginatus*, *P. m. marginatus*, and *P. m. oshimensis*, as the concatenated, *R35*, and *RAG1* phylogenies do not support the monophyly of the latter subspecies, by placing the sample from Yoronjima (*P. m. oshimensis*) closest to *P. m. marginatus* from Okinawa. This result is concordant with a few previous studies that support a closer affinity of the southern Amami Islands (Yoronjima and Okinoerabujima) populations of *P. m. oshimensis* to *P. m marginatus* from the Okinawa Islands than to the 'consubspecific' populations from the northern Amami Islands (Kato *et al*., 1994; Honda *et al*., 2008).

Clade C

All of the species in clade C (Fig. 3) inhabit North and Central America, and there is a strong support for five major subclades. Although subject to numerous taxonomic studies (Taylor, 1935; Dixon, 1969; Robinson, 1979; Lieb, 1985), when compared with Asian *Plestiodon*, North American species have been subject to quite limited molecular phylogenetic analysis. Those studies including North American species have typically focused on a very narrow set of taxa (Murphy *et al*., 1983; Richmond & Reeder, 2002; Schmitz *et al*., 2004; Macey *et al*., 2006; Richmond, 2006), or have only included a few representatives in a larger analysis of skink relationships (Whiting *et al*., 2003; Brandley *et al*., 2005). Thus, there are few existing hypotheses with which to compare the present multilocus phylogenetic analysis.

Clade C1 is composed of taxa primarily inhabiting the central Mexican highlands. Most of these species were formerly placed in the *brevirostris* group (*sensu* Dixon, 1969; Robinson, 1979). Although the results of our current phylogenetic analyses support a close relationship between most of the formerly recognized *brevirostris* group species, the group is not monophyletic with respect to both *P. lynxe* and *P. sumichrasti*. The inclusion of *P. lynxe* is not surprising given that, as with the other *brevirostris* group taxa, it shares a miniaturized, elongate body plan (Griffith, 1991). However, *P. sumichrasti* is a large-bodied species that superficially resembles the American *fasciatus* group. It is possible that the *P. sumichrasti* lineage has simply retained the ancestral *Plestiodon* body plan. However, this would require multiple independent derivations of the miniaturized body form seen in other *brevirostris* group taxa and *P. lynxe* (depending on the resolution of the tree). Instead, a more parsimonious explanation is that *P. sumichrasti* represents an independent derivation of a large body from a miniaturized ancestor. However, this independent derivation of a large, stout body involves more than simply overall tissue growth, including the evolutionary loss of up to four pre-sacral vertebrae (Griffith, 1990; M.C. Brandley, unpubl. data), thereby making this a more remarkable phenomenon. Our phylogenetic results are highly concordant with phylogenetic analyses of mtDNA for most *brevirostris* group species. One notable difference between these studies is the placement of *P. parvirauriculatus*. Our concatenated data tree strongly places this species in a more derived position (Fig. 3). However, this discordance is explained by our addition of nuclear loci that may

conflict with the mtDNA gene tree. Indeed, our mtDNA results (Fig. S2) are highly similar to those of Fería-Ortíz *et al*. (2011).

Dixon's (1969) *brevirostris* group taxonomy correctly indicates the phylogenetic exclusivity of *P. copei*, *P. dugesii*, and *P. ochoteranae*, but nonetheless underestimates the phylogenetic diversity within *P. brevirostris*. The four sampled subspecies do not form a clade, and are instead distributed throughout clade C1. One subspecies, *P. b. indubitus*, is itself indubitably polyphyletic, with the western population individual (sample 1 in Fig. 3), representing the sister lineage to *P. dugesii*, and the eastern population sample is the sister lineage to *P. b. brevirostris* (sample 2 in Fig. 3). Therefore, with the exception of *P. b. indubitus*, our results provide strong phylogenetic evidence to recognize each of the *P. brevirostris* subspecies as species. Moreover, our results are congruent with the *P. brevirostris* species delimitation analysis of Fería-Ortíz *et al*. (2011), who, on the basis of both mtDNA and morphological data, elevated *P. b. brevirostris*, *P. b. bilineatus*, *P. b dicei*, and eastern and western populations of *P. b. indubitus* to species. The status of *P. b. pineus* (not sampled in this study) remains uncertain (see Fería-Ortíz *et al*., 2011).

The phylogenetic placement of the Bermudian endemic *P. longrostris* (Fig. 3; clade C2) has long puzzled skink researchers. In Taylor's (1935) taxonomic and 'phylogenetic' hierarchy, *P. longirostris* represents the sole member of one of the three major groups of *Eumeces s.l.*, implying a distant relationship from all other *Plestiodon*. The phylogenetic affinities of *P. longirostris* to other *Plestiodon* were ambiguous in a previous phylogenetic analysis (Brandley *et al*., 2005), but that study only included seven species of *Plestiodon*. The present analysis strongly supports the inclusion of *P. longirostris* with the other North American species, but only weakly supports its relationship to the large-bodied species of western North America (clade C3). Regardless, *P. longirostris* is the sole representative of a *Plestiodon* lineage that diverged very early in the history of the North and Middle American clade (clade C; Fig. 3). These results are consistent with those of Brandley *et al*. (2010a), and support the hypothesis that the island of Bermuda, an island that is just 1–2 Myr old, nonetheless harbours one of the oldest extant lineages of North American skinks that diverged ~12–20 Mya.

The strongly supported phylogenetic relationships within the *skiltonianus* group (*P. gilberti*, *P. lagunensis*, and *P. skiltonianus*; clade C3; Fig. 3) corroborate those previously inferred by Richmond & Reeder (2002), although the latter study included many more populations than our study. Richmond & Reeder (2002) did not make taxonomic changes to the group for a variety of reasons, one of which was the lack of support or resolution of the relationship between the *P. skiltonianus* group and other species of *Plestiodon*. Thus, they could not exclude the possibility of paraphyly (although unlikely) with respect to other recognized species. The results of the current study exhibit strong evidence that the *P. skiltonianus* complex is monophyletic, and that the current three-species taxonomy severely underestimates the species diversity in this group.

The membership of clade C4 (Fig. 3) is notable because it strongly supports the inclusion of *P. anthracinus* to the exclusion of *P. septentrionalis*, two species that were previously thought to be closely related (Taylor, 1935; but see Schmitz *et al*., 2004), but also because it corroborates conclusions from previous studies that the critically endangered sand skink *P. reynoldsi* is deeply nested within *Plestiodon* (Richmond & Reeder, 2002; Schmitz *et al*., 2004; Brandley *et al*., 2005).

Plestiodon reynoldsi has a body plan so radically different from its congeners that it was formerly placed in a separate genus (*Neoseps*). It has very short limbs, and only a single digit remains on the forelimb and one or two digits remain on the hindlimb (Telford, 1959). Additionally, the head is shovel like, with reduced eyes and no external ear opening. All of these characters are likely adaptations for burrowing in the sand dunes of Central Florida. Its sister species, *P. egregius*, is also notable for its trunk elongation and short limbs, but not nearly to the extent seen in *P. reynoldsi*.

The morphology and phylogenetic relationship of *P. reynoldsi* is notable because it represents a relatively recent evolution of a highly specialized body plan within a group of lizards that exhibit little morphological diversity. This suggests that the underlying developmental genetic mechanisms that constrain body form evolution in *Plestiodon* have been radically altered in *P. reynoldsi*. However, this body form transformation may have been 'easier' in the *P. reynoldsi* species lineage than in other *Plestiodon* species lineages. Although other *Plestiodon* species do not differ markedly in body plan, there is nonetheless a subtle diversity in relative body length ranging from large 'stocky' species with relatively short trunks composed of 26 pre-sacral vertebrae (e.g. the *chinensis* group) to the small, elongate species of the *brevirostris* group (except *P. sumichrasti*) and *P. egregius*, which possess up to 33 pre-sacral vertebrae (Griffith, 1990, 1991; M.C. Brandley, unpubl. data). Limb reduction is an extremely common phenomenon in squamate reptiles (Greer, 1991; Wiens *et al*., 2006; Brandley *et al*., 2008; Siler & Brown, 2011), and it is clear that body elongation and limb reduction are an adaptation for burrowing in many lizard lineages (Wiens *et al*., 2006; Brandley *et al*., 2008). The

common ancestor of *P. egregius* (31–33 pre-sacral vertebrae; M.C. Brandley, unpubl. data) and *P. reynoldsi* (41–42 pre-sacral vertebrae; M.C. Brandley, unpubl. data) was almost certainly elongate. Moreover, both species inhabit sandy soils, with *P. reynoldsi* restricted to sand dunes in central Florida, USA. We speculate that although there are other elongate *Plestiodon* species (especially in the *brevirostris* group), the unique combination of ecological (sandy soils), developmental genetic (body elongation), and selective forces (locomotion/burrowing) explains the radical body transformation in *P. reynoldsi*. Uncovering the underlying developmental genetic framework of this transformation would be a fruitful topic of research.

Clade C5 comprises primarily large-bodied species, many of which were once placed in multiple distinct species groups. The three species, *P. fasciatus*, *P. inexpectatus*, and *P. laticeps* are phenotypically similar, and are frequently subject to mistaken identification. *Plestiodon inexpectatus* was only described after careful analysis of specimens previously described as *P. fasciatus* or *P. laticeps* (Taylor, 1932). In fact, an early molecular analysis of the three species did not contain any additional out-groups, as monophyly was assumed (Murphy *et al*., 1983). However, recent studies have found evidence that these three species do not form a clade exclusive of other *Plestiodon* (Richmond & Reeder, 2002; Schmitz *et al*., 2004; Macey *et al*., 2006; Richmond, 2006), a result strongly supported by our phylogenetic analyses.

Although all three species do not form an exclusive clade, the analysis of the concatenated nine-locus data set (Fig. 3) as well as analysis of the individual *PRLR* (Fig. S5) and *R35* (Fig. S7) data sets nonetheless support the sister relationship of *P. inexpectatus* and *P. laticeps* (it is also very highly supported by the *SNCAIP* data; PP = 0.94; Fig. S9). On the basis of phylogenetic analyses of mtDNA, Richmond (2006) found that none of these three species are sister taxa, a result that is concordant with our analyses of mtDNA (Fig. S2). The proponderance of the DNA evidence therefore suggests that the mtDNA is not tracking species history. However, this claim can only be evaluated by extensively collecting more nuclear loci with which to compare the mtDNA results.

The relationships of the non-*fasciatus* group species in clade C5 are also notable because of their phenotypic dissimilarity. The juveniles of *P. obsoletus*, for example, have a deep black coloration – a trait only shared with the distantly related *P. chinensis* and *P. kishinouyei*. The phylogeny also rejects the previous hypothesis of a close relationship between *P. callicephalus* and *P. tetragrammus*, as well as a close relationship of these species to *P. anthracinus* (Lieb, 1985).

Potential sources of gene tree conflict

There are numerous examples of strongly supported conflict between phylogenetic relationships inferred by the gene trees and the concatenated data analysis (the species tree), and these conflicting phylogenetic hypotheses have bearing on the subsequent interpretation of *Plestiodon* biology. Below, we outline several potential explanations for incongruent hypotheses of species relationships in two clades, including: (1) mtDNA and nuclear loci conflict in the East Asian *P. elegans*, *P. marginatus*, and *P. stimpsonii*; and (2) different phylogenetic resolutions of species in the Middle American *brevirostris* group (*sensu* this study) in all loci.

As phylogenetic analyses incorporate more independently evolving loci, it is becoming apparent that significant conflict between gene trees is the norm rather than the exception (for a review, see Edwards, 2009). There are many potential sources for this conflict, including error in the phylogenetic reconstruction, ancestral polymorphism, incomplete lineage sorting (Maddison & Knowles, 2006; Carstens & Knowles, 2007), and hybridization and mitochondrial introgression (e.g. Leaché & Cole, 2007; McGuire *et al*., 2007; Brandley *et al*., 2010b). Any of these phenomena may ultimately explain the incongruent relationships inferred by our data, and in the absence of significantly more data from independently evolving nuclear loci, we cannot confidently exclude any of them. However, we can nonetheless provide varying support for each of these hypotheses.

Homoplasy, shared similarities among taxa that do not arise by common ancestry, could introduce sufficient 'phylogenetic noise' that may potentially mislead our phylogenetic reconstruction (Felsenstein, 1978, 1985; Huelsenbeck, 1995; Brandley *et al*., 2009). Indeed, in their molecular divergence dating analysis of *Plestiodon*, Brandley *et al*. (2011) found that the rapid evolution of mtDNA effectively obliterated any evidence of an underlying rate of evolution. As the current study uses the same quickly evolving mtDNA gene, it is highly likely that this explains many of the numerous strongly supported conflicting relationships between the mtDNA and nuclear and concatenated data sets.

The *P. elegans* + *P. marginatus* +*P. stimpsonii* clade (B2) is a notable example of conflict between the mtDNA tree and those of the other data sets. The mtDNA analysis supports the sister relationship of *P. elegans* and *P. stimpsonii*, yet the concatenated data and *BEAST analyses of seven of the eight nuclear loci (*UBN1* was excluded) support the sister relationship of *P. marginatus* and *P. stimpsonii*. Could this conflict be explained by error in phylogenic reconstruction as a result of homoplasy?

Simply re-rooting the mtDNA tree with *P. elegans* results in a relationship identical to the concatenated and *BEAST trees. However, it is important to note that the probability of convergently evolving the same nucleotide state increases with both the rate of evolution and time. Thus, we expect levels of homoplasy to be highest in deeper relationships of the tree. In the case of *Plestiodon* erroneous phylogenetic reconstruction is less likely to explain the conflict seen in the *P. elegans* + *P. marginatus* + *P. stimpsonii* clade. It is also an unlikely explanation of the phylogenetic conflict amongst genes in the *brevirostris* group. Such an explanation would require the failure of phylogenetic analysis for most or all loci. Because there is conflict amongst the slowly evolving nuclear genes, this explanation is highly unlikely.

Additional explanations for gene tree and gene tree/species tree conflict include incomplete lineage sorting (ILS) and ancestral polymorphism (e.g. Carstens & Knowles, 2007; McGuire *et al*., 2007; Leaché, 2009). These are phenomena where ancestral alleles (or mtDNA haplotypes) that are present before a lineage splits are retained in its descendant lineages after the divergence (i.e. not lost to genetic drift; Maddison, 1997). Because the chance of retaining these ancestral alleles increases with recent divergences (e.g. Carstens & Knowles, 2007; McGuire *et al*., 2007; Leaché, 2009), this may be a plausible explanation for the incongruence between the mtDNA and nuclear loci analyses for the relationships of *P. elegans*, *P. marginatus*, and *P. stimpsonii*. However, this is an unlikely explanation for the incongruence between the mtDNA and nuclear loci analyses for the relationships of *P. elegans*, *P. marginatus*, and *P. stimpsonii*, because the rapid evolution of the mtDNA results in the rapid production and loss of haplotypes as a result of drift.

On the other hand, ancestral polypmorphism and ILS may be plausible explanations for the gene tree conflict amongst the *brevirostris* group species. Although the concatenated data analysis strongly supports many of the relationships within this group, inspection of the individual gene trees reveals that many of the 'backbone' relationships are poorly resolved. Our additional gene tree/species tree analyses using the multispecies coalescent in *BEAST revealed almost no phylogenetic structure in the *brevirostris* group. This suggests that these loci represent different evolutionary histories, and we lack sufficient loci to infer the genealogical relationships among species. Moreover, the unresolved relationships amongst the species across most loci may also be evidence that these lineages rapidly radiated. Because ancestral polymorphisms are lost because of drift, incomplete lineage sorting is fundamentally an issue of time and population size. Coalescent theory predicts that the maintenance of large population sizes in a short time period increases the probability of retaining ancestral polymorphisms (Degnan & Rosenberg, 2006; Kubatko & Degnan, 2007; Belfiore, Liu & Moritz, 2008). This explanation can only be tested with the collection of many more independently evolving nuclear loci, and is a fruitful area of future research.

Hybridization (or mitochondrial introgression) between one or more species lineages may be an additional explanation for the conflicting relationships among *P. elegans*, *P. marginatus*, and *P. stimpsonii* between the mtDNA and other phylogenies. The geological history of the Ryukyu Archipelago is complex, but is it widely agreed that reduced sea levels caused by glaciation in the Pliocene and Pleistocene resulted in terrestrial connections between many Ryukyu Islands (Hikida & Ota, 1997; Ota, 1998, 2000, 2003). During the Pleistocene, there may have been a continual or nearly continual terrestrial connection from continental China through Taiwan, where *P. elegans* occurs, and the southern Ryukyu Islands, where *P. stimpsonii* occurs, terminating at the central Ryukyu Islands, where *P. marginatus* occurs (Kizaki & Oshiro, 1980; Ota, 1998, 2000). Thus, one hypothesis to explain the gene tree conflict is that there was significant gene flow among these islands during these time periods when some of the islands were either connected or geographically much closer (and thus, making oceanic dispersal more likely). However, this explanation predicts two unlikely outcomes. Assuming that hybridization was not female biased, if interbreeding occurred in the past we would also expect evidence of this in the nuclear genes, of which there is none. Second, if only mitochondria introgressed into other species, this would require at least two independent events between two of these species, and that these introgressed mitochondria were present in all of the samples used in this study.

The current parapatric distribution of several highland species in the *brevirostris* group has permitted some hybridization in the recent past, or even currently (Fería-Ortíz *et al*., 2011). This may be the case for *P. bilineatus* and western populations of *P. indubitus* (and perhaps even *P. dugesii* in the western portion of the Mexican Transvolcanic Belt and southern end of the Sierra Madre Occidental), *P. brevirostris* and *P. indubitus* of the central portion of the Mexican Transvolcanic Belt, and *P. b. dicei* and *P. b. pineus* (not included in this study) in the northern portion of the Sierra Madre Oriental. In fact, the existence of 'intergradation' between the species in each of these areas (except for *P. dugesii*) has been suggested previously (Axtell, 1960; Dixon, 1969;

Robinson, 1979), although the morphological evidence for this is not extensive (e.g. individuals of a given species with mtDNA from some other species; Fería-Ortíz *et al*., 2011).

Many of the *brevirostris* group species inhabit moderately high mountain ranges in Mexico, west of the Isthmus of Tehuantepec, exclusive of the Peninsula de Baja California. They may be classic 'sky island' species (e.g. Knowles, 2001; Shepard & Burbrink, 2008) in that, although their geographical distribution is currently restricted, during times of climate cooling, these disjunct populations are joined by contiguous suitable habitat, thereby facilitating gene flow among species. The distribution of cloud forest and mesic forests in general was likely to be far more widespread during colder and wetter times in the Pleistocene (Toledo, 1982), which may have facilitated gene flow among multiple *brevirostris* group lineages in the southern end of the Sierra Madre Occidental and the Central portion and western end of the Mexican Transvolcanic Belt. Such episodes, alternating with drier and warmer periods that re-isolated the genetic lineages, could have also resulted in differentiation of the three groups of populations of *P. brevirostris*. Finally, colder and wetter episodes during the Pleistocene would certainly have permitted, or made easier, hybridization between all of the above taxa and other highland species, including *P. colimensis*, *P. copei*, *P. lynxe*, and *P. ochoterenae*; however, there is little morphological evidence for this hypothesis.

In summary, although we can only speculate on the cause of the conflicting phylogenetic relationships inferred by individual genes and the concatenated data, our analyses nonetheless provide varying support for several causal hypotheses. Error in phylogenetic reconstruction resulting from an abundance of homoplastic character changes is an unlikely explanation for the conflicting relationships between the mtDNA and nuclear loci in both the *P. elegans* + *P. marginatus* + *P. stimpsonii* and *brevirostris* group clades. Incomplete sorting of gene lineages and retention of ancestral polymorphism is perhaps the strongest hypothesis for gene tree conflict among the *brevirostris* group species, but less likely in the *P. elegans* + *P. marginatus* + *P. stimpsonii*. Finally, past hybridization may have played a role in both clades, but this hypothesis requires significantly more data to test.

A NEW *PLESTIODON* TAXONOMY

Our results demonstrate that the existing supraspecific taxonomy of *Plestiodon* (Taylor, 1935; Lieb, 1985; Hikida, 1993) does not accurately reflect monophyletic species groups, and therefore requires substantial revision. Although our study infers the close phylogenetic relationships of the *Eumeces s.l.* genera (*Eumeces s.s.*, *Eurylepis*, *Mesoscincus*, and *Plestiodon*), sinking these genera into *Eumeces* for convenience is not justified, as this clade would also contain *Scincus* and *Scincopus*. As *Scincus* Laurenti, 1768 has a priority, any attempt to lump these lineages into a single genus would instead require that the name *Scincus* be applied to this larger assemblage. As there is absolutely nothing to be gained by this action, we therefore retain the present generic taxonomy.

If one purpose of taxonomy is to promote the efficient dissemination of phylogenetic information, then clearly the current superspecific taxonomy of *Plestiodon* requires reorganization. There has been extensive and continuing debate on the relative merits of Linnean ranks (e.g. Dominguez & Wheeler, 1997; Cantino *et al*., 1999; Cantino, 2000; de Queiroz & Cantino, 2001; Nixon, Carpenter & Stevenson, 2003; de Queiroz, 2006), as well as the criteria for applying names to a phylogenetic tree (e.g. node based versus stem based; de Queiroz & Gauthier, 1990, 1992, 1994). All of these arguments may have merits to a varying degree. In the case of *Plestiodon*, we have chosen to preserve the use of the species 'groups' and 'series' informal names rather than develop new names for each node. First, there is a long history of use of '*Eumeces*' species groups beginning with Taylor (1935) and continuing through the present day. Thus, provided they are revised to reflect the most recent phylogenetic information, these groupings may continue to be useful. Secondly, the taxonomic history of *Plestiodon* has changed little over time, and there exist few junior generic synonyms (other than *Neoseps* Stejneger, 1910 and *Pariocela* Fitzinger, 1843) that may be resurrected as familiar clade uninominal names. Therefore, in this case, adopting a uninominal clade naming system, in which new names are created, would defeat taxonomy's goal of efficient transfer of information in this case. Third, maintaining these ranks does not preclude incorporating some criteria of phylogenetic taxonomy, and we adopt some of these principles in naming clades below.

Our phylogeny demonstrates that those morphological characters once thought to diagnose supraspecific groups of *Plestiodon* species (Taylor, 1935; Lieb, 1985) are instead cases of convergent evolution or retention of plesiomorphies. Indeed this explains why the results of our phylogenetic analysis differ so markedly to the phylogenetic/taxonomic analyses of Taylor (1935) and Lieb (1985), which relied on morphological characters. Therefore, in the context of our phylogeny, there exist very few characters that diagnose interspecific relationships in *Plestiodon*, and we must instead rely on several admittedly subjective

criteria to determine which clades to name. First, we attempt to preserve much of the historical taxonomy that was not radically changed by our phylogenetic analysis (e.g. the *latiscutatus* group and *capito* group). Secondly, when possible, we name clades with some biogeographic cohesion (e.g. the *brevirostris group* that inhabits Middle America; see also Ferría-Ortíz *et al*., 2011). Finally, in some cases, we name clades based on their unique morphology when compared with close relatives (e.g. *P. reynoldsi* and *P. quadrilineatus*).

All names are considered node-based names and are defined as the least inclusive clade containing all of the listed taxa (i.e. 'specifier taxa'; Sereno, 2005; PhyloCode, 2007), except where noted. Note that the subspecies of *P. brevirostris* are elevated to species, bringing the total number of species to 43. However, we emphasize that this is likely to underestimate species diversity, especially within the *brevirostris* group (clade C1 in Fig. 3).

Species that are not monophyletic are indicated to note that this revised taxonomy does not necessarily capture the species diversity, and is in need of additional phylogenetic and taxonomic study. We emphasize that these taxonomic ranks by themselves are not comparable in terms of either genetic diversity or evolutionary time (however, estimates of their ages can be found in Brandley *et al*. (2011).

Plestiodon Duméril & Bibron, 1849
- *fasciatus* species series (clade C in Fig. 3)
  - *anthracinus* species group
    - *P. anthracinus* Baird, 1849
  - *brevirostris* species group
    - *P. bilineatus* Cope, 1880
    - *P. brevirostris* (Günther, 1860)
    - *P. colimensis*[1] (Taylor 1935)
    - *P. copei* (Taylor, 1933)
    - *P. dicei* (Ruthven & Gaige, 1933)
    - *P. dugesii* (Thominot, 1883)
    - *P. indubitus*[2] (Taylor, 1933)
    - *P. lynxe* (Wiegmann, 1834)
    - *P. ochoteranae* (Taylor, 1933)
    - *P. parviauriculatus* (Taylor, 1933)
    - *P. parvulus* (Taylor, 1933)
    - *P. sumichrasti* (Cope, 1867)
  - *egregius* species group
    - *P. egregius* (Baird, 1859)
  - *fasciatus* species group
    - *P. callicephalus* (Bocourt, 1879)
    - *P. fasciatus* (Linnaeus, 1758)
    - *P. inexpectatus* (Taylor, 1932)
    - *P. laticeps* (Schneider, 1801)
    - *P. multilineatus*[1] (Tanner, 1957)
    - *P. multivirgatus* Hallowell, 1857
    - *P. obsoletus* Baird & Girard, 1852
    - *P. septentrionalis* Baird, 1859
    - *P. tetragrammus* Baird, 1859
  - *longirostris* species group
    - *P. longirostris* Cope, 1861
  - *reynoldsi* species group
    - *P. reynoldsi* (Stejneger, 1910)
  - *skiltonianus* species group
    - *P. gilberti*[2] (Van Denburgh, 1896)
    - *P. lagunensis* (Van Denburgh, 1895)
    - *P. skiltonianus*[2] Baird & Girard, 1852
- *latiscutatus* species series (clade B in Fig. 3)
  - *capito* species group
    - *P. capito* (Bocourt, 1879)
    - *P. liui*[1] (Hikida & Zhao 1989)
    - *P. popei*[1] (Hikida 1989)
    - *P. tunganus* (Stejneger, 1924)
  - *latiscutatus* species group (defined by the presence of a fan-shaped upper secondary temporal scale with emarginated posterior margin and keeled postanal scales (Hikida, 1993)
    - *P. barbouri* (Van Denburgh, 1912)
    - *P. elegans* (Boulenger, 1887)
    - *P. japonicus* (Peters, 1864)
    - *P. latiscutatus* Hallowell, 1861
    - *P. marginatus* Hallowell, 1861
    - *P. stimpsonii* (Thompson, 1912)
- *chinensis* species series (clade A in Fig. 3)
  - *chinensis* species group
    - *P. chinensis* (Gray, 1838)
    - *P. coreensis*[1] (Doi & Kamita, 1937)
    - *P. kishinouyei* (Stejneger, 1901)
    - *P. tamdaoensis* (Bouret, 1937)
  - *quadrilineatus* species group
    - *P. quadrilineatus* Blyth, 1853

[1] Not sampled in this study and thus not included as specifier taxa of the clade name. Inclusion of these species is based solely on previous taxonomic studies based on morphological data.

[2] Molecular evidence indicates that this species is not monophyletic.

ACKNOWLEDGEMENTS

We thank: A. Leaché, J. McGuire, J. Richmond, A. Seago, C. Siler, M. Toda, M. Toyama, and an anonymous reviewer for helpful discussion and/or comments on the manuscript; J. Aguilar López, K. Ashton, J. Campbell, S. Daniels, U. García Vázquez, L. Kitson, J. Lazell, I. López Hernández, R. Macey, A. Mendoza Hernández, M.E. Mociño Deloya, R. Murphy, E. Pérez Ramos, T. Reeder, J. Richmond, California Academy of Sciences, Field Museum of Natural History, Kyoto University Zoological Collection, Lousiana State University Museum of Zoology, Museum of Vertebrate Zoology, University of Michigan Museum of Zoology, and the Yale Peabody Museum, for providing tissue samples; J. Ichikawa,

I. Katsube, A. Mendoza Hernández, E. Pérez Ramos, F. Sato, A. Seago, and Y. Yamamoto for fieldwork assistance; and the facilities and staff of the Yale University Faculty of Arts and Sciences High Performance Computing Center for computer access. This project was financially supported by the National Science Foundation East Asia and Pacific Program grants (OISE 0513295 and OISE 0611646) in conjunction with the Japan Society for the Promotion of Science (as an Opportunity Fund for the International Summer Program), National Science Foundation Doctoral Dissertation Improvement grant (DEB 0709885), Museum of Vertebrate Zoology grants, and Linnean Society Systematics Fund awarded to M.C.B.

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APPENDIX

Specimens used in this study with locality information and GPS coordinates, when available. Museum abbreviations follow Leviton *et al*. (1985), except AMH (Andrés Alberto Mendoza Hernández), EMD (María Estrella Mociño Deloya), EPR (Edmundo Pérez Ramos), IDLH (Isaías Daniel López Hernández), JG (Justin Gerlach), JLAL (José Luís Aguilar López), KUZ (Kyoto University Zoological Collection), LK (Lisa Kitson), MCB (Matthew C. Brandley), MFO (Manuel Fería Ortíz), SD (Savel Daniels), and UOGV (Uri Omar García Vázquez).

Out-groups

Gerrhosauridae: *Gerrhosaurus major* (MVZ 241366): Somalia: Awdal: 8 km north (by air) of Borama: 10.00566, –43.18333. **Scincidae**: *Amphiglossus melanopleura* (UMMZ 208656) – Madagascar: Antsiranana: Montagne D'Ambre Antomboka River. *Brachymeles bonitae* (FMNH 259449) – Philippines: Luzon: Kalinga. *Chalcides ocellatus* (MVZ 242790) – Somalia: Bari: Hotel Kamal, Bosasso: 11.28550, 49.17883. *Emoia caeruleocauda* (MVZ 239361) – Indonesia: Sulawesi: Tenggara: –3.81784, 121.20506. *Eumeces schneiderii* (MVZ 234475) – Iran: Tehran: Cheshmeh Shah, 3 km south Caravansarie, Kavir National Park. *Eurylepis taeniolatus* (MVZ 246017) – Iran: Semnan: 2.85 km north-west of Delbar Field Station, Touran Protected Area, ~120 km (by air) ESE of Shahrud: 5.97681, 58.03856. *Janetaescincus braueri* (JG, uncatalogued) – Seychelles. *Lygosoma brevicaudis* (MVZ 249721) – Ghana: Volta: South Repeater Station, Kyabobo National Park: 8.34842, 0.60111. *Melanoseps occidentalis* (CAS 207873) – Equatorial Guinea: Bioko: Coast road ~5 km south (by road) of Luba: 3.46606, 8.52231. *Mesoscincus schwartzei* (UTA R–50296) – Guatemala: Peten: Tikal. *Ophiomorus punctatissimus* (MVZ 230221) – Turkey: Antalya: Kekova Adasi: 36.16667, 29.88333. *Paracontias hildebrandti* (UMMZ 209166) – Madagascar: Antsiranana: Montagne D'Ambre Antomboka River. *Scincopus fasciatus* (MVZ 242724) – Niger: Guesselbodi, 30 km south-east Niamey on road to Dosso: 13.41317, 2.35350. *Scincus scincus* (MVZ 234537) – Iran: Khuzestan: sand dunes 53 km east of Ahvaz via Ahvaz-Haftgel Rd. 31.27317, 49.23650. *Trachylepis perrotetii* (MVZ 245351) – Ghana: Greater Accra: ~34 km north-east of Accra: 5.84137, 0.11555. *Typhlosaurus* sp. (MVZ 164850) – No Locality. *Voeltzkowia rubricaudata* (MVZ 238841) – Madagascar: Toliary: –23.26650, 43.63617. **Xantusiidae**: *Xantusia vigilis* (MVZ 249144) – USA: California: San Bernardino County Burns Piñon Ridge Reserve: 34.14028, –116.45417.

Plestiodon

Plestiodon anthracinus (SDSU 802) – no locality. *Plestiodon barbouri* 1 (MCB 666) – Japan: Kagoshima Prefecture: Tokunoshima: Foothills of Tanhatsu Mountain: 27.77897, 128.96381. *Plestiodon barbouri* 2 (MCB 669) – Japan: Kagoshima Prefecture: Amamioshima: On unnamed road off of Highway 85 between Highways 79 and 58: 28.24003, 129.33823. *Plestiodon barbouri* 3 (MCB 644) – Japan: Okinawa Prefecture: Kumejima: On road to small dam: 26.36612, 126.76346. *Plestiodon brevirostris bilineatus* 1 (EMD 16) – México: Chihuahua: Namiquipa: 25.06967, –105.62869. *Plestiodon brevirostris bilineatus* 2 (EPR 1405) – México: Durango: Pueblo Nuevo: 23.71519, –105.48675. *Plestiodon brevirostris brevirostris* 1 (IDLH 16) – México: Tlaxcala: Huamantla: 19.39122, –97.92164. *Plestiodon brevirostris brevirostris* 2 (MFO 293) – México: Oaxaca: Macultianguis: 17.33000, –96.55000. *Plestiodon brevirostris indubitus* 1 (AMH 404) – México: Jalisco: Ciudad Guzmán:

19.61689, –103.56031. *Plestiodon brevirostris indubitus* 2 (MFO 303) – México: Morelos: Huitzilac: 19.02378, –99.28047. *Plestiodon callicephalus* (MFO 307) – México: Sonora: Approximately 4 km east of Uvalama: 26.99343, –108.97540. *Plestiodon capito* 1 (CAS 182575) – China: Shaanxi Province: Xian: base of the Qin Ling Mtns south of Xian: 34.26667, 108.90000. *Plestiodon capito* 2 (MCB 1051) – China: Sichuan Province: Nanjiang County In mountains ~13.5 miles north (by air) of Yangba town: 32.53437, 106.76136. *Plestiodon chinensis* 1 (MCB 675) – China: Taiwan: Hsingchu Province: road near Ji-Ding train station: 24.72158, 120.87086. *Plestiodon chinensis* 2 (MCZ Z39481) – China: Guangdong Province: Nan Ao Island. *Plestiodon copei* 1 (AMH 315) – México: México: Desierto de los Leones: 19.26733, –99.32183. *Plestiodon copei* 2 (MVZ 143455) – México: México: 1 mile west of Rio Frio on old road to Puebla: 19.33778, –98.67611. *Plestiodon dicei* 1 (MFO 316) – México: Tamaulipas: Ejido 'La Cima': 23.05814, –99.19375. *Plestiodon dicei* 2 (UOGV 552) – México: Cohuila: Rancho El Manzano: 24.35233, –100.19333. *Plestiodon dugesii* 1 (IDLH 105) – México: Jalisco: Atemajac de Brizuela: 20.11853, –103.72692. *Plestiodon dugesii* 2 (MCB 1054) – México: Michuocán: Quendaro Municipality: ~9.5 km west of the town of San José de la Cumbre: 19.68612, –100.87945. *Plestiodon egregius onocrepis* 1 (CAS 214309) – USA: Florida: Citrus County east. McMullen Rd. 28.69108, –82.33742. *Plestiodon egregius onocrepis* 2 (MVZ 150132) – USA: Florida: Highlands County north-west Avon Park, 3.6 miles north (by road) junction of Route 29 and Route 64, off Route 29: 27.59460, –81.50370. *Plestiodon elegans* 1 (MCZ Z39486) – China: Guangdong Province: Nan Ao Island: San Jian Shan. *Plestiodon elegans* 2 (MVZ 231241) – China: Fujian Province: Dehua: Dai Yun village: 25.66083, 118.22183. *Plestiodon elegans* 3 (MCB 673) – China: Taiwan: Hsingchu Province: Ji-Ding beach park near Ji-Ding train station: 24.72050, 120.86520. *Plestiodon fasciatus* (MCB 249) – USA: Kentucky: Henderson County Sloughs Wildlife Management Area, creek overpass on road west of Gary Aldrich Rd. 37.80861, –87.81333. *Plestiodon gilberti* A (MVZ 147888) – USA: California: Kern County, east slope Temblor Range, Highway 58, 11 miles north-west of Highway 33: 35.34427, –119.80670. *Plestiodon gilberti* I (MVZ 162079) – USA: California: Calaveras County 1.9 mi WNW Highway 4 at Avery on Avery-Sheep Ranch Rd. 38.22836, –120.37336. *Plestiodon inexpectatus* 1 (CAS 214312) – USA: Florida: Citrus County Inverness, Sandpiper Rd. *Plestiodon inexpectatus* 2 (MVZ 162086) – USA: North Carolina: Brunswick County 5 miles north of Supply: 34.09380, –78.26640. *Plestiodon japonicus* 1 (MCB 635) – Japan: Kagoshima Prefecture: Yakushima: City of Nagata, road south of hotel: 30.40454, 130.43059. *Plestiodon japonicus* 2 (MCB 682) – Japan: Kyoto Prefecture: Kyoto City: East wall of Imperial Palace grounds: 35.01425, 135.75115. *Plestiodon japonicus* 3 (KUZ R61221) – Japan: Miyagi Prefecture: Sendai. *Plestiodon kishinouyei* 1 (MCB 652) – Japan: Okinawa Prefecture: Iriomotejima: 24.41701, 123.79899. *Plestiodon kishinouyei* 2 (MCB 658) – Japan: Okinawa Prefecture: Ishigakijima: Park off of Highway 79 in central part of island: 24.45178, 124.19494. *Plestiodon lagunensis* (SDNHM-CIBNOR 151) – México: Baja Califorinia del Sur: Sierra Guadalupe, San Jose de Magdalena. *Plestiodon laticeps* (CAS 218689) – USA: Florida: Liberty County Forest Road 181: 30.05889, 84.94731. *Plestiodon latiscutatus* 1 (KUZ R58387) – Japan: Tokyo Prefecture: Aogashima: 32.46811, 139.76421. *Plestiodon latiscutatus* 2 (MCB 683) – Japan: Shizuoka Prefecture: Numazu: 35.01425, 135.75115. *Plestiodon longirostris* 1 (SK1) – Bermuda: Castle Island. *Plestiodon longirostris* 2 (SK2) – Bermuda: Castle Island. *Plestiodon lynxe* 1 (LSUMZ H14823) – México: San Luis Potosi. *Plestiodon lynxe* 2 (LSUMZ H14966) – México: Hidalgo. *Plestiodon marginatus marginatus* (MCB 646) – Japan: Okinawa Prefecture: Kumejima: 26.33560, 126.76669. *Plestiodon marginatus oshimensis* 1 (MCB 639) – Japan: Kagoshima Prefecture: Kodakarajima: 29.22642, 129.33011. *Plestiodon marginatus oshimensis* 2 (MCB 672) – Japan: Kagoshima Prefecture: Amamioshima: unnamed road at the eastern terminus of Highway 607: 28.32269, 129.52980. *Plestiodon marginatus oshimensis* 3 (MCB 668 – Japan: Kagoshima Prefecture: Tokunoshima: City of Amagi, near the port: 27.81952, 128.89296. *Plestiodon marginatus oshimensis* 4 (MCB 632) – Japan: Kagoshima Prefecture: Yoronjima: City of Nankaiso: 27.04921, 128.41551. *Plestiodon multivirgatus* (ADL 274) – USA: Colorado: Montezuma County US Route 666, Yellow Jacket Canyon: 37.52000, –108.70122. *Plestiodon obsoletus* (MVZ 137633) – USA: Arizona: Cochise County Highway 80, 15–20 miles south Rodeo: 31.63070, –109.19830. *Plestiodon ochoteranae* 1 (MFO 287) – México: Guerrero: Agua del Obispo: 17.32192, –99.47006. *Plestiodon ochoteranae* 2 (UOGV 250) – México: Guerrero: Agua del Obispo: 17.32192, –99.47006. *Plestiodon parviauriculatus* (IDLH 85) – México: Sonora: Los Alamos: 26.99342, –108.97539. *Plestiodon parvulus* 1 (ANMO 1141) – México: Michoacán: Pueblo Nuevo: 18.56130, –103.59437. *Plestiodon parvulus* 2 (ANMO 1173) – México: Colima: Manzanillo: 21.60425, –105.17211. *Plestiodon quadrilineatus* (MVZ 230445) – China: Hong Kong: Cheung Chau: 22.20000, 114.01667. *Plestiodon reynoldsi* 2 (NR390) – Florida: Highlands County Archbold Biological

Station *Plestiodon reynoldsi* 1 (NR383) – Highlands County Archbold Biological Station. *Plestiodon septentrionalis* 1 (LSUMZ H1231) – USA: Wisconsin. *Plestiodon septentrionalis* 2 (LSUMZ H1230) – USA: Wisconsin. *Plestiodon skiltonianus* F (MVZ 162314) – USA: California: Mendocino County 6.6 miles west of Willits on Highway 20: 39.39721, –123.45057. *Plestiodon skiltonianus* G (MVZ 162089) – USA: California: San Diego County 1 mile west of junction Route S6 on Route S7: 33.31347, –116.88200. *Plestiodon stimpsonii* 1 (MCB 657) – Japan: Okinawa Prefecture: Iriomotejima: 24.41701, 123.79899. *Plestiodon stimpsonii* 2 (MCB 664) – Japan: Okinawa Prefecture: Ishigakijima: Park off of Highway 79 in the northwest part of the island: 24.44786, 124.13341. *Plestiodon sumichrasti* (JLAL 141) – México: Veracruz: 2 km south of Cañahuatal: 18.83497, –98.85067. *Plestiodon tamdaoensis* 1 (ROM 25817) – Vietnam: Hia Duong, Chi Linh. *Plestiodon tamdaoensis* 2 (ROM 26948) – Vietnam: Cao Bang, Qyang Thanh. *Plestiodon tetragrammus* (UOGV 525) – México: Tamaulipas: ~1 km east of Marmolejo: 24.62217, –99.03194. *Plestiodon tunganus* 1 (MCB 1020) – China: Sichuan Province: Luding County ~5 km south-east (by air) of Pengba town on mountain road following the eastern shore of the Tung River: 29.99377, 102.21052. *Plestiodon tunganus* 2 (MCB 1025) – China: Sichuan Province: Luding County ~0.5 km south of Pengba on side of highway: 30.01844, 102.18371.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Figure S1. The inter-relationships of the major lineages of Scincidae, including the placement of *Plestiodon*, inferred by partitioned Bayesian analyses of the individual locus data sets. Taxa once considered part of the genus *Eumeces s.l.* are shaded in grey. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S2. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the mtDNA data set. Out-groups are not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S3. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *BDNF* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S4. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *MKL1* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S5. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *PRLR* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S6. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *PTGER4* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S7. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *R35* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S8. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *RAG1* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S9. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *SNCAIP* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.
Figure S10. The inter-relationships of *Plestiodon* species inferred by partitioned Bayesian analysis of the *UBN1* DNA data set. Out-groups not shown. Branch lengths represent means of the posterior distribution. Values above or below the nodes represent posterior probabilities.

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