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Partitioned Bayesian Analyses, Partition Choice, and the Phylogenetic Relationships of Scincid Lizards

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Abstract.—Partitioned Bayesian analyses of ∼2.2 kb of nucleotide sequence data (mtDNA) were used to elucidate phylogenetic relationships among 30 scincid lizard genera. Few partitioned Bayesian analyses exist in the literature, resulting in a lack of methods to determine the appropriate number of and identity of partitions. Thus, a criterion, based on the Bayes factor, for selecting among competing partitioning strategies is proposed and tested. Improvements in both mean $-\ln L$ and estimated posterior probabilities were observed when specific models and parameter estimates were assumed for partitions of the total data set. This result is expected given that the 95% credible intervals of model parameter estimates for numerous partitions do not overlap and it reveals that different data partitions may evolve quite differently. We further demonstrate that how one partitions the data (by gene, codon position, etc.) is shown to be a greater concern than simply the overall number of partitions. Using the criterion of the 2ln Bayes factor >10, the phylogenetic analysis employing the largest number of partitions was decisively better than all other strategies. Strategies that partitioned the ND1 gene by codon position performed better than other partition strategies, regardless of the overall number of partitions. Scincidae, Acontinae, Lygosominae, east Asian and North American "*Eumeces*" + *Neoseps*; North African *Eumeces*, *Scincus*, and *Scincopus*, and a large group primarily from sub-Saharan Africa, Madagascar, and neighboring islands are monophyletic. *Feylinia*, a limbless group of previously uncertain relationships, is nested within a "scincine" clade from sub-Saharan Africa. We reject the hypothesis that the nearly limbless dibamids are derived from within the Scincidae, but cannot reject the hypothesis that they represent the sister taxon to skinks. *Amphiglossus*, *Chalcides*, the acontines *Acontias* and *Typhlosaurus*, and Scincinae are paraphyletic. The globally widespread "*Eumeces*" is polyphyletic and we make necessary taxonomic changes. [Bayes factors; Bayesian hypothesis testing; "Eumeces"; mixed-model analyses; partitioning; "Scincinae."]

Maximum likelihood (ML) methods have become increasingly popular tools for the analysis of DNA sequence data. Unlike maximum parsimony, ML methods better incorporate models of DNA sequence evolution and are thus less likely to be misled by the complexities of this process (Huelsenbeck and Crandall, 1997, and references therein). ML methods also consistently outperform parsimony and distance methods under a variety of simulated conditions (Huelsenbeck 1995a, 1995b; Swofford et al., 2001). Concurrent with the rise of ML methods was the development and implementation of more complex and realistic models of DNA sequence evolution that allow different rates of nucleotide base substitution (Kimura, 1980; Yang, 1994a), base composition (Felsenstein, 1981), and site rate heterogeneity (Gu et al., 1995; Hasegawa et al., 1985; Yang, 1993, 1994b). Recent models can also incorporate sequence gaps (McGuire et al., 2001), secondary structure (Muse, 1995; Tillier and Collins, 1995), and amino acid codons (Goldman and Yang, 1994; Muse and Gaut, 1994). Despite these advances, ML analyses of data sets with multiple genes and/or gene regions exhibiting different models of evolution (e.g., stems and loops, codon positions) have generally been limited to using a single specified nucleotide substitution model and associated parameter estimates to explain the entire data set. The resultant model represents a compromise among these various partitions (hereafter defined as any subset of the entire data set) and may be inadequate to account for the vagaries of the entire data set. This "compromise model" can introduce a major source of systematic error and mislead the phylogenetic analysis (Leaché and Reeder, 2002; Reeder, 2003; Wilgenbusch and de Queiroz, 2000). Systematic error may be defined as error in estimating a parameter due to incorrect or violated assumptions in the method of estimation (Swofford et al., 1996). This differs from random error, which is stochastic error in a parameter estimate due to a limited sample size. Systematic error is particularly troublesome in that it may result in well-supported, yet erroneous, relationships (e.g., long branch attraction), or decrease support for legitimate relationships (Swofford et al., 1996).

In other words, despite continuing advances in our ability to incorporate more realistic individual models of molecular evolution, the use of a single model (and associated parameters) with data composed of differently evolving subsets may result in mismodeling and significant systematic error.

A common kind of mismodeling occurs when a single "compromise model," actually inappropriate for both partitions, is employed for multiple data partitions best explained by separate models of DNA evolution (e.g., GTR+I+Γ versus JC). Another form of mismodeling results when multiple partitions, explained by the same underlying general model (e.g., GTR+I+Γ), differ drastically in the specific model parameter estimates that maximize the likelihood (e.g., different relative substitution rates). For example, Reeder (2003) found the relative rate of C $\leftrightarrow$ T transitions was 27.2 for structural RNAs, but only 4.0 for the ND4 protein-coding gene, a sevenfold difference. The estimate of the same parameter for the combined mtDNA data was 14.7; half the best estimate for the structural RNAs, and over

three times the estimate for ND4. Whereas the separate data analyses used specific and seemingly appropriate models for the two individual data partitions (i.e., structural RNAs and ND4 protein-coding), the combined (single-model) mtDNA analysis did not accommodate all that was known about the partitions (i.e., specific parameter estimates). A solution to these problems would be to apply appropriate models and their specified parameter estimates to each data partition and subsequently incorporate this into a single ML tree search (Yang, 1996; a partitioned or mixed-model ML analysis). Methods of conducting such partitioned analyses using Bayesian/Markov chain Monte Carlo (MCMC) methods have recently become available (MrBayes 3.0; Huelsenbeck and Ronquist, 2001; See Nylander et al., 2004). Bayesian analyses generate posterior probability distributions using the likelihood function and incorporate the same models of DNA evolution commonly used with ML. Bayesian analyses using uniform priors are expected to yield similar results as ML, and generally do (Huelsenbeck et al., 2002; Larget and Simon, 1999; Leaché and Reeder, 2002). Because it more accurately models the data, the use of partition-specific modeling should reduce systematic error, resulting in better likelihood scores and more accurate posterior probability estimates.

The use of partitioning analyses also impacts the "combined versus separate" phylogenetic analysis debate (Bull et al., 1993; Chippendale and Wiens, 1994; de Queiroz, 1993; Kluge, 1989). Much of the debate centers upon how to cope with the different evolutionary characteristics of different data partitions. Fully combining the data into a single analysis allows for a phylogenetic reconstruction based on more characters, and under ideal conditions may infer better resolved or supported relationships than those inferred by separate analyses of each partition. However, this practice ignores the fact that different partitions of the data may have evolved under different models of evolution. Thus, some proponents advocate separate analyses in order to more accurately accommodate the evolutionary complexity of each partition. Our approach addresses both of these issues by employing partition-specific modeling in a combined analysis (see also Nylander et al., 2004).

We use partitioned Bayesian analyses to demonstrate the effect of partitioning on phylogeny reconstruction using multiple mitochondrial gene sequences from scincid lizards. We focus on the extent that partitioning improves the ability to explain the DNA data and the effects on clade support (i.e., posterior probabilities) compared to traditional, unpartitioned Bayesian analyses. We also introduce a method, based on the Bayes factor, to select the best partitioning strategy. This is significant because it provides an objective criterion for choosing among the countless ways of partitioning data, from the traditional, non-partitioned analyses, to partitioning by every character (i.e., the parsimony model [Tuffley and Steel, 1993]). As partitioning increases, the amount of data within each partition becomes smaller, resulting in increased random error associated with estimating model parameters. Thus, the Bayes factor is a method for determining whether a specific partitioning strategy is superior to another and evaluates the trade-off between increasing overall partition number (and thus number of estimated parameters) and minimizing random error.

The Current State of Scincid Phylogenetics

With over 1300 species, Scincidae is one of the largest families of squamate reptiles (Pough et al., 2004), yet little is known about their higher-level relationships. In fact, for many groups, relationships above the species level are only recently becoming better understood (e.g., Mausfeld and Schmitz, 2003; Mausfeld et al., 2002; Reeder, 2002; Schmitz et al., 2004, 2005; Whiting et al., 2003). This lack of phylogenetic information is an impediment to the study of the complex morphological evolution within skinks, including the evolution of limb reduction and loss. Indeed, inferring the phylogenetics of skinks based on morphological variation is problematic due to the presumably highly convergent evolution of limb reduction. Skinks are distributed worldwide and inhabit a variety of habitats. Scincid morphology is diverse; they range from being large (490 mm snout-vent-length) to small (23 mm snout-vent-length) (Greer, 2001), and from being robustly limbed to completely limbless. Despite the ubiquity and diversity of skinks, as well as their significance in elucidating the evolution of limblessness, their phylogenetic relationships are poorly known. Much of our current understanding of the phylogeny and taxonomy of skinks is based on the morphological work of Greer (1970a). In his pioneering scincid study, Greer recognized the following four subfamilies: Acontinae, Feylininae, Lygosominae, and Scincinae. Greer (1970a) hypothesized that the former three subfamilies were independently derived from within the scincines, and that scincines represent the most "primitive" group. This hypothesis that scincines represent the ancestral stock from which the other subfamilies are derived effectively implies that "Scincinae" is not monophyletic. Thus, to infer the higher-level phylogenetics of Scincidae, elucidating the relationships among the "scincines" is critical. The monophyly of Acontinae, Feylininae, and Lygosominae appears to be well supported by numerous morphological synapomorphies (Greer, 1970a, 1986); however, their phylogenetic placement within the "Scincinae" has not been adequately tested.

"Scincinae" consists of ~32 genera that inhabit Africa, North and Central America, Europe, and Asia. Greer (1970a) acknowledged that no derived characters support "scincine" monophyly and provided little evidence supporting relationships among major "scincine" groups. In a subsequent study, Greer (1970b) hypothesized various natural groups of some "scincine" genera: (1) *Janetaescincus* and *Pamelaescincus* (Seychelles) + *Gongylomorphus* (Mauritius), (2) *Proscelotes* and *Sepsina* (southern Africa), and (3) *Scelotes*, *Melanoseps*, *Scolecoseps*, and *Typhlacontias* (sub-Saharan Africa). Although Greer and Shea (2000) were careful to avoid making formal

taxonomic designations, their identification of a diagnostic head scale character nonetheless implied several higher-level relationships, including the placement of Acontinae and Feylininae within a diverse assortment of Malagasy, African, Central Asian, and European skinks (based on a bell-shaped frontal scale); and a group including the remaining sub-Saharan African, Malagasy "scincines," and the North American genus *Neoseps* (based on an hourglass-shaped frontal scale).

Recently, Whiting et al. (2003) focused on the phylogenetic relationships of the sub-Saharan African "scincines." Results from their DNA sequence analysis differed from Greer (1970b) in that they inferred a sister-group relationship between *Proscelotes* and *Scelotes*, and a close relationship between *Melanoseps*, *Typhlacontias*, and *Feylinia* (Fig. 1A). Their analysis also included other scincid representatives and supported Acontinae as the sister taxon to all remaining scincids. Given the numerous morphological synapomorphies that define the Lygosominae, it is surprising that Whiting et al. (2003) inferred the paraphyly of the group with respect to North American *Eumeces*.

The "scincine" *Eumeces* (sensu lato) is widespread, with members in North and Central America, North Africa, and Central and Southeast Asia. A recent morphological phylogenetic analysis by Griffith et al. (2000) rejected the monophyly of *Eumeces* and inferred the relationships among the hypothesized major species groups (Fig. 1B). They proposed splitting the paraphyletic *Eumeces* into four genera: *Mesoscincus* ("*E.*" *schwartzei* group), *Eurylepis* ("*E.*" *taeniolatus* group), and "*Novoeumeces*" (*E. schneideri* group, which contains the type for *Eumeces* sensu lato, *E. pavimentatus*), and *Eumeces* (sensu stricto) for all of the remaining species, which primarily inhabit East Asia and North America. However, this study was based on few morphological characters and did not rigorously evaluate the relationships of *Eumeces* (sensu lato) with respect to most other "scincines." In this study, we reconsider the taxonomic recommendations of Griffith et al. (2000) through an explicitly phylogenetic analysis including a greater diversity of "scincines."

In addition to reducing taxonomic chaos, a well-resolved phylogeny of skinks (especially non-lygosomines) will improve evolutionary studies on the group allowing, for example, a clearer understanding of the evolution of body size (Greer, 2001) and external ear morphology (Greer, 2002). In addition, limb reduction may have evolved as many as 25 times in the group, including multiple times within "Scincinae" (Greer, 1991); approximately half of the "scincine" genera (Greer, 2001) and the subfamilies Acontinae and Feylininae are completely limbless. A phylogenetic hypothesis would facilitate discovery of patterns and provide a framework for testing the numerous hypotheses about the evolution of the limbless body plan (e.g., Gans, 1975, 1986, 1994). For example, a recent phylogenetic study (Reeder, 2003) demonstrated that limb reduction has occurred independently more times in Australian

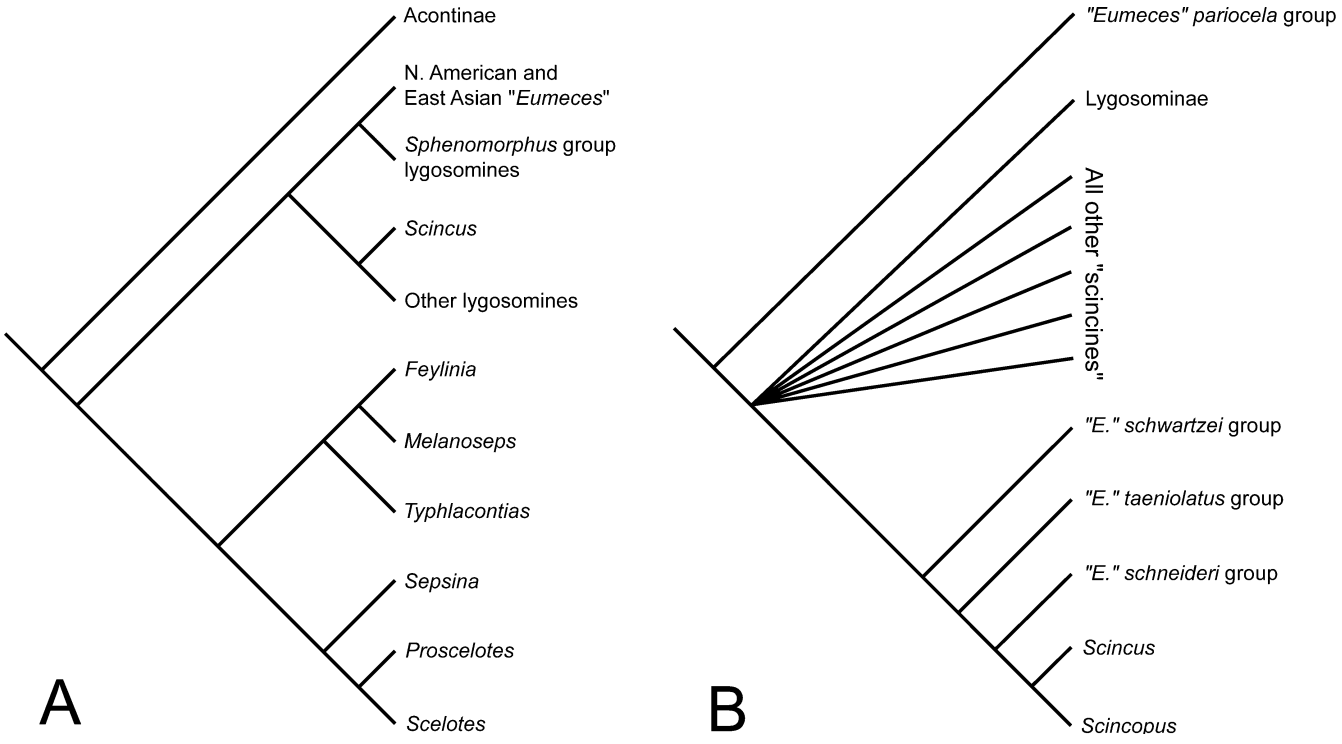

FIGURE 1. (A) Whiting et al.'s (2003) simplified hypothesis of scincid phylogenetic relationships. (B) Griffith et al.'s (2000) hypothesis of the phylogenetic relationships of the *Eumeces* (sensu lato) species groups.

lygosomine skinks than previously hypothesized by Greer (1991).

Using the partitioned Bayesian approach, we inferred the higher-level phylogeny of the Scincidae and the relationships among most "scincine" genera, including the first rigorous test of "scincine" monophyly. Additionally, we address the phylogenetic placements of *Feylinia* and *Dibamus*, two taxa for which scincid affinities have been debated. And finally, we also evaluate the monophyly of Lygosominae and "*Eumeces*," and test the previously hypothesized close relationship between the endemic Mauritian (*Gongylomorphus*) and the Seychellois (*Janetaescincus* and *Pamelaescincus*) "scincines."

Materials and Methods

Taxon sampling.—We sampled broadly from all currently recognized subfamilies, especially the "Scincinae," including (1) representatives of 21 of the ~32 currently recognized "scincine" genera, (2) all three genera of Acontinae, (3) one of the two genera of Feylininae, and (4) five representative genera of the speciose (600 + species) Lygosominae (Table 1). Where possible, multiple representatives of each speciose genus were used, especially within the putatively polyphyletic "*Eumeces*" (Griffith et al., 2000) and *Amphiglossus* (Schmitz et al., 2005). Species from three of the four major groups of "*Eumeces*" were sampled (Table 2), but samples were unavailable for the "*E.*" *taeniolatus* group (*Eurylepis* sensu; Griffith et al., 2000). We did not sample extensively from the Lygosominae because the goals of this study are to elucidate the placement of the acontines, feylinines, and lygosomines within the "Scincinae," as well as interrelationships among "scincine" genera. The lygosomine genera we sampled represent the five major strongly supported clades within Lygosominae (Honda et al., 2000; Reeder, 2003).

Because of the unavailability of tissue samples, we did not include the following "scincines": *Sepsina* and *Scolecoseps* from Africa, *Cryptoscincus* of Madagascar, and *Davewakeum* from Thailand. Their exclusion, however, is meliorated by the comparatively large sampling of other African and Malagasy "scincines" and should have little effect on our ability to identify major clades within the "Scincinae." Furthermore, whereas Greer (1970b) hypothesized the sister relationship between *Proscelotes* and *Sepsina*, Whiting et al. (2003) placed *Sepsina* sister to a *Proscelotes* + *Scelotes* clade; therefore, the phylogenetic affinities of *Sepsina* seem to be with other sub-Saharan "scincines." The limbless *Scolecoseps* is currently placed in a clade with other limbless sub-Saharan "scincines" (*Melanoseps* and *Typhlacontias*; Greer, 1970b). *Cryptoscincus* and *Davewakeum* are morphologically very similar to *Voeltzkowia* and *Brachymeles*, respectively, the latter two which are included in this study. Tissues were also unavailable for all four genera from India and Sri Lanka (*Barkudia*, *Chalcidoseps*, *Nessia*, and *Sepsophis*).

The family Cordylidae is hypothesized to be closely related to scincids (Estes et al., 1988; Lee, 1998, 2002; Schwenk, 1988; Townsend et al., 2004; Vicario et al., 2003; Whiting et al., 2003). Two taxa (*Cordylus* and *Zonosaurus*) representing the two basal clades of cordylids (Lang, 1991; Odierna et al., 2002) were used as the first outgroup. More distant outgroup taxa, representing other scleroglossan families (Anguidae, Lacertidae, and Dibamidae), were also included and the ingroup was not constrained to be monophyletic. The phylogenetic affinities of dibamids to other squamates are unclear (Greer, 1985; Rieppel, 1984), although several studies have hypothesized a close relationship between dibamids and skinks (Boulenger, 1884; Camp, 1923; Cope, 1885; Estes et al., 1988; Rieppel, 1981, 1984). Nevertheless, because of its inclusion as an outgroup taxon, we can evaluate the hypothesis that dibamids evolved from within the Scincidae.

Molecular methods and DNA alignment.—DNA was isolated from tissue using standard phenol/chloroform methods or Qiagen DNeasy™ columns. Segments of the mitochondrial genome were amplified, including the complete ND1, $tRNA^{GLU}$, $tRNA^{ILE}$, $tRNA^{GLN}$ genes, as well as partial gene sequences of the 12S rRNA, 16S rRNA, and $tRNA^{MET}$ for a total of ~2700 bp (see Table 3 for primers). Polymerase chain reaction (PCR) products were purified using PEG/NaCl precipitation or cut from 2.5% to 5% polyacrylamide gels and extracted using elution buffer (0.5 M ammonium acetate, 0.001 M EDTA, pH = 8.0). Purified templates were dye-labeled using BigDye (ABI) and sequenced on an ABI 377 automated DNA sequencer.

Alignment of the structural rRNA and tRNA gene sequences was aided by published secondary structure information (12S: Titus and Frost, 1996; 16S: Gutell and Fox, 1998; tRNAs: Kumazawa and Nishida, 1993). Insertions and deletions in these structural genes may make homology determination difficult for some regions. To aid in the identification of possibly ambiguously aligned positions, the sequences were aligned using various opening gap costs (= 6, 9, and 12) implemented by Clustal X (Thompson et al., 1997). Alignment of nucleotide positions that differed under any of these gap costs was considered to be ambiguous and were excluded from phylogenetic analysis (Gatesy et al., 1993).

Model determination.—An initial ML tree for the entire data set was created using the JC model with 10 random addition replicates and TBR branch swapping. The appropriate model of sequence evolution for each partition and combination of partitions (see below) was determined using the likelihood ratio test (LRT) implemented with MrModeltest (a variant of Posada and Crandall's [1998] ModelTest; Nylander, 2002) using this same initial tree for all partitions.

Bayesian phylogenetic analyses.—All phylogenetic analyses were conducted using MrBayes 3.0b4 (Huelsenbeck and Ronquist, 2001). Each analysis consisted of 2.0×10^7 generations with a random starting tree, default priors, the same set of branch lengths for each partition, and four Markov chains (with default heating values) sampled every 1000 generations. The common practice

TABLE 1. Species used in this study, their museum numbers, GenBank accession numbers, and collecting localities. Acronyms: AMB, Aaron Bauer field series; AMS, Australian Museum, Sydney; CAS, California Academy of Sciences; DCC, David C. Cannatella field series, University of Texas at Austin; DMH, David M. Hillis, University of Texas at Austin; JG, Justin Gerlach; LK, Lisa Kitson; MRSN, Museo Regionale di Scienze Naturali; MVZ, Museum of Vertebrate Zoology; RAN, Ronald Nussbaum field series; SAMA, South Australian Museum; SD, Savel Daniels; SDSU, San Diego State University; TNHC, Texas Natural History Collection; TWR, Tod Reeder field series; SDSU, San Diego State University; SDNHM, San Diego Natural History Museum; UADBA-MV, Universite d'Antananarivo, Departement de Biologie Animale; UMMZ, University of Michigan Museum of Zoology; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig.

Taxon	Museum no.	GenBank accession numbers			Locality
		12S	16S	ND1 and tRNAs	
Outgroups					
Takydromus sp.	SDNHM 69010	AY649136	AY649177	AY649218	Commercially purchased
Elgaria multicarinata	SDSU 3858	AY649110	AY649151	AY649192	USA: California: El Dorado Co.; south fork of the American River
Dibamus sp.	ROM 19108	AY649108	AY649149	AY649190	Philippines: Negros Island: Valencia
Cordylus sp.	DMH photo voucher	AY315471	AY315520	AY315566	South Africa
Zonosaurus sp.	TNHC 55947	AY315472	AY315521	AY315567	Commercially purchased
Acontinae					
Acontias meleagris	DMH photo voucher	AY649100	AY649140	AY649181	South Africa: Eastern Cape Region: N. Joubertina
Acontias percivali	ZFMK 72253	AY649101	AY649141	AY649182	Tanzania
Acontophiops lineatus	SD, uncataloged	AY649102	AY649142	AY649183	South Africa
Typhlosaurus caecus	ZFMK 18575	AY649138	AY649179	AY649220	South Africa: Saldanha Bay
Typhlosaurus lineatus	ZFMK 60582	AY649139	AY649180	AY649221	Botswana: Tsodilo Hills
Feylininae					
Feylinia cf. polylepis	BMNH, uncataloged	AY649119	AY649160	AY649201	Sao Tomé and Principé
Feylinia polylepis	CAS 219164	AY649120	AY649161	AY649202	Sao Tomé and Principé: Principe Id.: Cerracao Sur Pina
Lygosominae					
Egernia whitii	SAMA R34781	AY649109	AY649150	AY649191	Australia: South Austrlia: Kangaroo Island: Cape Hart
Eugongylus rufescens	AMS R122480	AY649111	AY649152	AY649193	Papua New Guinea: Bobole
Lygosoma fernandi	SDSU 3945	AY649124	AY649165	AY649206	Commercially purchased
Euprepis perrotetii	TWR 426 (uncataloged TNHC specimen)	AY649118	AY649159	AY649200	Commercially purchased
Scincella lateralis	DCC 2842 (uncataloged TNHC specimen)	AY649131	AY649172	AY649213	USA: Texas: Sutton: 0.7–1.2 mi W of bridge over I-10 on FM 3130
"Scincinae"					
Amphiglossus macrocercus	UMMZ 195924	AY315480	AY315529	AY315575	Madagascar: Toamasina: Moramanga: Mantady Park
Amphiglossus melanopleura	UMMZ 208656	AY315481	AY315530	AY315576	Madagascar: Antsiranana: Montagne D'Ambre Antomboka River
Amphiglossus mouroundavae	UMMZ 201592	AY315486	AY315535	AY315581	Madagascar: Antsiranana: Montagne D'Ambre Antomboka River
Amphiglossus ornaticeps	UMMZ 196048	AY315488	AY315537	AY315583	Madagascar: Toliara: Tolanaro: Manantantely Forest
Amphiglossus splendidus	UMMZ 208789	AY315495	AY315544	AY315590	Madagascar: Toliara: Tolanaro: east side of Summit Ambatorongorongo
Amphiglossus stumpffi	UMMZ 201595	AY315496	AY315545	AY315591	Madagascar: Antsiranana: Montagne D'Ambre Antomboka River
Brachymeles talinis	ZFMK 73806	AY649103	AY649143	AY649184	Philippines: NW Panay
Brachymeles gracilis	TNHC 59948	AY649104	AY649144	AY649185	Philippines: Mindanao Is.: Davao City Prov.: Municipality of Calinan: Barangay Malagos, at or near the Malagos Eagle Station
Chalcides chalcides	ZFMK 77801	—	AY649145	AY649186	France: Banjuls
Chalcides mionecton	ZFMK uncataloged	AY649105	AY649146	AY649187	Morocco: Sidi Kaouki
Chalcides ocellatus	TNHC 55635	AY649106	AY649147	AY649188	Commercially purchased
Chalcides polylepis	No voucher	AY649107	AY649148	AY649189	Morocco: Plage Blanche: Atlantic coast
"Eumeces" egregius	—	NC000888	NC000888	NC000888	GenBank accession number NC000888
"Eumeces" elegans	MVZ 231239	AY649112	AY649153	AY649194	China: Fujian Province: Dehua County: Dai Yun village: Qi-Li-Yang
"Eumeces" fasciatus	SDSU 3836	AY315505	AY315554	AY315600	USA: Missouri: Camden Co.: Lake of the Ozarks, Sunrise Beach
"Eumeces" longirostris	LK, uncataloged	AY649113	AY649154	AY649195	Bermuda
"Eumeces" lynxe	MVZ 190185	AY649114	AY649155	AY649196	Mexico: San Luis Potosi; 39 km E of San Luis Potosi

(Continued on next page)

TABLE 1. Continued

Taxon	Museum # no.	GenBank accession numbers 12S	16S	ND1 and tRNAs	Locality
"Eumeces" managuae	ZFMK 57771	AY649115	AY649156	AY649197	Costa Rica: Guanacaste
"Eumeces" obsoletus	SDNHM 69011	AY649116	AY649157	AY649198	USA: New Mexico: Mora Co.: 3.8 mi S of Wagon Mound
"Eumeces" schneideri	TNHC 55948	AY315506	AY315555	AY315601	Commercially purchased
"Eumeces" schwartzei	UTA R-50296	AY649117	AY649158	AY649199	Guatemala: Peten: Tikal
Gongylomorphus bojeri	BMNH, uncataloged	AY649121	AY649162	AY649203	Mauritius: Round Island
Hakaria simonyi	No voucher	AY649122	AY649163	AY649204	Yemen: Socotra Island
Janetaescincus braueri	JG, uncataloged	AY649123	AY649164	AY649205	Seychelles: Silhouette Island
Melanoseps occidentalis	CAS 207873	AY649125	AY649166	AY649207	Equatorial Guinea: Bioko Id.: coast road ca 5 km S (by road) of Luba
Neoseps reynoldsi	USNM 541741	AY649126	AY649167	AY649208	USA: Florida: Orange Co.: Walt Disney World
Ophiomorus punctatissimus	MVZ 230221	AY649127	AY649168	AY649209	Turkey: Antalya Province: Kekova Adasi
Pamelaescincus gardineri	JG, uncataloged	AY649128	AY649169	AY649210	Seychelles: Silhouette Island
Paracontias brocchii	UMMZ 209153	AY315507	AY315556	AY315602	Madagascar: Antsiranana: Montagne D'Ambre Antomboka River
Paracontias holomelas	UMMZ 201644	AY315509	AY315558	AY315604	Madagascar: Antsiranana: Sambava: Marojejy Reserve along Manantenina River
Proscelotes eggeli	FMNH 250585	AY315512	AY315561	AY315607	Tanzania: Korogwe Dist.: West Usambara Mts.
Pseudoacontias menameinty	MRSN R1826	AY315511	AY315560	AY315606	Madagascar: Berara Forest
Pygomeles braconnieri	UMMZ 229882	AY315513	AY315562	AY315609	Madagascar: Toliara: Betioky
Scelotes bipes	SD, uncataloged	AY649129	AY649170	AY649211	South Africa
Scelotes mirus	No voucher	AY649130	AY649171	AY649212	Swaziland: Malolotja Reserve
Scincopus fasciatus	ZFMK uncataloged	AY649132	AY649173	AY649214	Mauritania: ca. 30 km NW Rosso
Scincus mitranus	BMNH, uncataloged	AY649133	AY649174	AY649215	United Arabian Emirates
Scincus scincus	TNAC 55667	AY315515	AY712942	AY315611	Commercially purchased
Sphenops boulengeri	ZFMK uncataloged	AY649134	AY649175	AY649216	Mauritania: ca. 30 km NW Rosso
Sphenops sphenopsiformis	ZFMK uncataloged	AY649135	AY649176	AY649217	Morocco: southern Tan Tan Plage
Typhlacontias brevipes	AMB 7030	AY649137	AY649178	AY649219	Namibia
Voeltzkowia fierinensis	UADBA-MV 2000.569	AY315516	AY315563	AY315612	Madagascar: Arboretum, Tulear
Voeltzkowia lineata	UMMZ 197125	AY315517	AY315564	AY315613	Madagascar: Toliara: Amboasary: Beraketa

of detecting stationarity in MCMC analyses by plotting $-\ln L$ against generation time is problematic (especially at detecting slow convergence; Gelman, 1996); therefore, we tracked the cumulative posterior probabilities of individual clades using the *cump* and *slide* command in Converge v0.1 (Warren et al., 2003). Stationarity was assumed when the cumulative posterior probabilities of all clades stabilized. Burn-in trees were discarded and the remaining trees and associated parameter estimates saved, with the frequency of inferred relationships representing estimated posterior probabilities. To decrease the chance of reaching apparent stationarity on local optima, two separate analyses were performed for each partitioning strategy. Posterior probability estimates for each clade were then compared between the two analyses using a scatterplot created by the *compare2trees* command in Converge. If posterior probability estimates for clades were similar in both analyses, the results of both analyses were combined.

Unlike nonparametric bootstrap values, which are known to be conservative estimates of clade confidence (Hillis and Bull, 1993), recent simulation studies (e.g., Alfaro et al., 2003; Erixon et al., 2003; Wilcox et al, 2002) have demonstrated that Bayesian posterior probabilities are less biased estimators of confidence and thus generally represent much closer estimates of true clade probabilities (referred to as "*Pp*" throughout). Also, whereas the Bayesian approach may be more sensitive to signal in the sequence data (i.e., provide higher confidence for short internodes; Alfaro et al., 2003), there is also an increased chance of the Bayesian method assigning higher confidence to incorrectly inferred short internodes because of the stochastic nature of the underlying model of evolution (Alfaro et al., 2003; Erixon et al.,

TABLE 2. Traditional taxonomy of "*Eumeces*" (sensu lato) species used in this study (Lieb, 1985).

pariocela species group
"Eumeces" egregius
"Eumeces" elegans
"Eumeces" fasciatus
"Eumeces" longirostris
"Eumeces" lynxe
"Eumeces" obsoletus
schwartzei species group
"Eumeces" managuae
"Eumeces" schwartzei
schneideri species group
"Eumeces" schneideri

TABLE 3. Primers used in this study.

Primer name	Sequence (5′ → 3′)	Position[1]	Source
tPHE	AAA GCA CRG CAC TGA AGA TGC	44	Wiens and Reeder, 1997
12a	AAA CTG GGA TTA GAT ACC CCA CTA T	526	Kocher et al., 1989
12g	TAT CGA TTA TAG GAC AGG CTC CTC TA	630	Leaché and Reeder, 2002
12e	GTR CGC TTA CCM TGT TAC GAC T	984	Wiens and Reeder, 1997
16aR2	CCC GMC TGT TTA CCA AAA ACA	1928	Schmitz et al., 2005
16d	CTC CGG TCT GAA CTC AGA TCA CGT AG	2456	Reeder, 1995
16dR	CTA CGT GAT CTG AGT TCA GAC CGG AG	2481	Leaché and Reeder, 2002
ND1-INTF	CTA GCW GAA ACM AAY CGA GCC CC	3309	Schmitz et al., 2005
ND1-INTF2	AAY CGV GCV CCW TTY GAC CTW ACA GA	3323	Schmitz et al., 2005
ND1-INTF3	ATA ATR TGR TTY ATY TCN ACN CTA GCA GA	3293	This study
ND1-INTF4	TAY CCN CGN TTH CGN TAY GAY CA	3567	This study
ND1-INTR	TAT TCT GCT AGG AAG AAW AGG GCG	3379	Schmitz et al., 2005
ND1-INTR2	CRA AKG GGC CDG CTG CRT AYT CTA C	3356	Schmitz et al., 2005
tMET	TCG GGG TAT GGG CCC RAR AGC TT	3836	Leaché and Reeder, 2002

[1]Position of the terminal 3′ base of the *Eumeces egregius* mt genome (GenBank accession number NC_000888; Kumazawa and Nishida, 1999).

2003). Given this, clades with $Pp \geq 0.95$ were generally considered strongly (significantly) supported, but with the caveat that relatively high posterior probabilities for short internodes (particularly those that might receive low bootstrap values) may be overestimates of confidence.

Choosing the Best Partitioning Strategy

The goal of partitioning is to divide the data into sequence regions that have evolved under different models of evolution. The more partitions, the more accurately the data are modeled. However, as the number of nucleotide positions per partition decreases, the amount of random error associated with estimating parameters for each partition increases. Therefore, we attempted to achieve a balance between partitioning the data into similar units and overpartitioning. To determine the best partitioning strategy, we developed a method that compares strategies using the Bayes factor. The method consists of three general steps.

1. Choose data partitions.—Partitions were chosen a priori based on gene identity (i.e., ND1, 12S, 16S, and tRNAs) and general biochemical or evolutionary constraints (i.e., codon positions, stems, and loops). In this study, the separate tRNAs were combined due to their small size (~80 bp) and given that they are expected to evolve similarly due to similar functional and evolutionary constraints. Appropriate models of sequence evolution were chosen for each partition using the LRT on the same initial ML tree (see above). All partition strategies are denoted with a capital P and a numerical subscript identifying the number of data partitions (e.g., P_1, P_9, etc.). Additional subscript letters identify multiple partitioning strategies that have the same number of data partitions but partition the data differently (e.g., P_{4A}, P_{4B}, etc.).

2. Best and alternative analyses.—A partitioned Bayesian analysis of the total data set with the most logical number of partitions was implemented by applying the previously determined models to each data partition. Additional analyses combining data partitions (thereby reducing the overall number of partitions; "alternative analyses") were performed, and the appropriate models of sequence evolution of the various combined partitions were also re-determined using the LRT with the same initial ML tree. With four or more total data partitions, the number of possible partition combinations becomes too large to evaluate practically; therefore, we used background information regarding how these partitions evolve to test logical combinations of partitions (e.g., combining the first and second codon positions but not second and third; Table 4).

3. Evaluating alternative partitioning strategies.—The results for each partitioning strategy were then compared to the strategy with the best arithmetic mean $-\ln L$ using the Bayes factor. The Bayes factor measures the amount by which one's opinion is changed after viewing the data. This is interpreted as the change in odds in favor of a hypothesis and can be measured as the change in odds from the prior to the posterior (Lavine and Schervish, 1999; see Huelsenbeck and Imennov, 2002, for a phylogenetics example using this method), or as the relative success of two hypotheses (H) at predicting the

TABLE 4. Partitioning strategies used in this study.

Partition strategy	Partition identity
P_1	All data combined
P_2	ND1; 12S, 16S, and tRNAs combined
P_3	ND1; one partition each for the combined stems and loops of the 12S, 16S, and tRNAs
P_{4A}	ND1 codon positions; 12S, 16S, and tRNAs combined
P_{4B}	ND1; one partition each for 12S, 16S, and tRNAs
P_5	ND1 codon positions; one partition each for the stems and loops of the combined 12S, 16S, and tRNAs
P_6	ND1 codon positions; one partition each for the 12S, 16S and tRNAs
P_7	ND1; one partition each for the stems and loops of the 12S, 16S, and tRNAs
P_9	ND1 codon positions; one partition each for the stems and loops of the 12S, 16S, and tRNAs

data (Kass and Raftery, 1995). In the latter case, it can be computed by the following formula:

$$B_{01} = \frac{\Pr(D \mid H_0)}{\Pr(D \mid H_1)},$$

where B_{01} is the Bayes factor of the comparisons of H_0 and H_1 and corresponds to the ratios of the marginal likelihoods of the two hypotheses (Kass and Raftery, 1995; Newton and Raftery, 1994; Raftery, 1996). The marginal likelihood is the probability of the data with all of the model parameters integrated out (Holder and Lewis, 2003; Raftery, 1996). This integral is difficult to compute directly, and instead can be estimated by calculating the harmonic mean of the likelihood values (*not* ln*L*s) sampled from the posterior distributions of the two analyses (Newton and Raftery, 1994). The Bayes factor, therefore, is the ratio of the harmonic means of the likelihoods (sampled from the posterior) of the two analyses being tested:

$$B_{01} = \frac{\text{Harmonic Mean } L_0}{\text{Harmonic Mean } L_1}$$

Ln*L*s were sampled from the posterior distribution (at stationarity), retransformed into likelihoods, and the harmonic mean of these likelihoods was calculated using Mathematica®. For convenience, Bayes factors were then ln-transformed. Note that a harmonic mean can be more conveniently estimated using slightly less precise scaling procedure by using the *sump* command in MrBayes. We therefore also calculated the harmonic mean using the *sump* command and compared it to the value calculated from Mathematica®. For the remainder of the paper, harmonic means will be referred to as such, whereas arithmetic means will simply be referred to as "means."

Unlike the LRT and other familiar frequentist methods, rejection of the null hypothesis is not evaluated using critical values. Instead, the Bayes factor (and therefore, one's change in opinion) can be evaluated using a table provided by Jeffreys (1935, 1961) and further modified by Raftery (1996; Table 5). At this point, the investigator must choose a cutoff for determining support for the alternative hypothesis. Selecting a Bayes factor cutoff is essentially equivalent to selecting an arbitrary *P* value (such as 0.05) in frequentist statistics. In this study, we used the traditional criterion of 2ln Bayes factor of ≥ 10 as very strong evidence against the alternative hypothesis (Kass and Raftery, 1995; Table 5). Ultimately, the alternative partitioning strategy that explains the data as well as the best strategy (if any), but with fewer partitions is considered the optimal strategy (i.e., the one that best explains the data while incurring the least random error).

TABLE 5. Interpretations of the 2ln Bayes factor. Modified from Kass and Raftery (1995).

2ln Bayes factor	Evidence for H_1
<0	Negative (supports H_0)
0 to 2	Barely worth mentioning
2 to 6	Positive
6 to 10	Strong
>10	Very strong

Testing Alternative Phylogenetic Hypotheses

Because Bayesian methods infer sets of trees proportional to their posterior probability rather than a single estimate of phylogeny, common frequentist statistical methods for testing alternative phylogenetic hypotheses, such as the SH test (Shimodaira and Hasegawa, 1999), are not practical. Instead, we employed a Bayesian approach to hypothesis testing and built 95% credible sets of unique trees (sampled at stationarity) using the *sumt* command in MrBayes. This methodology was used to test whether alternative phylogenetic hypotheses not supported with high posterior probabilities (i.e., $Pp < 0.95$) could be rejected by the data. If a phylogenetic hypothesis of interest was absent in all of the trees of the 95% credible set, it could be rejected statistically (Buckley et al., 2002; Reeder, 2003).

RESULTS

We obtained sequence data for all genes and taxa except for *Chalcides chalcides*, for which we were unable to obtain 12S sequence data. We excluded 483 positions from the phylogenetic analyses due to ambiguous alignment. The remaining 2195 unambiguously aligned positions consisted of 1154 variable sites, with 950 being parsimony informative. Results of the model selection regime are provided in Table 6. For most partitions, the most general model (GTR+I+Γ) was selected even if the data partition was quite small. All Bayesian analyses achieved apparent stationarity by 1.2×10^7 generations.

TABLE 6. Data partitions, their estimated models of sequence evolution, and total number of characters of each partition used in phylogenetic analysis.

Partition	Model	Number of characters in partition
All data	GTR+I+Γ	2195
ND1	GTR+I+Γ	954
ND1 1st codon	GTR+I+Γ	318
ND1 2nd codon	GTR+I+Γ	318
ND1 3rd codon	GTR+I+Γ	318
12S	GTR+I+Γ	620
12S stems	SYM+I+Γ	371
12S loops	GTR+I+Γ	249
16S	GTR+I+Γ	416
16S stems	SYM+I+Γ	177
16S loops	GTR+I+Γ	239
tRNA	GTR+I+Γ	205
tRNA stems	GTR+Γ	126
tRNA loops	GTR+I+Γ	83
12S + 16S + tRNAs	GTR+I+Γ	1241
All stems	GTR+I+Γ	674
All loops	GTR+I+Γ	571

TABLE 7. Mean $-\ln L$ and 95% credible interval results of each partitioning strategy.

Partition strategy	Mean $-\ln L$	Upper 95% CI	Lower 95% CI
P_1	39644.890	39626.765	39665.156
P_2	39485.383	39466.286	39506.404
P_3	39380.875	39360.992	39403.023
P_{4A}	39195.204	39175.253	39217.330
P_{4B}	39422.659	39402.659	39444.721
P_5	39091.425	39070.575	39114.233
P_6	39126.173	39105.566	39149.412
P_7	39339.302	39318.083	39362.659
P_9	39030.845	39008.647	39056.012

Effect of Partitioning on Mean $-\ln$L

We used mean $-\ln L$ to measure the ability of data partitioning to explain the entire data set and found that partitioning does, in fact, greatly improve mean $-\ln L$ (Table 7 and Fig. 2). Simply adding partitions does not necessarily further improve the mean $-\ln L$. Rather, the identity of each partition is extremely important. For example, partitioning the ND1 data by codon positions (partition strategies P_{4A}, P_5, P_6, and P_9) has the largest effect on the mean $-\ln L$. Partition strategy P_7, which does not partition the ND1 by codon, includes three more partitions than strategy P_{4A}; yet, the mean $-\ln L$ of P_{4A} is almost 150 likelihood units better than P_7 (Table 7). With rRNA genes, partitioning by combined stems and loops improves the $-\ln L$ more dramatically than partitioning by gene (P_3 versus P_{4B}, P_5 versus P_6), suggesting that the stems and loops of these different structural genes evolve similarly. Partitioning by codon position and rRNA gene specific stems and loops (strategy P_9) yields the greatest improvement of mean $-\ln L$.

Effects of Partitioning on Topology, Posterior Probabilities, and the Bayes Factor

The consensus tree topologies inferred from all nine analyses differed, yet all of these differences involved

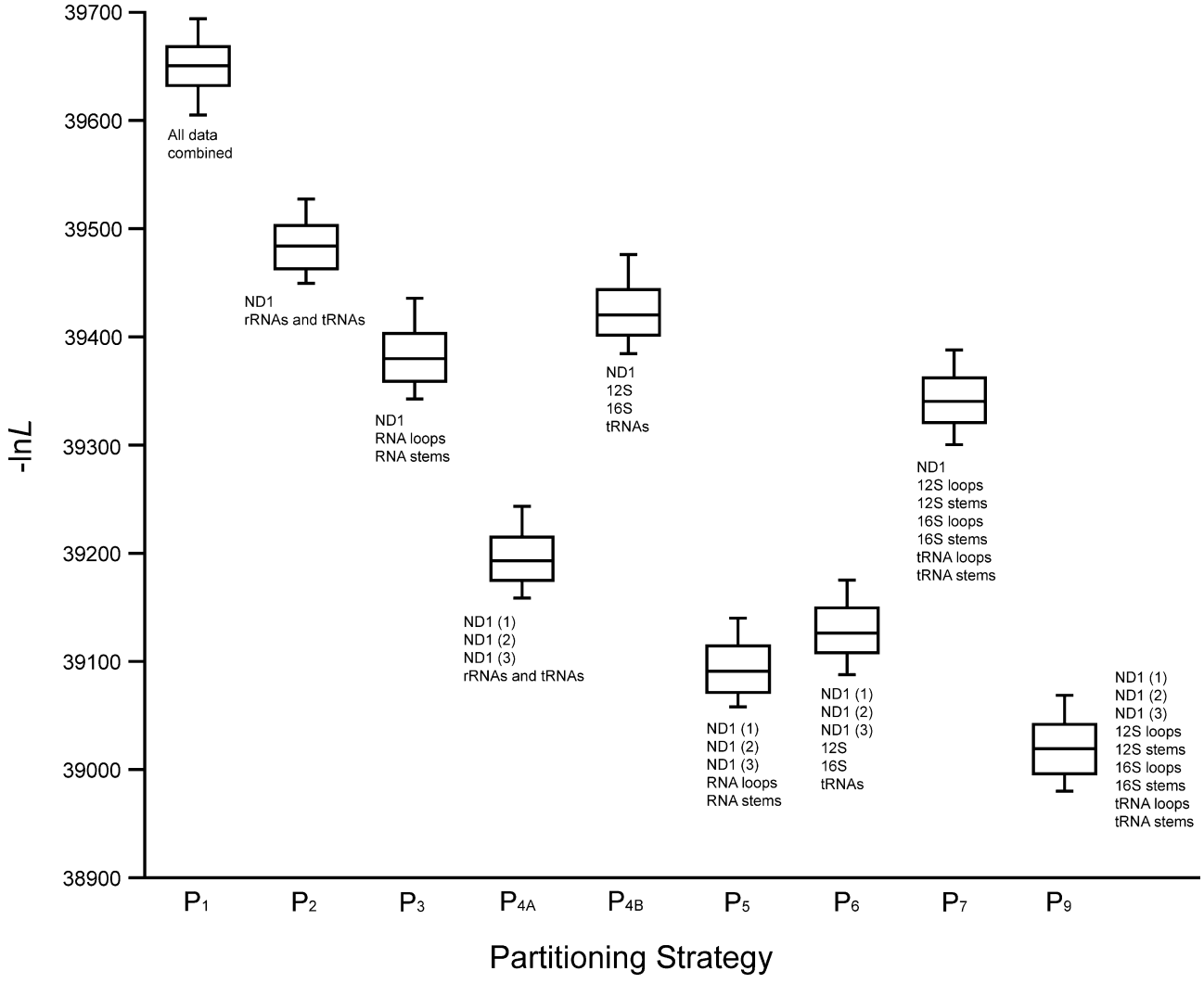

FIGURE 2. Box plots of the $-\ln L$ of all trees sampled from the posterior distribution (at stationarity) for each partitioning strategy. The top and bottom bars, box, and center line represent the upper and lower bounds of the 100% interval, 95% interval, and the mean of the distribution, respectively.

alternative placements of weakly supported nodes (i.e., <0.95). There were notable differences in posterior probabilities between the analyses depending on whether the ND1 sequences were partitioned by codon position (compare P_{4A}, P_5, P_6, and P_9 to others; Table 7, Fig. 2). The analysis that did not include any partitions (P_1; Fig. 3) and the nine-partition analysis (strategy P_9; Fig. 4) are generally representative of these two partitioning strategy groups. The most dramatic difference can be seen in the deepest nodes in the tree, as well as basal relationships in the clade containing *Chalcides*, *Sphenops*, and the Malagasy (and surrounding islands) "scincines" (clade B in Figs. 3 and 4). All analyses that do not partition the ND1 by codon infer very weak support for these relationships. In contrast, all analyses that partitioned ND1 by codon position inferred greater support for these same clades, with posterior probabilities increasing from <0.50 to significant ($Pp \geq 0.95$) or marginally nonsignificant (defined here as $0.90 \leq Pp < 0.95$) for clades B and D.

The absolute difference between the 2ln Bayes factor estimates using Mathematica and MrBayes ranged from 19.1 to 0.6 (Table 8). We attribute these differences to calculation errors due to the programs' handling of extremely small likelihood values, the fact that MrBayes excludes "extreme values" when calculating the harmonic means, or both. Nonetheless, given that all Bayes factor estimates were much larger than the criterion for strong evidence against a hypothesis (see below), the differences between these estimates are within an acceptable range. The analysis using nine partitions was a decisively better explanation of the data than all other analyses according to the Bayes factor (Table 8). Thus, it is our preferred hypothesis of the phylogeny of scincid lizards, and subsequent discussion will be limited to this tree (Fig. 4). Additional Bayes factor analyses demonstrate that every partitioning strategy is decisively different from each other (Table 8). This holds even for partitioning strategies with somewhat similar mean $-\ln L$s, such as strategies P_3 and P_{4B}, and P_5 and P_6.

TABLE 8. 2ln Bayes factors results of comparisons of all partitioning strategies. The top matrix represents Bayes factors calculated from the harmonic means of likelihoods sampled directly from the posterior distribution using Mathematica®. The bottom matrix represents Bayes factors calculated from estimated harmonic means of likelihoods by the *sump* command in MrBayes 3b4. Bold values indicate comparisons used in determining the optimal partitioning strategy. A positive value indicates evidence against alternative hypotheses.

	Partitioning strategies								
	P_9	P_7	P_6	P_5	P_{4B}	P_{4A}	P_3	P_2	P_1
P_1	**1221.0**	607.6	1031.0	1104.8	432.0	891.4	514.0	320.6	—
P_2	**900.4**	287.0	710.4	784.2	111.4	570.8	193.4	—	
P_3	**707.0**	93.6	517.0	590.8	−82.0	377.4	—		
P_{4A}	**329.6**	−283.8	139.6	213.4	−459.4	—			
P_{4B}	**789.0**	175.6	599.0	672.8	—				
P_5	**116.2**	−497.2	−73.8	—					
P_6	**190.0**	−423.4	—						
P_7	**613.4**	—							
P_9	—								
P_1	**1227.8**	613.9	1038.6	1100.7	447.0	895.7	526.9	318.8	—
P_2	**909.0**	295.1	719.8	781.9	128.2	576.9	208.1	—	
P_3	**701.0**	87.0	511.7	573.8	−79.9	368.8	—		
P_{4A}	**332.1**	−281.8	142.9	205.0	−448.7	—			
P_{4B}	**780.8**	166.9	591.6	653.7	—				
P_5	**127.2**	−486.8	−62.1	—					
P_6	**189.3**	−424.7	—						
P_7	**614.0**	—							
P_9	**—**								

Higher-Level Phylogeny of the Scincidae

The monophyly of Scincidae (relative to cordylids and *Dibamus*) is strongly supported ($Pp = 1.0$; Fig. 4). Thus, the hypothesis that dibamids are nested within Scincidae is not supported by the mtDNA. The monophyly of the subfamilies Acontinae and Lygosominae (including the *Sphenomorphus* group taxon, *Scincella*) is also strongly supported (both $Pp = 1.0$). Not surprisingly, the monophyly of the "Scincinae" is not supported, with the independent derivation of the other scincid subfamilies from within various more exclusive "scincine" clades. The interrelationships of the basal-most clades (North American/east Asian "*Eumeces*" + *Neoseps*, *Brachymeles*, lygosomines, and remaining skinks) are not well supported. Within the North American/east Asian "*Eumeces*" + *Neoseps* clade, the sister relationship between *Neoseps* and "*E*." *egregius* is strongly supported ($Pp = 1.0$). Within the Acontinae, *Typhlosaurus* and *Acontias* are each strongly supported as not monophyletic. The North African and Middle Eastern *Scincus*, *Scincopus*, and *E. schneideri* form a strongly supported clade ($Pp = 1.0$), but interrelationships among these three taxa are not well supported. The strongly supported Central American "*E*." *schwartzei* group ("*E*." *managuae* and "*E*." *schwartzei*) is weakly placed as the sister taxon of a strongly supported clade (clade A) containing the sub-Saharan African and Malagasy (and surrounding islands) "scincines," *Chalcides*, *Sphenops*, and *Feylinia*. Basal relationships within clade A are generally strongly supported. The two Seychellois genera (*Janetaescincus* and *Pamelaescincus*) strongly form a clade ($Pp = 1.0$) that is also strongly placed as the sister taxon of all remaining members of clade A (= Clade B; $Pp = 0.96$). A clade containing *Feylinia*, *Typhlacontias*, and *Melanoseps* is well supported ($Pp = 1.0$), as is the sister relationship between *Feylinia* and the *Melanoseps* + *Typhlacontias* clade ($Pp = 0.98$). The remaining "scincines" (clade C; $Pp = 0.73$) form two major monophyletic groups (clades D and E). The marginally weakly supported clade D ($Pp = 0.93$) contains the sub-Saharan African *Proscelotes* and *Scelotes*, and the North African, central Asian, and European *Chalcides*, and *Sphenops*, whereas the weakly supported clade E ($Pp = 0.82$) contains species that inhabit Madagascar, Mauritius, and Socotra. The sister relationship between the two sub-Saharan African genera (*Proscelotes* and *Scelotes*) is strongly supported ($Pp = 1.0$), with this clade being placed as the sister taxon of the well-supported *Chalcides* + *Sphenops* clade ($Pp = 1.0$). However, *Chalcides* monophyly is not supported. With the exception of *Gongylomorphus* and *Hakaria*, the species of clade E all inhabit Madagascar. Basal relationships within clade E are not well resolved, but there is strong

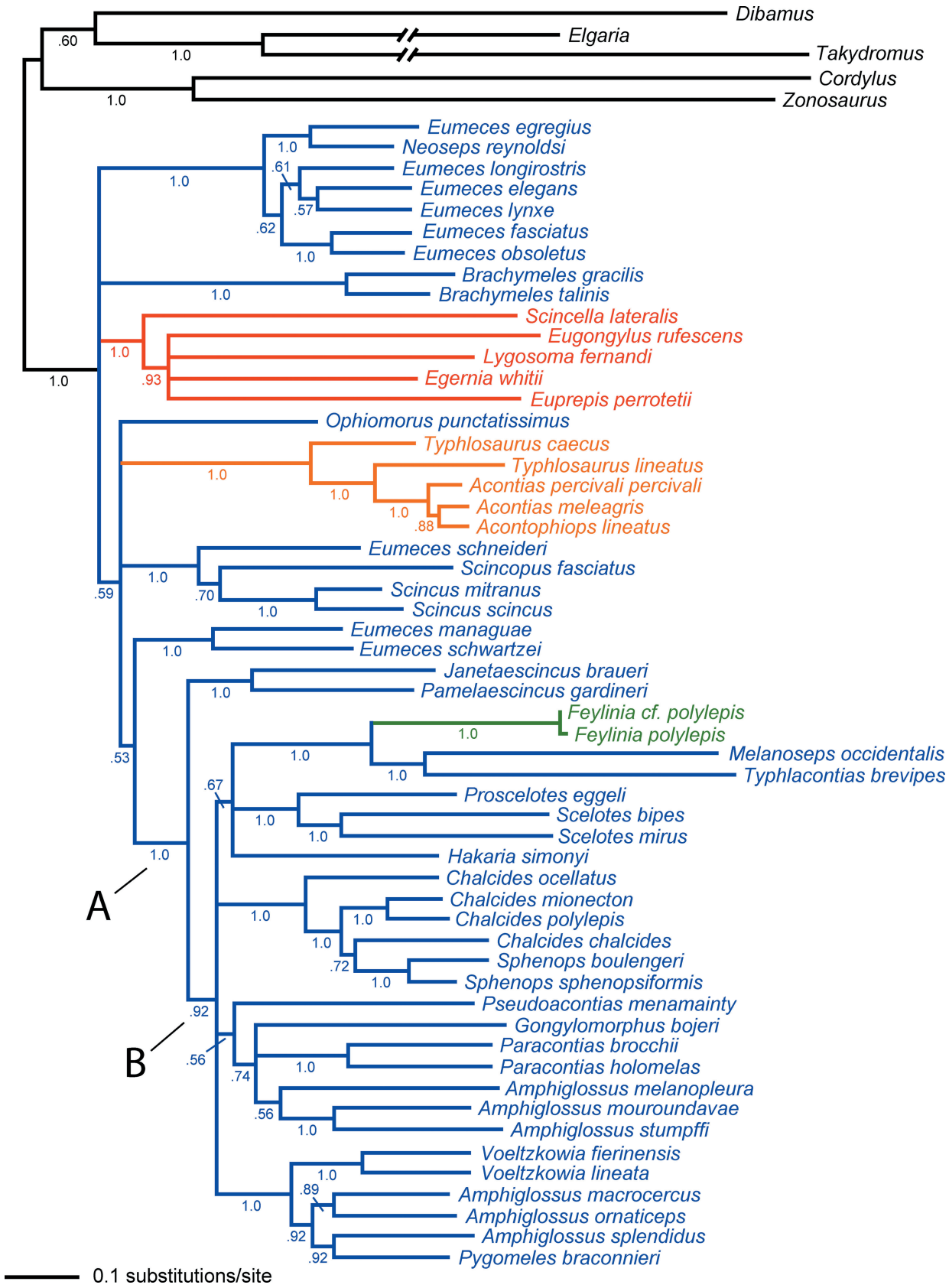

FIGURE 3. Fifty percent consensus of trees sampled from the posterior distribution (at stationarity) of the unpartitioned Bayesian analysis (strategy P_1). Branch lengths are calculated from means of the posterior probability density. Ingroup taxa shaded in blue represent the subfamily "Scincinae," red Lygosominae, green Feylininae, and orange Acontinae. Values below the nodes represent posterior probabilities. Clades A and B are discussed in the text.

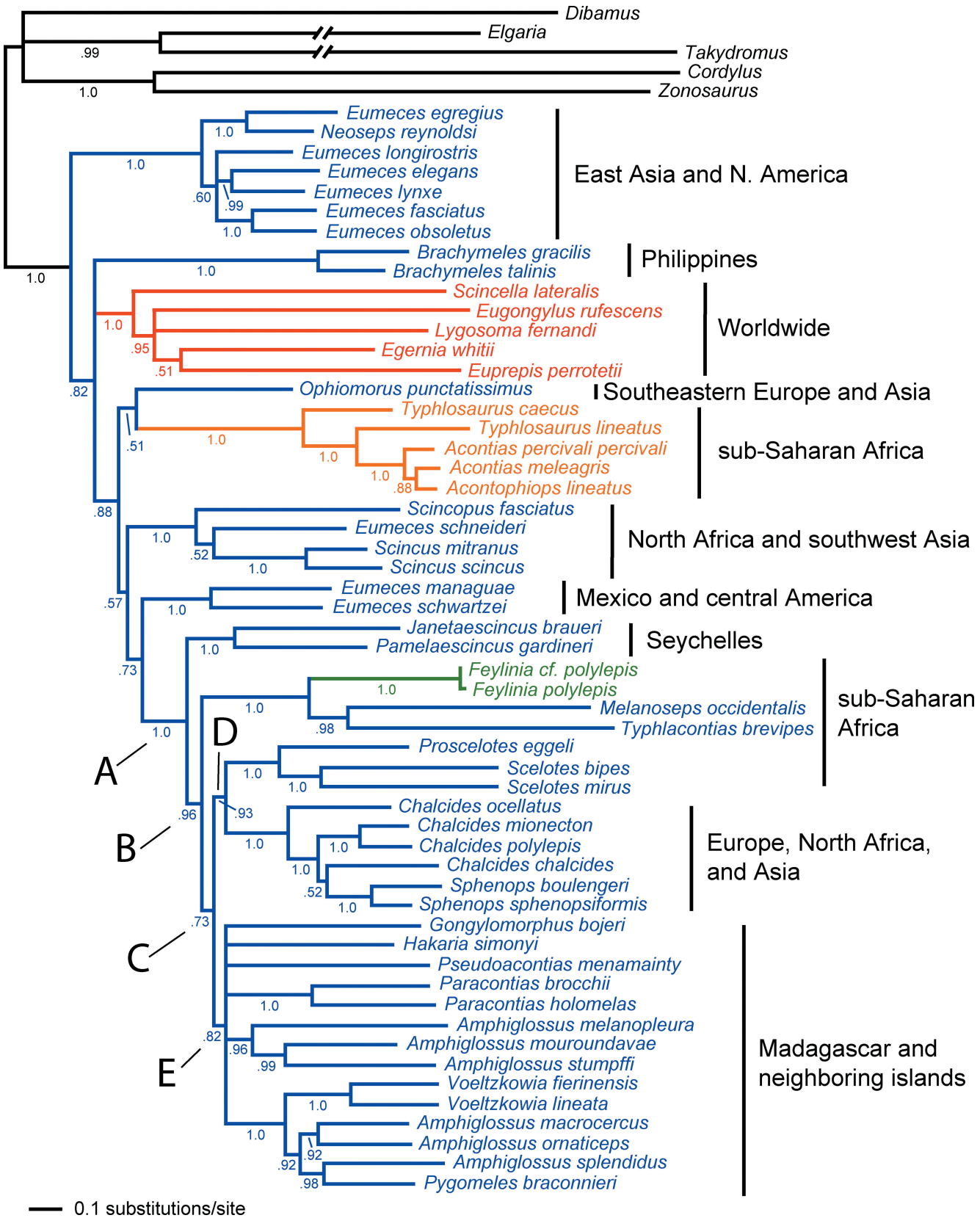

FIGURE 4. Fifty percent consensus of trees sampled from the posterior distribution (at stationarity) of the most-partitioned analysis (strategy P_9), and our best estimate of scincid lizard phylogeny. Branch lengths are calculated from means of the posterior probability density. Ingroup taxa shaded in blue represent the subfamily "Scincinae," red Lygosominae, green Feylininae, and orange Acontinae. Values below the nodes represent posterior probabilities estimated from all trees sampled at stationarity. Clades A, B, C, D, and E are discussed in the text. "Asia" refers to the Middle East and central and south Asia unless otherwise specified.

support for the paraphyly of *Amphiglossus* with respect to other Malagasy "scincine" genera (a result congruent with Schmitz et al., 2005).

Discussion

Partition Incongruence and Performance of Partitioned Analyses

To illustrate the significant heterogeneity among model parameter estimates for different data partitions, we compared 95% credible intervals (CIs) of each parameter sampled from the posterior distribution for strategies P_1 and P_9 (Table 9). There exists numerous instances of nonoverlap among parameter CIs, the most striking of which occurs among the ND1 codon positions where in 8 of the 11 estimated parameters, CIs do not overlap among two or more codon positions. In addition, the parameter CIs of each codon position do not overlap with at least one (and usually multiple) CI of every other partition. There are far more instances of parameter CI overlap among the rRNA and tRNA partitions, suggesting these partitions evolve similarly. Finally, every 95% CI for parameter values estimated from the total data (P_1) conflicts with at least one data partition of the P_9 analysis. These examples likely explain (1) why partitioned analyses may greatly reduce systematic error and improve $-\ln L$s and posterior probabilities with respect to traditional, single-model analyses, and (2) why this effect was so apparent with the ND1 codon positions and least noticeable with the rRNA genes. The ND1 codon positions displayed the largest differences in parameter estimates and are therefore the subset of the data that benefit most from partitioning. It is evident that simply including more partitions does not necessarily result in an improvement in mean $-\ln L$ (Fig. 2, Table 7) and that the identity of data partitions is far more important than their overall number.

In addition to its effect on mean $-\ln L$, partitioning also affected node support. This is important because it demonstrates that partitioning is doing more than simply modeling random elements of the data (i.e., improving mean $-\ln L$ but having little or no effect on topology and/or node support). Systematic error, due to poor modeling, for example, can mislead a phylogenetic analysis into inferring the wrong tree and may also affect estimates of clade confidence (making them artificially high or low) even if the true tree is inferred (Swofford et al., 1996). Thus, reducing systematic error in a partitioned Bayesian analysis should result in more accurate estimates of clade posterior probabilities. If this is the case, the difference between the posterior probabilities of the most partitioned and single-model analyses in our study may be inferred as actual *improvements* in our estimates of clade confidence if, in fact, systematic error was reduced. It should also be noted that better modeling will not necessarily result in *higher* clade posterior probabilities. If the posterior probability estimate for a clade is erroneously high due to systematic error caused by inadequate modeling, improved modeling (e.g., partitioning) should infer decreased support for this incorrect relationship.

Low support for deep nodes is a frequent problem in numerous phylogenetic analyses (e.g., Fishbein, 1999; Jackman et al., 1999; Poe and Chubb, 2004). This low support may be the result of rapid cladogenesis in a time period too brief to allow the accumulation of characters diagnostic for these clades. Thus, an optimal phylogenetic method would be one that, in a sense, does more with less data when compared to traditional single-model or maximum parsimony analysis. We demonstrated that certain partitioning strategies increase estimated posterior probabilities of many deep nodes when compared to single-model analyses. Although all but one of these increased estimates did not achieve significant (i.e., $\geq$0.95) levels, we assert that mixed-model analyses are potentially a powerful tool, even with rapid radiation phenomena. Because mixed-model phylogenetic methods may reduce systematic error, they may allow a researcher faced with a difficult phylogenetic problem (e.g., a rapid radiation) to collect far less data than that needed for single-model or parsimony analyses. This could result in a difference between

TABLE 9. Lower and upper ranges of the 95% credible interval for each parameter sampled from the posterior distribution. Values for the individual partitions are from the most-partitioned analysis (P_9). Values for the entire data set are from the non-partitioned analysis (P_1). Substitution rates are relative to the G ↔ T rate = 1.0.

	Base frequencies				Substitution rates					Rate heterogeneity	
	A	C	G	T	A ↔ C	A ↔ G	A ↔ T	C ↔ G	C ↔ T	I	Γ
All data	0.40–0.43	0.31–0.34	0.07–0.08	0.17–0.19	0.50–0.92	6.44–11.13	0.56–1.08	0.28–0.67	8.22–14.27	0.36–0.41	0.41–0.47
ND1 1st codon	0.31–0.39	0.33–0.40	0.13–0.19	0.12–0.16	0.14–0.65	2.12–5.89	1.09–3.28	<0.01–0.17	9.13–25.84	0.29–0.40	0.36–0.44
ND1 2nd codon	0.14–0.22	0.30–0.39	0.07–0.12	0.33–0.45	2.41–16.30	6.91–42.10	0.58–4.09	5.19–34.47	13.78–49.34	0.42–0.60	0.14–0.21
ND1 3rd codon	0.43–0.49	0.31–0.36	0.05–0.06	0.14–0.17	1.43–3.08	30.15–49.75	1.77–4.11	0.51–5.00	24.14–47.93	<0.01–0.06	0.85–1.24
12S loops	0.39–0.47	0.24–0.30	0.11–0.17	0.14–0.18	2.24–5.23	7.86–20.97	3.11–7.54	0.23–1.91	28.80–49.81	0.13–0.27	0.19–0.23
12S stems	—	—	—	—	2.83–6.41	27.16–48.84	3.43–7.36	0.04–1.25	30.19–49.74	0.08–0.20	0.18–0.21
16S loops	0.35–0.44	0.25–0.35	0.08–0.14	0.17–0.25	2.83–11.17	12.70–48.80	1.27–6.53	0.20–4.14	15.78–49.15	0.22–0.38	0.18–0.22
16S stems	—	—	—	—	2.19–8.43	7.65–29.44	0.74–5.03	0.15–2.78	28.43–49.77	0.33–0.52	0.17–0.21
tRNA loops	0.31–0.50	0.18–0.30	0.06–0.17	0.19–0.33	2.46–15.77	11.99–49.36	0.13–4.78	0.04–10.22	13.91–49.61	0.13–0.53	0.14–0.37
tRNA stems	0.27–0.39	0.25–0.38	0.11–0.20	0.17–0.25	0.01–2.24	4.70–49.30	0.53–2.71	<0.01–0.79	9.09–49.81	—	0.19–0.34

collecting a few kilobases and hundreds of kilobases. A second explanation for poor support for basal nodes may be inadequate modeling. Inadequate modeling may fail to account for the large amount of homoplasy, the erosion of synapomorphies due to multiple substitutions at a site, and heterogeneous evolution among genes or gene regions. This should be particularly acute in single-model analyses of rapidly evolving data and/or old clades, such as skinks (Estes, 1983). Partitioning allows for a more realistic modeling of the heterogeneous nature of DNA evolution and can potentially alleviate these problems.

Although improved modeling of the evolutionary process decreases the amount of systematic error in the analysis, little is known about how small partitions can become before random error becomes a significant influence on phylogeny and confidence estimation. Reducing systematic error is always beneficial, but partitioning is not a universal remedy for problematic phenomena and data. One must still sample appropriate taxa and sufficient characters and be aware of potential pitfalls of different model and partition selection schemes.

Performance of the Bayes Factor

The effects of partition identity on mean $-\ln L$ and estimated clade support highlight the importance of thoroughly exploring different partition strategies. This would be best accomplished by finding data regions that evolve according to a similar model (with similar parameter estimates) and combining them into one partition; in essence, estimating partitioning strategies concurrently with a tree search. However, because this is not currently feasible, we must choose partitions a priori. It is therefore essential to use an objective criterion to determine the optimal partitioning strategy from a set of alternate strategies. We accomplished this using the Bayes factor. For our data, the most partitioned analysis was decisively better than any other strategy using a 2ln Bayes factor $\geq$10 as the criterion for very strong support (Kass and Raftery, 1995). However, using this current criterion, all partitioning strategies were decisively different from each other (Table 8). This raises the question of whether or not a 2ln Bayes factor of $\geq$10 exacts a substantial enough penalty to additional partitions. Further study is needed to determine if the standard convention of evaluating Bayes factors (Table 5) requires refinement for use in phylogenetic analysis.

Phylogeny of Scincidae

Dibamus—The phylogenetic placement of dibamids (*Dibamus* and *Anelytropsis*) within Squamata has been problematic (Estes et al., 1988; Greer, 1985; Rieppel, 1984). Several authors have postulated scincid affinities for *Dibamus* (Boulenger, 1887; Camp, 1923; Cope, 1885, 1892, 1900; Rieppel, 1984). One of the characters that potentially supports this relationship is the presence of an extensive secondary palate resulting from scroll-like palatines, a trait that is unique to dibamids and some scincids. Our analyses reject the hypothesis that *Dibamus* is nested within Scincidae. The Scincidae (exclusive of *Dibamus*) is strongly supported ($Pp = 1.0$; Fig. 4). However, because of the weak placement of *Dibamus* in the unrooted tree (Fig. 4), we cannot reject the hypothesis that dibamids are sister to skinks. This relationship is also unlikely as Townsend et al. (2004) inferred that dibamids are, instead, probably one of the basal-most squamate lineages.

Basal scincid relationships and major "scincine" clades.—As long suspected (Greer 1970a), the "Scincinae" is not monophyletic, with all three of the other scincid subfamilies being nested within it. However, due to weak support for the basal nodes, determining the specific interrelationships among the major scincid clades (including between the currently recognized subfamilies) remains problematic. With the exception of the "scincine" clade inhabiting sub-Saharan Africa, Madagascar, and nearby islands (clade A), the relatively low posterior probabilities of the basal nodes makes identifying major "scincine" clades difficult. The single-scale character described by Greer and Shea (2000) appears to have little utility for defining major "scincine" clades. Our phylogeny suggests that their two defining two character states (bell- versus hourglass-shaped frontal scales) have evolved multiple times within "scincines."

The basal split between the east Asian/North American "*Eumeces*" clade and all remaining skinks is congruent with the morphological study of Griffith et al. (2000). However, the recent study by Whiting et al. (2003) inferred a basal scincid split between the Acontinae and all remaining skinks. Although such a relationship is less probable in our study, our mtDNA data cannot reject this hypothesis (Table 10).

Acontinae and Lygosominae.—The monophyly of Acontinae is strongly supported, but our data do not support the monophyly of the acontine genera *Acontias* and *Typhlosaurus*. Whiting et al. (2003) inferred Lygosominae to be paraphyletic with respect to east Asian and North American "*Eumeces*." More specifically, they inferred this clade of "*Eumeces*" as sister to the *Sphenomorphus* group lygosomines. In contrast, the monophyly of the Lygosominae (including the *Sphenomorphus* group taxon, *Scincella*) is supported by our analysis ($Pp = 1.0$) and is also supported by three morphological synapomorphies (Greer, 1970a, 1986). Whereas the Whiting et al. (2003) hypothesis is based on multiple independent mitochondrial and nuclear markers, they did not present separate analyses for each gene; thus, it is not possible at

TABLE 10. Results of tests of multiple phylogenetic hypotheses using the most partitioned analysis. The presence of any trees in the 95% credible interval of trees (sampled at stationarity) congruent with the hypothesis indicates that the hypothesis cannot be rejected by the data.

Phylogenetic hypothesis	Number of congruent trees
Total trees in 95% CI	18642
Basal split between Acontinae and all other skinks[1]	498
"Eumeces" + Neoseps + Scincopus + Scincus	0

[1]Whiting et al. (2003).

this time to determine which gene(s) suggest lygosomine paraphyly. Determining the exact nature of the incongruencies between these two studies (as well as between the independent genes) deserves further inquiry.

Other African and Malagasy scincines.—A major clade containing the genera from sub-Saharan Africa, Madagascar, and offshore islands of these two landmasses, as well as *Sphenops* and *Chalcides* of northern Africa and the Middle East (*Chalcides* also extends into Europe) is strongly supported by the mtDNA data ($Pp = 1.0$; clade A of Fig. 4). The sub-Saharan African "scincines" are placed in two strongly supported clades, but are not each other's closest relatives, while the Malagasy "scincines" (plus *Gongylomorphus* and *Hakaria*) are restricted to a single, marginally well-supported clade (clade E). In clade D, a strongly supported *Sphenops* + *Chalcides* clade is not surprising given their distribution and the presence of a shared derived karyotype ($2N = 28$; references in Greer and Shea, 2000). However, *Chalcides* is strongly supported as paraphyletic with respect to *Sphenops*. The previous hypothesis that *Scelotes* is closely related to *Melanoseps* and *Typhlacontias* (Greer, 1970b) is clearly refuted by our data. Instead, the sub-Saharan *Scelotes* + *Proscelotes* clade is more closely related to the *Chalcides* + *Sphenops* clade of northern Africa and the Middle East. The restriction of all the Malagasy "scincines" to a single clade (clade E) suggests a single "scincine" origin for the island (assuming *Hakaria* and *Gongylomorphus* dispersed to Socotra and Mauritius, respectively). The inclusion of Indian and Sri Lankan genera in future phylogenetic analyses may help determine whether the origin of the Malagasy "scincines" resulted from an over-water invasion from Africa or vicariance due to the break-up of Gondwanaland in the Late Cretaceous (i.e., a close relationship between Malagasy, Seychellois, and south Asian taxa). The interrelationships among the Malagasy "scincines" are currently weakly supported. However, a generally well-supported conclusion is that the species-rich genus *Amphiglossus* is not monophyletic with respect to other Malagasy lineages with limb-reduced taxa. A more detailed phylogenetic study of the group, including many more sampled species, further explores the phylogenetic relationships within this diverse "scincine" clade (Schmitz et al., 2005).

Janetaescincus and *Pamelaescincus* (from the Seychelles) and *Gongylomorphus* (from Mauritius) were all previously thought to be closely related based on the shared derived condition of a complete secondary palate formed by the medial apposition of both the palatines and palatal rami of the pterygoids, which is unique among "scincines" (Greer, 1970b). Greer (1970b) acknowledged that the hypothesized close relationship of these genera poses a biogeographical problem as these taxa inhabit two different remote island banks, but dismissed the notion that the complete secondary palate evolved twice. Our phylogenetic analysis indicates that while *Janetaescincus* and *Pamelaescincus* are sister taxa ($Pp = 1.0$), they are not closely related to *Gongylomorphus*. Thus, our analyses provide evidence that the complete secondary palate indeed evolved twice among the "scincines." The convergent nature of the complete secondary palate should not be too surprising given this condition has evolved repeatedly in lygosomine skinks (Reeder, unpublished data). The closest relatives of *Gongylomorphus* inhabit Madagascar, so dispersal from this island to nearby Mauritius seems likely. The source of the Seychellois taxa is unclear, as its sister taxon includes all the remaining African and Malagasy "scincines." The inclusion of the Indian and Sri Lankan "scincines" may help unravel the mystery behind the origin of these Seychellois taxa.

Feylinia.—Although never widely accepted, Rieppel (1981) suggested that feylinines are not scincid lizards and deserve taxonomic rank at par with Scincidae. The limbless feylinines possess a highly derived morphology including numerous morphological autapomorphies. Our study provides strong support for the phylogenetic placement of *Feylinia* as the sister taxon of the sub-Saharan *Melanoseps* + *Typhlacontias* clade, which also exhibit extreme limb reduction. Additional evidence of the close relationship between these three genera is that they share a three base pair insertion between the $tRNA^{GLU}$ and $tRNA^{MET}$ genes absent in all other sampled skinks. Within this clade, our data strongly support the sister relationship between *Melanoseps* and *Typhlacontias* ($Pp = 0.98$). However, Whiting et al. (2003) hypothesized a sister relationship between *Feylinia* and *Melanoseps*. Both of these relationships are incongruent with morphology in that both *Feylinia* and *Typhlacontias* lack jugal bones (a presumably derived condition). However, because the reduction or loss of the jugal is a common phenomenon among strongly fossorial squamates (lost in some amphisbaenians, some anguids, dibamids, pygopodids, and snakes), convergent loss of this bone is not unlikely.

The Phylogeny and Taxonomy of "Eumeces"

Not surprisingly, our study does not support the monophyly of *Eumeces* (sensu lato). Our sampled "*Eumeces*" fall within three different, well-supported clades: (1) east Asian and North American species + *Neoseps*, (2) *E. schneideri* + *Scincus* + *Scincopus*, and (3) "*E.*" *managuae* + "*E.*" *schwartzei* (= "*E.*" *schwartzei* species group). In our preferred phylogeny (Fig. 4), the east Asian/North American clade is the sister taxon of all remaining skinks and the other two "*Eumeces*" clades are nested within this more exclusive skink clade. Although each of these three clades is strongly supported, their specific placement among scincids is only weakly supported by the mtDNA data. However, in no phylogenies of the 95% credible set do these three clades form a clade to the exclusion of all the remaining skinks (Table 10). Thus, we are confident in our assessment of "*Eumeces*" paraphyly.

Although Griffith et al. (2000) based their conclusions on relatively few morphological characters, their recognition of these three "*Eumeces*" clades is in general agreement with our study. Both studies support

the placement of the *E. schneideri* group with the other north African and southwest Asian genera *Scincus* and *Scincopus*, but the specific relationships between these three taxa differ. Whereas Griffith et al. (2000) hypothesized a sister-group relationship between *Scincus* and *Scincopus*, our results suggest a closer relationship between *Scincus* and the *E. schneideri* group. Although weakly supported, this hypothesis is congruent with that of Arnold and Leviton (1977). The basal position of the east Asian/North American "*Eumeces*" clade is also congruent with the findings of Griffith et al. (2000). However, our data also strongly support the placement of the monotypic, limb-reduced *Neoseps* within the east Asian/North American clade as the sister species of the geographically proximate "*E.*" *egregius*, which is consistent with Richmond and Reeder (2002) and Schmitz et al. (2004) and inconsistent with Griffith et al. (2000), who implied that *Neoseps* was nested within the large clade containing all the skinks to the exclusion of the east Asian/North American "*Eumeces*" clade.

In order to correct for obvious polyphyly of "*Eumeces*," taxonomic changes are clearly needed. However, for reasons outlined by Schmitz et al. (2004), we do not support all of Griffith et al.'s (2000) taxonomic recommendations. Designating the "*E.*" *taeniolatus* group as *Eurylepis*, and the "*E.*" *schwartzei* group as *Mesoscincus* (Griffith et al., 2000) is warranted, but redesignating the type species to preserve the name *Eumeces* for the east Asian/North American "*Eumeces*" and the creation of *Novoeumeces* (for the *E. schneideri* group) is not justifiable. Instead, we retain *Eumeces* (sensu stricto) for the *E. schneideri* group that contains the type species, *E. pavimentatus*. *Eumeces pavimentatus*, although not included in this study, is frequently treated as a subspecies of *E. schneideri*. A recent study by Schmitz et al. (2004) included a specimen of *E. schneideri* collected from a locality proximate to the type locality of *E. s. pavimentatus* and found strong support for its inclusion in a clade of other recognized subspecies of *E. schneideri*. We also designate *Plestiodon* (Duméril and Bibron, 1839) as the generic name for the all species of the east Asian/North American + *Neoseps* clade.

Conclusions and Recommendations

Until very recently, practitioners of model-based phylogenetic methods have generally been limited to the use of a single model for combined analyses of multiple genes and gene regions. If subsets of the data (such as different genes, codon positions, stems and loops, etc.) evolve under very different models of evolution, the use of a single, compromise model may result in a large amount of systematic error. By comparing 95% credible intervals of parameters estimated for each partition, we demonstrate numerous instances of incongruence among character partitions and thus the partitions are not adequately represented by a single model. We further show that allowing subsets of the data to evolve under different models and parameters (i.e., partitioned analyses) greatly improves our ability to explain the evolution of the data (as measured by mean $-\ln L$) and provides presumably more accurate posterior probability estimates. Because how data are partitioned is far more important than the overall number of partitions, we propose an objective method of partition selection based on the Bayes factor.

The use of partition-specific modeling represents an enormous advance in phylogenetic methodology. Given the heterogeneous nature of DNA evolution even within genes (e.g., codon positions), we urge researchers to make full use of partitioned analyses. We additionally advocate the use of an objective criterion to evaluate and test alternative partitioning strategies using the Bayes factor. This methodology is easily implemented by calculating the difference in the harmonic means of the likelihoods sampled from the posterior either directly (as in this study) or by using the *sump* command of MrBayes 3.0.

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References

Alfaro, M. E., S. Zoller, and F. Lutzoni. 2003. Bayes or bootstrap? A simulation study comparing the performance of Bayesian Markov chain Monte Carlo sampling and bootstrapping in assessing phylogenetic confidence. Mol. Biol. Evol. 20:255–266.

Arnold, E. N., and A. E. Leviton. 1977. A revision of the lizard genus *Scincus* (Reptilia: Scincidae). Bull. Br. Mus. Nat. Hist. 31:187–248.

Boulenger, G. A. 1884. Synopsis of the families of existing Lacertilia. Annu. Mag. Nat. Hist. 5:117–122.

Brown, W. C. 1956. A revision of the genus *Brachymeles* (Scincidae), with descriptions of new species and subspecies. Breviora 54:1–19.

Buckley, T. R., P. Arensburger, C. Simon, and G. K. Chambers. 2002. Model mispecification and probabilistic tests of topology: Evidence from empirical data sets. Syst. Biol. 51:509–523.

Bull, J. J., J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford, and P. J. Waddell. 1993. Partitioning and combining data in phylogenetic analysis. Syst. Biol. 42:384–397.

Camp, C. L. 1923. Classification of the lizards. Bull. Am. Mus. Nat. Hist. 48:289–481.

Chippindale, P. T., and J. J. Wiens. 1994. Weighting, partitioning, and combining characters in phylogenetic analysis. Syst. Biol. 43:278–287.

Cope, E. D. 1885. A contribution to the herpetology of Mexico. I. The collection of the Comisión Científica. Proc. Am. Phil. Soc. 22:379–382.

Cope, E. D. 1892. On degenerate types of scapular and pelvic arches in the Lacertilia. J. Morph. 7:223–244.

Cope, E. D. 1900. The crocodilian, lizards and snakes of North America. Ann. Report U.S. Nat'l. Mus. for 1898. Part II:153-1270. Government. Printing Office, Washington D.C.

de Queiroz, A. 1993. For concensus (sometimes). Syst. Biol. 42:368–372.

Duméril, A. M. C., and G. Bibron. 1839. Erpétologie général ou histoire naturelle complete des reptiles, V.

Erixon, P., B. Svennblad, T. Britton, and B. Oxelman. 2003. Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. Syst. Biol. 52:665–673.

Estes, R. 1983. The fossil record and early distribution of lizards. Pages 365–398 *in* Advances in herpetology and evolution: Essays in honor of Ernest E. Williams (A. Rhodin and K. Miyata, eds.). Museum of Comparative Zoology, Cambridge, Massachusetts, USA.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. Pages 119–281 *in* Phylogenetic relationships of the Lizard families (R. Estes and G. Pregill, eds.). Stanford University Press, Stanford, California, USA.

Felsenstein, J. 1981. Evolutionary trees from DNA sequences: A maximum likelihood approach. J. Mol. Evol. 17:368–376.

Fishbein, M., C. Hibsch-Jetter, D. E. S Oltis, and L. Hufford. 2001. Phylogeny of Saxifragales (Angiosperms, Eudicots): Analysis of a rapid, ancient radiation. Syst. Biol. 50:817–847.

Gans, C. 1975. Tetrapod limblessness: Evolution and functional corollaries. Am. Zool. 15:455–467.

Gans, C. 1986. Locomotion of limbless vertebrates: Patterns and evolution. Herpetologica 42:33–46.

Gans, C. 1994. Approaches to the evolution of limbless locomotion. Cuadernos Herpetol. 8:12–17.

Gatesy, J., R. DeSalle, and W. Wheeler. 1993. Alignment-ambiguous nucleotide sites and the exclusion of systematic data. Mol. Phylogenet. Evol. 2:152–157.

Gelman, A. 1996. Inference and monitoring convergence. Pages 131–144 *in* Markov Chain Monte Carlo in practice (W. R. Gilks, S. Richardson, and D. J. Spiegelhalter, eds.). Chapman and Hall, New York, USA.

Goldman, N., and Z. Yang. 1994. A codon-based model of nucleotide substitution for protein coding DNA sequences. Mol. Biol. Evol. 11:725–736.

Greer, A. E. 1970a. A subfamilial classification of scincid lizards. Bull. Mus. Comp. Zool. 139:151–183.

Greer, A. E. 1970b. The systematics and evolution of the Subsaharan Africa, Seychelles, and Mauritius scincine scincid lizards. Bull. Mus. Comp. Zool. 140:1–23.

Greer, A. E. 1985. The relationships of the lizard genera *Anelytropsis* and *Dibamus*. J. Herpetol. 19:116–156.

Greer, A. E. 1986. Lygosomine (Scincidae) monophyly: A third, corroborating character and a reply to critics. J. Herpetol. 20:123–126.

Greer, A. E. 1987. Limb reduction in the lizard genus *Lerista*. 1. Variation in the number of phalanges and presacral vertebrae. J. Herpetol. 21:267–276.

Greer, A. E. 1990. Limb reduction in the scincid lizard genus *Lerista*. 2. Variation in the bone complements of the front and rear limbs and the number of postsacral vertebrae. J. Herpetol. 24:142–150.

Greer, A. E. 1991. Limb reduction in squamates: Identification of the lineages and discussion of the trends. J. Herpetol. 25:166–173.

Greer, A. E. 2001. Distribution of maximum snout-vent length among species of scincid lizards. J. Herpetol. 35:383–395.

Greer, A. E. 2002. The loss of the external ear opening in scincid lizards. J. Herpetol. 36:544–555.

Greer, A. E., V. Caputo, B. Lanza, and R. Palmieri. 1998. Observations on limb reduction in the scincid lizard genus *Chalcides*. J. Herpetol. 32:244–252.

Greer, A. E., and G. M. Shea. 2000. A major new head scale character in non-lygosomine scincid lizards. J. Herpetol. 34:629–634.

Griffith, H., A. Ngo, and R. W. Murphy. 2000. A cladistic evaluation of the cosmopolitan genus *Eumeces* Wiegmann (Reptilia, Squamata, Scincidae). Russ. J. Herpetol. 7:1–16.

Gu, X., Y. X. Fu, and W. H. Li. 1995. Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. Mol. Biol. Evol. 12:546–557.

Gutell, R. R., and G. E. Fox. 1988. A compilation of large subunit RNA sequences presented in a structural format. Nucleic Acids Res. 16:r175–r269.

Hasegawa, M., H. Kishino, and T. Yano. 1985. Dating the human-ape split by a molecular clock of mitochondrial DNA. J. Mol. Evol. 22:160–174.

Holder, M., and P. O. Lewis. 2003. Phylogeny estimation: Traditional and Bayesian approaches. Nat. Rev. Genet. 4:275–284.

Honda, M., H. Ota, M. Kobayashi, J. Nabhitabhata, H. Yong, and T. Hikida. 2000. Phylogenetic relationships, character evolution, and biogeography of the subfamily Lygosominae (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. Mol. Phylogenet. Evol. 15:452–461.

Huelsenbeck, J. P. 1995a. The performance of phylogenetic methods in simulation. Syst. Biol. 44:17–48.

Huelsenbeck, J. P. 1995b. The robustness of two phylogenetic methods: Four-taxon simulations reveal a slight superiority of maximum likelihood over neighbor joining. Mol. Biol. Evol. 12:843–849.

Huelsenbeck, J. P, and K. A. Crandall. 1997. Phylogeny estimation and hypothesis testing using maximum likelihood. Annu. Rev. Ecol. Syst. 28:437–466.

Huelsenbeck, J. P., and N. S. Imennov. 2002. Geographic origin of human mitochondrial DNA: Accommodating phylogenetic uncertainty and model comparison. Syst. Biol. 51:155–165.

Huelsenbeck, J. P., B. Larget, R. E. Miller, and F. Ronquist. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. Syst. Biol. 51:673–688.

Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754–755.

Jackman, T.R., A. Larson, K. de Queiroz, and J.B. Losos. 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. Syst. Biol. 48:254–285.

Jeffreys, H. 1935. Some tests of significance, treated by the theory of probability. P. Camb. Philos. Soc. 31:203–222.

Jeffreys, H. 1961. Theory of probability. Oxford University Press, Oxford.

Kass, R. E., and A. E. Raftery. 1995. Bayes factors. J. Am. Stat. Assoc. 90:773–795.

Kimura, M. 1980. A simple method for estimating evolutionary rate of base substitution through comparative studies of nucleotide sequences. J. Mol. Evol. 16:111–120.

Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae: Serpentes). Syst. Zool. 38:7–25.

Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Pääbo, F. X. Villablanca, and A. C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals—amplification and sequencing with conserved primers. Proc. Nat. Acad. Sci. USA. 86:6196–6200.

Kumazawa, Y., and M. Nishida. 1993. Sequence evolution of mitochondrial tRNA genes and deep-branch animal phylogenetics. J. Mol. Evol. 37:380–398.

Kumazawa, Y., and M. Nishida. 1999. Complete mitochondrial DNA sequences of the green turtle and blue-tailed mole skink: Statistical evidence for archosaurian affinity of turtles. Mol. Biol. Evol. 16:784–792.

Lang, M. 1991. Generic relationships within Cordyliformes (Reptilia: Squamata). Bull. Inst. Roy. Sci. Nat. Belgique 61:121–188.

Larget, B., and D. L. Simon. 1999. Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. Mol. Biol. Evol. 16:750–759.

Lavine, M., and M. J. Schervish. 1999. Bayes factors: What they are and what they are not. Am. Stat. 53:119–122.

Leaché, A. D., and T. W. Reeder. 2002. Molecular systematics of the Eastern Fence Lizard (*Sceloporus undulatus*): A comparison of parsimony, likelihood, and Bayesian approaches. Syst. Biol. 51:44–68.

Lee, M. S. Y. 1998. Convergent evolution and character correlation in burrowing reptiles: Towards a resolution of squamate relationships. Biol. J. Linn. Soc. 65:369–453.

Lee, M. S. Y. 2002. Soft anatomy, diffuse homoplasy, and the relationships of lizards and snakes. Zool. Scr. 29:101–130.

Lieb, C. S. 1985. Systematics and distribution of the skinks allied to *Eumeces tetragrammus* (saurie: scincidae). Contrib. Sci. Los Angel. 357:1–19.

Mausfeld, P., and A. Schmitz. 2003. Molecular phylogeography, intraspecific variation and speciation of the Asian scincid lizard

genus *Eutropis* Fitzinger, 1843, (Squamata: Reptilia: Scincidae): taxonomic and biogeographic implications. Org. Divers. Evol. 3:161–171.

Mausfeld, P., A. Schmitz, W. Böhme, B. Misof, D. Vrcibradic, and C. F. D. Rocha. 2002. Phylogenetic affinities of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean Archipelago of Fernando de Noronha (Brazil): Necessity of partitioning the Genus *Mabuya* Fitzinger, 1826 (Scincidae: Lygosominae). Zool. Anz. 241:281–193.

McGuire, G., M. C. Denham, D. J. Balding. 2001. Models of sequence evolution for DNA sequences containing gaps. Mol. Biol. Evol. 18:481–490.

Muse, S. V. 1995. Evolutionary analyses of DNA sequences subject to constraints on secondary stucture. Genetics 139:1429–1439.

Muse, S. V., and B. S. Gaut. 1994. A likelihood approach for comparing synonymous and nonsynonymous substitution rates, with application to the chloroplast genome. Mol. Biol. Evol. 11:715–724.

Newton, M. A., and A. E. Raftery. 1994. Approximate Bayesian inference with the weighted likelihood bootstrap. J. R. Stat. Soc. B 56:3–48.

Nylander J. A. A. 2002. MrModeltest v1.0b. Program distributed by the author (http://www.ebc.uu.se/systzoo/staff/nylander.html).

Nylander, J. A. A., F. Ronquist, J. P. Huelsenbeck, and J. L. Nieves-Aldrey. 2004. Bayesian phylogenetic analysis of combined data. Syst. Biol. 53:47–67.

Odierna, G., A. Canapa, F. Andreone, G. Aprea, M. Barucca, T. Capriglione, and E. Olmo. 2002. A phylogenetic analysis of Cordyliformes (Reptilia: Squamata): comparison of molecular and karyological data. Mol. Phylogenet. Evol. 23:37–42.

Poe, S., and A. L. Chubb. 2004. Birds in a bush: Five genes indicate explosive evolution of avian orders. Evolution 58:404–415.

Posada, D., and K. A. Crandall. 1998. Modeltest: Testing the model of DNA substitution. Bioinformatics 14:817–818.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 2004. Herpetology, 3rd edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Raftery, A. 1996. Hypothesis testing and model selection. Pages 163–187 *in* Markov Chain Monte Carlo in Practice (W. R. Gilks, S. Richardson, and D. J. Spiegelhalter, eds.). Chapman and Hall, New York, USA.

Reeder, T. W. 1995. Phylogenetic relationships among phrynosomatid lizards as inferred from mitochondrial ribosomal DNA sequences: Substitutional bias and information content of transitions relative to transversions. Mol. Phylogenet. Evol. 4:203–222.

Reeder, T. W. 2003. A phylogeny of the Australian *Sphenomorphus* group (Scincidae: Squamata) and the phylogenetic placement of the crocodile skinks (*Tribolonotus*): Bayesian approaches to assessing congruence and obtaining confidence in maximum likelihood inferred relationships. Mol. Phylogenet. Evol. 27:384–397.

Richmond, J. Q., and T. W. Reeder. 2002. Evidence for parallel ecological speciation in scincid lizards of the *Eumeces skiltoniatus* species group (Squamata: Scincidae). Evolution 56:1498–1513.

Rieppel, O. 1981. The skull and the jaw adductor musculature in some burrowing scincomorph lizards of the genera *Acontias*, *Typhlosaurus*, and *Feylinia*. J. Zool. (Lond.) 195:493–528.

Rieppel, O. 1984. The cranial morphology of the fossorial lizard genus *Dibamus* with a consideration of its phylogenetic relationships. J. Zool. (Lond.) 204:289–327.

Schmitz, A., M. C. Brandley, P. Mausfeld, M. Vences, F. Glaw, R. A. Nussbaum, and T. W. Reeder. 2005. Opening the black box: Phylogenetics and morphological evolution of the malagasy fossorial lizards of the subfamily "Scincinae." Mol. Phylogenet. Evol. 34:118–133.

Schmitz, A., P. Mausfeld, and D. Embert. 2004. Molecular studies on the genus *Eumeces* Wiegmann, 1834: phylogenetic relationships and taxonomic implications. Hamadryad 28:73–89.

Schwenk, K. 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. Pages 569–598 *in* Phylogenetic relationships of the Lizard families (R. Estes and G. Pregill eds.). Stanford Univ. Press, Stanford, California, USA.

Shimodaira, H., and M. Hasegawa. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Mol. Biol. Evol 16:1114–1116.

Swofford, D. L., G. J. Olsen, P. J. Waddell, and D. M. Hillis. 1996. Phylogenetic inference. Pages 407–543 *in* Molecular systematics, 2nd edition (D. M. Hillis, C. Moritz, and B. K. Mable, eds.), Sinauer Associates, Sunderland, Massachusetts, USA.

Swofford, D. L., P. J. Waddell, J. P. Huelsenbeck, P. G. Foster, P. O. Lewis, and J. S. Rogers. 2001. Bias in phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. Syst. Biol. 50: 525–539.

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin, and D. G. Higgins. 1997. The ClustalX windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 24:4876–4882.

Tillier, E. R. M., and R. A. Collins. 1995. Neighbor joining and maximum likelihood with RNA sequences: Addressing the interdependence of sites. Mol. Biol. Evol. 12:7–15.

Titus, T. A., and D. R. Frost. 1996. Molecular homology assessment and phylogeny in the lizard family Opluridae (Squamata: Iguania). Mol. Phylogenet. Evol. 6:49–62.

Townsend, T. M., A. Larson, E. Louis, and J. R. Macey. 2004. Molecular phylogenetics of squamata: The position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. Syst. Biol. 53:735–757.

Tuffley, C., and M. Steel. 1997. Links between maximum likelihood and maximum parsimony under a simple model of site substitution. Bull. Math. Bio. 59:581–607.

Vicario, S., A. Caccone, and J. Gauthier. 2003. Xantusiid "night" lizards: A puzzling phylogenetic problem revisited using likelihood-based Bayesian methods on mtDNA sequences. Mol. Phylogenet. Evol. 26:243–261.

Warren, D. L., J. Wilgenbusch, and D. L. Swofford. 2003. Converge: A program for implementing MCMC convergence diagnostics. Available from the authors at danwarren@ucdavis.edu.

Whiting, A. S., A. M. Bauer, and J. W. Sites, Jr. 2003. Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). Mol. Phylogenet. Evol. 29:582–598.

Wiens, J. J., and T. W. Reeder. 1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. Herp. Monog. 11:1–101.

Wilcox, T. P., D. J. Zwickl, T. A. Heath, D. M. Hillis. 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. Mol. Phylogenet. Evol. 25:361–371.

Wilgenbusch, J., and K. de Queiroz. 2000. Phylogenetic relationships among the phrynosomatid sand lizards inferred from mitochondrial DNA sequences generated by heterogeneous evolutionary processes. Syst. Biol. 49:592–612.

Yang, Z. 1993. Maximum likelihood estimation of phylogeny from DNA sequences when substitution rates differ over sites. Mol. Biol. Evol. 10:1396–1401.

Yang, Z. 1994a. Estimating the pattern of nucleotide substitution. J. Mol. Evol. 39:105–111.

Yang, Z. 1994b. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: Approximate methods. J. Mol. Evol. 39:306–314.

Yang, Z. 1996. Maximum likelihood models for combined analyses of multiple sequence data. J. Mol. Evol. 42:587–596.

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