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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

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Abstract

Australian scincid lizards are a diverse squamate assemblage (~385 species), divided among three major clades (*Egernia*, *Eugongylus*, and *Sphenomorphus* groups). The *Sphenomorphus* group is the largest, comprising 61% of the Australian scincid fauna. Phylogenetic relationships within the Australian *Sphenomorphus* group and the phylogenetic placement of *Tribolonotus* are inferred using mtDNA (12S and 16S rRNA genes, ND4 protein-coding gene, and associated tRNA genes; 2185 bp total). These data were analyzed separately (structural RNA vs protein-coding partitions) and combined using maximum likelihood. Confidence in inferred clades was assessed using non-parametric bootstrapping and Bayesian analysis. Analysis of the combined data strongly supports *Sphenomorphus* group (as well as the Australian subgroup) monophyly. *Notoscincus* is strongly placed as the sister taxon of the remaining Australian *Sphenomorphus* group taxa, with this more exclusive clade being divided into two major groups (one restricted to mesic eastern Australia and the other continent wide). The speciose Australian "*Eulamprus*" and "*Glaphyromorphus*" are both polyphyletic. All remaining non-*Sphenomorphus* group lygosomine skinks strongly form a clade, with *Tribolonotus* placed as the sister taxon of the Australian *Egernia* group.

1. Introduction

Scincid lizards (skinks) of Australia are a diverse assemblage, with all species belonging to the widespread subfamily Lygosominae (Greer, 1970a). In the first formal taxonomic subdivision of Australian scincids, Greer (1979a) recognized three major clades (*Egernia*, *Eugongylus*, and *Sphenomorphus* groups), each of which also includes non-Australian taxa. Of these major Australian clades, the *Sphenomorphus* group exhibits the greatest species diversity, as well as morphological (e.g., strongly limbed to completely limbless; varied body size) and ecological diversity (e.g., diurnal and nocturnal; arboreal, terrestrial, and fossorial; oviparous and viviparous). Of the ~385 currently recognized Australian scincid species (Cogger, 2000), 235 belong to the *Sphenomorphus* group. A great deal is known about the basic biology and ecology for many species within this assemblage (reviewed by Greer, 1989) and yet the higher-level phylogenetic relationships among (as well as within) the 14 Australian *Sphenomorphus* group genera are poorly understood. There are essentially no published phylogenies for Australian *Sphenomorphus* group intergeneric relationships. The handful of studies that do exist only deal with smaller hypothesized clades and are generally taxonomic in nature, augmented with brief phylogenetic scenarios (e.g., Choquentot and Greer, 1989; Greer, 1979b, 1983; Greer and Cogger, 1985). Hypotheses of relationships within the more speciose genera are also lacking, as well as support for the

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monophyly of some genera (e.g., *Eulamprus*, *Glaphyromorphus*).

The Australian *Sphenomorphus* group presumably represents a clade within the more cosmopolitan *Sphenomorphus* group. The *Sphenomorphus* group reaches it greatest diversity in Australia and southeast Asia, but also extends into East Asia and the New World (Greer, 1974, 1979a, 1997; Greer and Parker, 1967, 1974). There are currently thirteen non-Australian *Sphenomorphus* group genera (Allison and Greer, 1986; Darevsky and Orlov, 1997; Greer, 1979a; Greer and Simon, 1982). Monophyly of the *Sphenomorphus* group appears to be well supported by numerous morphological apomorphies (parietal scales meet behind interparietal; medial pair of preanal scales overlap outer preanals; iris of eye essentially as dark as pupil; deeply forked hemipenes; Greer, 1979a). However, evidence supporting the monophyly of the Australian group has never been presented. The phylogenetic scenario by Greer (1974, his Fig. 38) is the only hypothesis of higher-level relationships for the *Sphenomorphus* group. If this hypothesis accurately represents the evolutionary history of the *Sphenomorphus* group, then the genus "*Sphenomorphus*" is clearly paraphyletic. Greer (1974) hypothesized that the two diverse groups (i.e., *fasciatus* and *variegatus* species groups) within "*Sphenomorphus*" gave rise to the other more morphologically distinct genera of the *Sphenomorphus* group. As with the Australian subgroup, the intergeneric relationships between the non-Australian genera is unclear, as well as their exact relationship to the Australian taxa.

The spinose Crocodile Skinks of the genus *Tribolonotus* are a small (seven species) and bizarre group of lizards restricted to New Guinea, the Solomon Islands, and the Bismarck Archipelago (Cogger, 1972; Greer and Parker, 1968; Zweifel, 1966). Besides spiny scalation (rare among scincids), *Tribolonotus* is unique among lizards in their possession of volar (= soles of feet) pores and abdominal glands (Greer and Parker, 1968; Parker, 1940). Because of these unique attributes, the monophyly of *Tribolonotus* has not been questioned. However, despite their peculiar morphology, little is known about the biology of this enigmatic group (reviewed in Greer and Parker, 1968).

Although presumed to be a lygosomine, the specific phylogenetic placement of *Tribolonotus* within this large clade is uncertain. Few studies have speculated on the phylogenetic placement of *Tribolonotus* and these have generally implicitly assumed that its affinities lie with the Australian scincids. In diagnosing the Australian subgroups, Greer (1979a) hypothesized that *Tribolonotus* was a member of the *Egernia* group, but did not list the morphological characters supporting such a relationship. Alternatively, Greer (1979a) suggested that if *Tribolonotus* was not related to the *Egernia* group, then its affinities might be with the *Sphenomorphus* group. Based on immunoelectrophoretic evidence, Hutchinson (1980) postulated that *Tribolonotus* was more closely related to the *Egernia* and *Eugongylus* groups than to the *Sphenomorphus* group, with the *Tribolonotus* plasma reacting strongest (though only slightly) with the antiserum from the *Eugongylus* group. Baverstock and Donnellan (1990) used microcomplement fixation to assess the phylogenetic affinities of the three major Australian scincid clades and concluded that the *Eugongylus*, *Egernia*, and *Sphenomorphus* groups (as well as *Lamprolepis*) were approximately equally divergent from *Tribolonotus*. Such a finding suggests that *Tribolonotus* may be a relatively basal lygosomine. Unfortunately, no explicitly character based phylogenetic analyses (using morphology or molecules) have been conducted to elucidate the phylogenetic placement of this bizarre clade of skinks.

In this study, I use mtDNA data and maximum likelihood to infer phylogenetic relationships among lygosomine scincid lizards. One specific objective is to perform a phylogenetic analysis of the Australian *Sphenomorphus* group, with three specific goals: (1) determine the phylogenetic placement of the *Sphenomorphus* group within the Lygosominae, (2) test the monophyly of the Australian *Sphenomorphus* group, and (3) provide a preliminary phylogenetic hypothesis of the higher-level relationships within the Australian group. An additional objective is to determine the phylogenetic placement of *Tribolonotus*, relative to the three major Australian lygosomine clades. A Bayesian approach is used to test congruence between data partitions and assess confidence in the inferred relationships.

2. Materials and methods

2.1. Choice of terminal taxa

In all, 36 lygosomine species (Appendix A) were included in this study. Multiple species of the *Egernia*, *Eugongylus*, and *Sphenomorphus* groups were represented, as well as several lygosomines of uncertain placement. All currently recognized genera of the Australian *Sphenomorphus* group (except *Coggeria*) were included in an attempt to cover most of the phyletic diversity. In addition, three non-Australian species of the *Sphenomorphus* group were included. This sampling strategy allowed a preliminary test of the monophyly of the Australian *Sphenomorphus* group. *Tribolonotus* was represented by a single exemplar (*Tribolonotus gracilis*). Lygosomine monophyly appears to be well supported by morphological evidence (Greer, 1970a, 1986). One acontine (*Acontias melagris*) and two "scincine" (*Eumeces septentrionalis* and *Eumeces egregius*) skinks were simultaneously used to root the lygosomine phylogeny.

2.2. DNA amplification, sequencing, and alignment

DNA was extracted following Hillis et al. (1996) and portions of the mitochondrial genome (i.e., 12S, 16S, ND4 [plus two 3′ flanking tRNAs]) were amplified (primers in Table 1). Unincorporated primers and nucleotides were removed using PEG/NaCl precipitation. Purified PCR templates were sequenced using dye-labeled dideoxy terminator cycle sequencing and an ABI 377 automated DNA sequencer.

DNA sequences were aligned using Clustal W (Thompson et al., 1994). Secondary structure models, following the protocol of Wiens and Reeder (1997), aided alignment of the rRNA and tRNA gene sequences. 12S and 16S stem and loop regions were identified using the Van de Peer et al. (1994) and Gutell and Fox (1988) models. The Kumazawa and Nishida (1993) secondary structure models assisted in the alignment of tRNA gene sequences. Ambiguously aligned regions were identified based on various gap cost sequence alignments (gap opening penalties = 6, 9, or 12) and were excluded from phylogenetic analyses. Because of conserved codon reading frame, the ND4 sequences were unambiguously aligned. All DNA sequences are deposited in GenBank (Accession Nos. AB016606, AY046420, AY046462, AY169563–AY169674) and the PAUP* matrix is available upon request and/or can be downloaded from the author's web site (http://www.bio.sdsu.edu/pub/tod/homepage.html).

2.3. Phylogenetic analysis

Phylogenetic analyses were conducted using maximum parsimony (MP) and maximum likelihood (ML) methods, as implemented in PAUP* (versions 4.0b2-6; Swofford, 1999). Although the data were evaluated using MP and ML approaches, the phylogenetic hypotheses inferred using ML were preferred. Uniformly weighted heuristic MP analyses (TBR branch swapping; 500 random taxon addition replicates per analysis) were performed to obtain an initial tree(s) for testing models of sequence evolution (see below).

The ML phylogenies were estimated following a successive approach similar to that described by Swofford et al. (1996) and Wilgenbusch and de Queiroz (2000), with Modeltest 3.0 (Posada and Crandall, 1998) being used to test alternative models of sequence evolution. The best model (and model parameters) estimated from the initial MP tree was used in a ML heuristic tree search, with the initial MP tree serving as a starting tree. If the resulting ML tree differed from the initial starting tree, then all models were re-tested on the new tree, followed by a new ML tree search.

The mtDNA regions sequenced code for two very different products, structural RNAs (i.e., rRNAs and tRNAs) and the ND4 protein, which may be evolving under different models of sequence evolution. Following separate analyses and assessment of congruence between the structural RNA and protein-coding data sets, all the mtDNA data were combined for phylogenetic analysis. In the combined ML analysis, the best model for the combined data may be a compromise between the best models of the individual partitions. Ideally, it would be preferred to conduct such a combined analysis implementing different models for specific partitions of the data. However, currently it is not possible to conduct mixed-model ML analyses in PAUP*. The impact of this "compromise" model on the inferred relationships was investigated by analyzing the combined data with the best models for the separate protein-coding and structural RNA gene regions.

2.4. Confidence and congruence assessment

The computational limitations of ML make it difficult (if not impossible) to perform extensive non-parametric bootstrap (Felsenstein, 1985) analyses on data sets with large numbers of taxa (Sanderson and Kim, 2000). Because of this limitation, MP derived bootstrap proportions have been used as proxies of support for relationships inferred by ML. Recently, Larget and Simon (1999) demonstrated that complex nucleotide substitution models and the likelihood function can be implemented quickly and efficiently for large data sets

Table 1
Oligonucleotide primers used in this study

Gene	Primer name	Sequence (5′–3′)	Position[a]	Source
12S	tPhe	AAAGCACRGCACTGAAGATGC	618	Wiens et al. (1999)[b]
	12e	GTRCGCTTACCWTGTTACGACT	1558	Wiens et al. (1999)
16S	16aR2	CCCGMCTGTTTACCAAAAACA	2509	This study[c]
	16d	CTCCGGTCTGAACTCAGATCACGTAG	3057	Reeder (1995)
ND4	ND4	TGACTACCAAAAGCTCATGTAGAAGC	11,427	Forstner et al. (1995)
	LEU	TRCTTTTACTTGGATTTGCACCA	12,314	Forstner et al. (1995)

[a] 3′ nucleotide position in the human mtDNA sequence of Anderson et al. (1981).
[b] Modified version of primer L2172 of Titus and Frost (1996).
[c] Modified version of primer 16aR of Reeder (1995).

by incorporating Bayesian methods (see Leaché and Reeder, 2002 for empirical example). Thus, Bayesian analysis was used to estimate posterior probabilities for the phylogenetic relationships inferred in the ML analyses.

Bayesian analyses were performed using MrBayes 2.0 (Huelsenbeck and Ronquist, 2001), using the general models previously identified using Modeltest. Bayesian analyses were launched with random starting trees and run for 1.0×10^6 generations, sampling the Markov chains at intervals of 100 generations. To more thoroughly explore tree and parameter space, four incrementally heated Markov chains (using default heating values) were used. To determine whether the Bayesian analyses had reached stationarity, likelihoods of sample points were plotted against generation time. Sample points generated before reaching stationarity were discarded as "burn-in" samples. To ensure the Bayesian analyses were not trapped on local optima, analyses were performed twice for each data set and apparent stationarity levels were compared for convergence (Huelsenbeck and Bollback, 2001). In all analyses, the likelihood values stabilized by 2.0×10^5 generations, with the last 9000 sampled trees being used to estimate the Bayesian posterior probabilities. In addition, the estimated posterior probabilities of inferred clades from independent analyses (for a given data set) were compared for congruence (Huelsenbeck et al., 2001). Similarity of clade posterior probabilities is indicative of the Bayesian analyses converging on essentially identical posterior probability distributions.

The percentage of samples (pooled for a given data set) recovering any particular clade represents that clade's posterior probability (Huelsenbeck and Ronquist, 2001; Huelsenbeck et al., 2001). Unlike non-parametric bootstrap proportions which are known to be conservative estimates of clade confidence (Hillis and Bull, 1993), a recent simulation study (Wilcox et al., 2002) suggests Bayesian posterior probabilities represent much closer estimates of true clade probabilities (referred to as "*Pc*" throughout). Thus, clades with $Pc \geqslant 95\%$ were considered strongly (significantly) supported. For comparison, support was also assessed by non-parametric bootstrapping. Uniformly weighted MP bootstrap analyses were conducted on all data sets and based on 1000 heuristic tree searches (three random taxon addition searches/pseudoreplicate; TBR branch swapping).

Two different approaches were taken to assess incongruence between data partitions. One involved comparing posterior probabilities between trees (following similar methodology outlined by Wiens, 1998), with strongly supported conflicting clades being indicative of significant incongruence (= heterogeneity). A Bayesian approach (similar to that proposed by Buckley et al., 2002) was also used to test for significant incongruence between data partitions. For each data partition, the 0.95 posterior probability interval was estimated, with this interval representing the set of phylogenies contained within the cumulative 0.95 posterior probability distribution. If the preferred ML phylogeny from one data partition was contained within the 0.95 interval of a different data partition (which yielded a different ML phylogeny), then one could not statistically reject the possibility that the phylogeny of interest gave rise to the different observed data partition (= no statistically significant incongruence or heterogeneity).

Alternative phylogenetic hypotheses were tested against the preferred combined data phylogeny using the Shimodaira–Hasegawa test (S–H test; Goldman et al., 2000; Shimodaira and Hasegawa, 1999). The S–H tests were performed by PAUP* 4.08, using the following parameters: same substitution model (and estimated parameters) as original ML analysis, RELL, and 10,000 bootstrap replicates.

3. Results

3.1. Separate phylogenetic analyses

Structural RNAs. A total of 1475 nucleotide positions were unambiguously aligned. Of these, 705 were variable (678 within lygosomines; 542 within the *Sphenomorphus* group) and 517 being parsimony informative (492 within lygosomines; 337 within the *Sphenomorphus* group). The ML tree search using the $GTR + I + \Gamma$ model (parameters given in Table 2) yielded a single optimal tree ($-\ln L = 16005.865$, Fig. 1). The phylogeny based on the structural RNA gene data can be rooted such that the lygosomines form a monophyletic group. However, this grouping is weakly supported ($Pc = 0.77$). The monophyly of the *Sphenomorphus* group is well supported ($Pc = 1.0$) and this large clade is the sister taxon of all remaining lygosomines in this study. Within the

Table 2
Maximum likelihood model parameter estimates for the mitochondrial DNA

	Substitution rates					Site rates		Nucleotide frequencies			
	A ↔ G	C ↔ T	A ↔ C	A ↔ T	C ↔ G	I	Γ	A	C	G	T
Structural	13.500	27.255	4.761	3.912	0.688	0.380	0.643	0.359	0.241	0.188	0.212
Protein	5.647	4.044	0.170	0.381	0.150	0.375	0.493	0.399	0.347	0.064	0.189
Combined	8.234	14.707	1.964	2.119	0.407	0.417	0.661	0.380	0.284	0.131	0.203

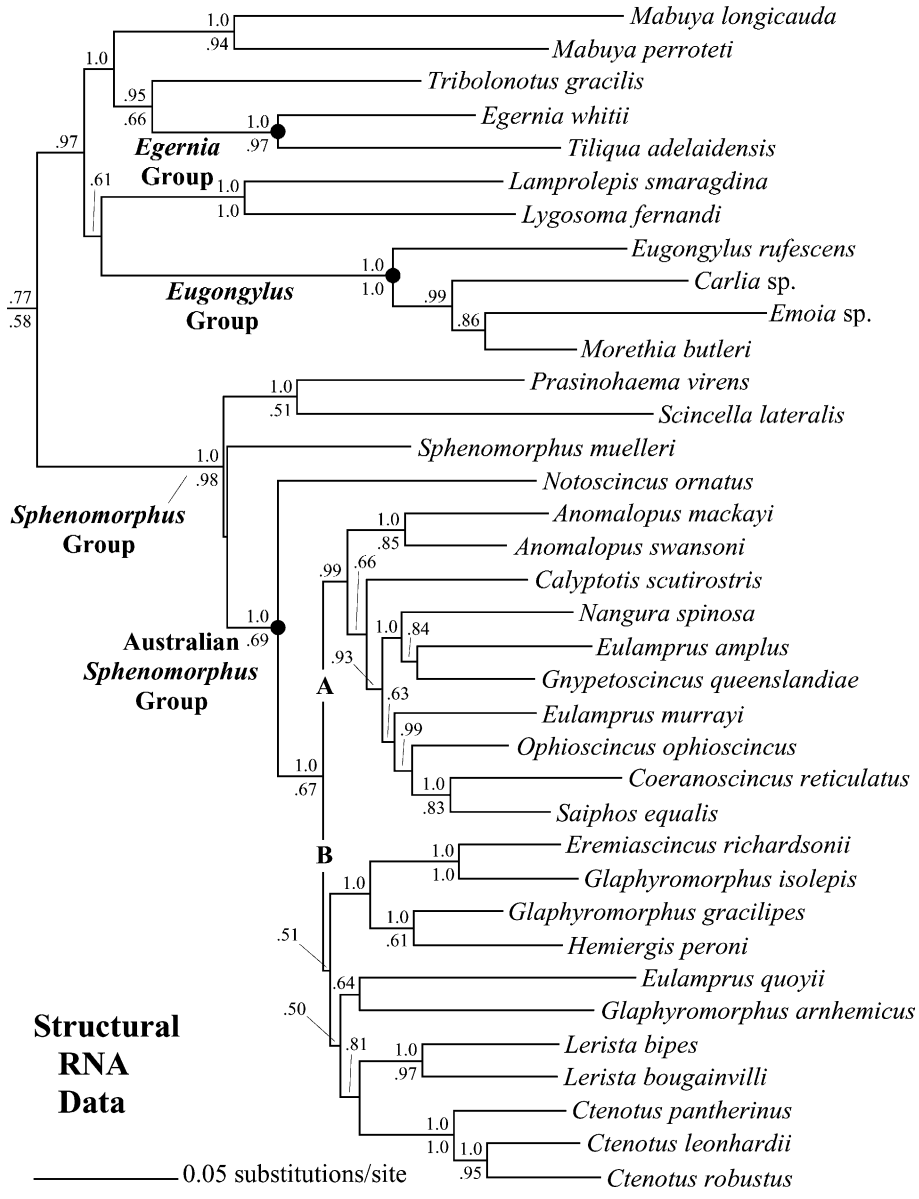

Fig. 1. Maximum likelihood phylogeny of lygosomines inferred from the separate analysis of the mitochondrial structural RNA coding data. Numbers above branches correspond to Bayesian posterior probabilities and numbers below branches correspond to bootstrap proportions from uniformly weighted parsimony analysis (proportions < 0.50 not shown).

Sphenomorphus group, there is also strong support ($Pc = 1.0$) for the monophyly of the Australian subgroup (= Australian *Sphenomorphus* group). *Notoscincus* is strongly supported ($Pc = 1.0$) as the sister taxon of the remaining members of the Australian *Sphenomorphus* group. This more exclusive clade is divided into two major monophyletic groups, one of which (Clade A; $Pc = 0.99$) is strongly supported by the structural RNA data. In all, 11 of the 20 inferred clades within the Australian *Sphenomorphus* group are strongly supported ($Pc \geqslant 0.95$).

Tribolonotus gracilis is marginally strongly placed ($Pc = 0.95$) as the sister taxon of a strongly supported ($Pc = 1.0$) monophyletic *Egernia* group. The *Eugongylus* group is also strongly supported as a clade ($Pc = 1.0$), which is weakly placed ($Pc = 0.61$) as the sister taxon of the well supported ($Pc = 1.0$) *Lamprolepis smaragdina* + *Lygosoma fernandi* clade.

ND4 protein-coding gene. A total of 710 nucleotide positions were unambiguously aligned, with 416 being variable (407 among lygosomines; 364 within the *Sphenomorphus* group). Of the variable positions, 370 were parsimony informative (357 among lygosomines; 308 within the *Sphenomorphus* group). The ML tree search using the GTR + I + Γ model (parameters given in Table 2) yielded a single optimal tree ($-\ln L =$ 12597.161, Fig. 2). The ML phylogeny inferred from the ND4 gene data could not be rooted to make the

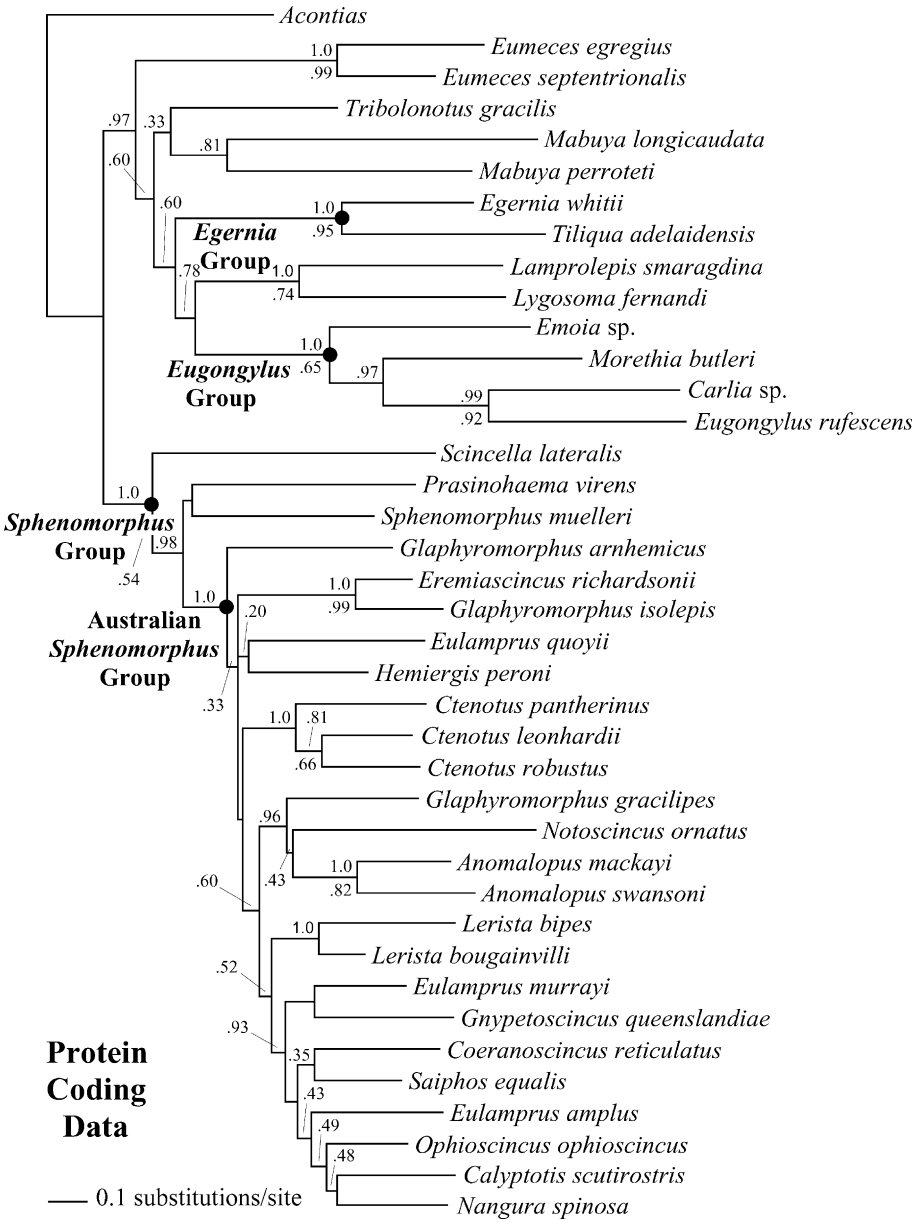

Fig. 2. Unrooted maximum likelihood phylogeny of lygosomines inferred from the separate analysis of the mitochondrial ND4 protein-coding data. Numbers above branches correspond to Bayesian posterior probabilities and numbers below branches correspond to bootstrap proportions from uniformly weighted parsimony analysis (proportions < 0.50 not shown).

lygosomines monophyletic, with the placement of *Acontias* or *Eumeces* among the lygosomines being apparently strongly supported ($Pc = 0.97$).

The *Sphenomorphus* group and the more exclusive Australian *Sphenomorphus* group are both well supported as clades ($Pc = 1.0$ and 0.98, respectively; Fig. 2). Within the Australian *Sphenomorphus* group, most relationships (14 of 19 inferred clades) are weakly supported ($Pc < 0.95$) by the protein-coding data. The non-*Sphenomorphus* group lygosomines are weakly supported as a clade ($Pc = 0.60$; Fig. 2), with *T. gracilis* being weakly placed as the sister taxon of *Mabuya*. These data strongly support *Eugongylus* group monophyly ($Pc = 1.0$) and places this clade as the sister taxon of the strongly supported ($Pc = 1.0$) *L. smaragdina* + *L. fernandi* clade. However, the sister group relationship between the *Eugongylus* group and the *Lamprolepis* + *Lygosoma* clade is only weakly supported in this analysis.

Incongruence between data partitions. Only 11 of 35 lygosomine clades are shared between the phylogenies inferred from the initial separate uniformly weighted MP analyses of the structural RNA and protein-coding data partitions (MP trees not shown). When explicit

models of sequence evolution are incorporated in the ML analyses, the number of congruent clades between the separate gene phylogenies increases by ~36% to 15 shared clades (i.e., nine shared clades strongly supported in both separate phylogenies; four strongly supported only by the structural RNA gene data; one weakly supported in both separate phylogenies). Using a Bayesian approach to test for incongruence between data partitions reveals that the separate phylogenies are statistically worse explanations of the alternative data partitions, with the structural RNA phylogeny not being present in the 0.95 posterior probability interval of the protein-coding data (and visa versa). Although the use of explicit models of sequence evolution in the ML analyses of the separate data sets increased the topological congruence (compared to the MP trees), significant incongruence apparently still exists. Thus, the differences between the phylogenies cannot be attributed solely to random error.

Comparison of the posterior probabilities of individual clades aids in the identification of conflicting relationships that may be contributing to the significant incongruence between the data partitions. In the structural RNA phylogeny (Fig. 1) there are four strongly supported relationships that appear to be in strong conflict with the ND4 phylogeny (Fig. 2). One of these conflicting relationships involves internal relationships within the *Eugongylus* group. The structural RNA data strongly support *Eugongylus* as the basal most taxon ($Pc = 0.99$; Fig. 1) whereas the protein-coding data strongly place *Emoia* as the sister taxon of the remaining *Eugongylus* group taxa ($Pc = 0.97$; Fig. 2). This apparent conflict is caused by alternative rooting of the *Eugongylus* group, with the inferred unrooted relationships being identical. The remaining instances of strongly supported incongruence are found within the *Sphenomorphus* group. The structural RNA data strongly supports a *Scincella lateralis* + *Prasinohaema virens* clade ($Pc = 1.0$), but the ND4 data strongly places *S. lateralis* as the basal most species of the *Sphenomorphus* group. The other two areas of incongruence involve the placement of *Glaphyromorphus gracilipes* and *Notoscincus ornatus*. The structural data strongly supports a *G. gracilipes* + *Hemiergis peroni* clade ($Pc = 1.0$) and strongly places *Notoscincus* as the sister taxon to all other Australian *Sphenomorphus* group taxa ($Pc = 1.0$) whereas the protein-coding data strongly places *G. gracilipes* in an exclusive clade containing *N. ornatus* and *Anomalopus* ($Pc = 0.96$).

3.2. Combined phylogenetic analysis

In the combined data set, a total of 2185 unambiguously aligned nucleotide positions were available for phylogenetic analysis. Of these, 1121 were variable (1085 among lygosomines; 906 within the *Sphenomorphus* group) and 887 were parsimony informative (849 among lygosomines; 645 within the *Sphenomorphus* group). The ML tree search using the GTR + I + Γ model (parameters given in Table 2) yielded a single optimal tree ($-\ln L = 28954.528$; Fig. 3).

The combined data support lygosomine monophyly; however, this clade is weakly supported ($Pc = 0.88$). The Lygosominae is divided into two major clades which are strongly supported ($Pc = 1.0$): the *Sphenomorphus* group and a clade containing all the remaining lygosomine species. Within the *Sphenomorphus* group, the Australian *Sphenomorphus* group is also strongly supported ($Pc = 1.0$). Although the Australian subgroup is well supported, the specific relationships of the three non-Australian taxa (*P. virens*, *S. lateralis*, and *Sphenomorphus muelleri*) to the Australian subgroup are weak. Within the Australian *Sphenomorphus* group, the mtDNA data strongly supports the monophyly of *Anomalopus*, *Ctenotus*, and *Lerista* ($Pc = 1.0$; Fig. 3), whereas *Eulamprus* and *Glaphyromorphus* are both polyphyletic. Overall, 13 of the 20 inferred clades (65%) within the Australian *Sphenomorphus* group are strongly supported by the mtDNA data.

Within the Australian *Sphenomorphus* group, *N. ornatus* is strongly placed ($Pc = 1.0$; Fig. 3) as the sister taxon to the remaining members of this diverse clade. Exclusive of *N. ornatus*, the Australian *Sphenomorphus* group is divided into two major clades (A and B; Fig. 3). Strongly supported Clade A ($Pc = 0.99$) is comprised solely of taxa from mesic eastern Australia whereas the marginally well supported ($Pc = 0.94$) Clade B contains taxa from essentially all regions of Australia. In both major clades, the majority of inferred relationships are strongly supported by the mtDNA data.

Within the non-*Sphenomorphus* group lygosomine clade, there is strong support ($Pc = 1.0$) for the placement of *T. gracilis* within a strongly supported clade ($Pc = 1.0$) containing *Mabuya* and the *Egernia* group. However, the specific placement of *Tribolonotus* within this clade is not well supported. The monophyly of the *Eugongylus* group is strongly supported ($Pc = 1.0$), but the interrelationships among the four representative species are not well supported by the mtDNA data.

In the separate and combined ML analyses, the GTR + I + Γ substitution model best explains the evolution of the observed data. However, it is evident in Table 2 that the estimated model parameters for the combined data are intermediate between those estimated from the individual structural RNA and protein-coding gene regions. This is most noticeable for the substitution rates. Thus, the specified model used in the combined ML analysis is a compromise between the specified models of the individual data partitions. However, when the combined data are analyzed using the parameters based on the separate partitions, the resulting

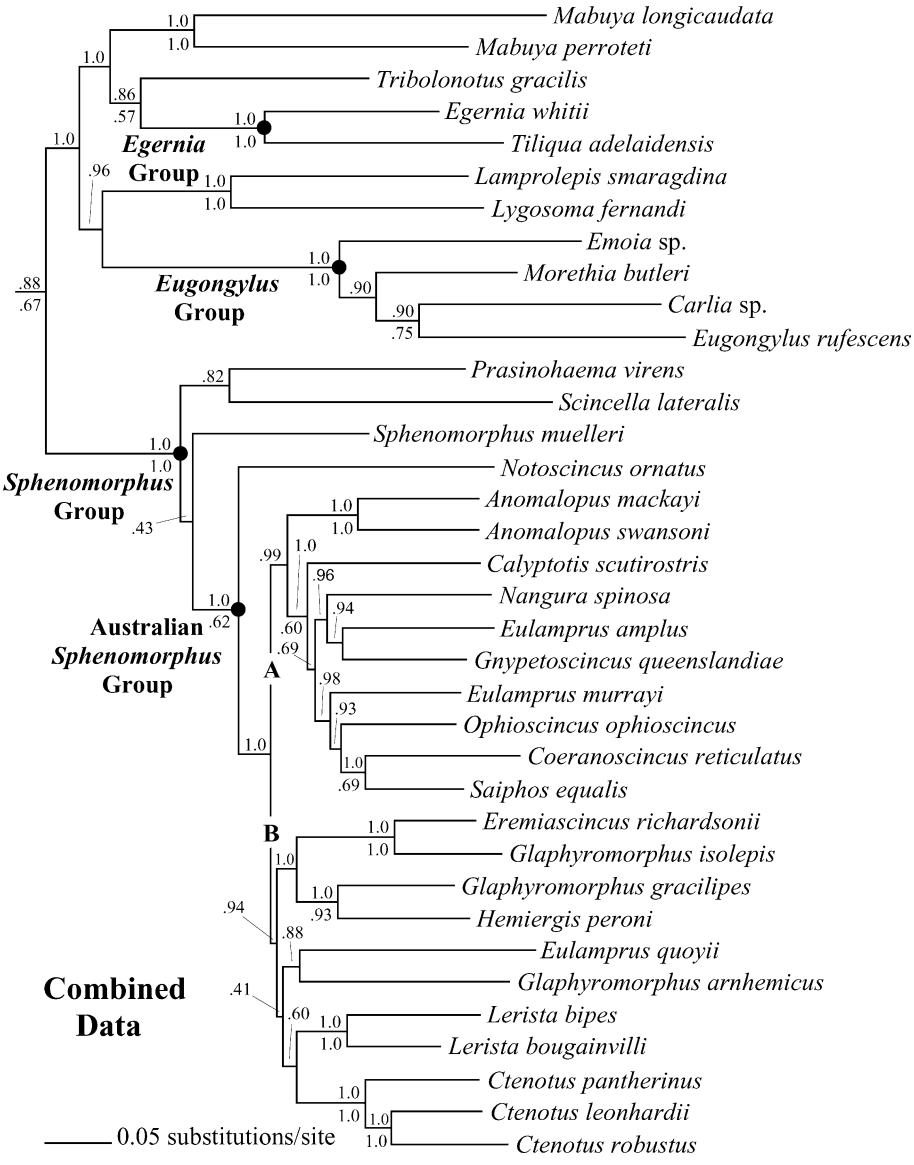

Fig. 3. Maximum likelihood phylogeny of lygosomines inferred from the combined analysis of mitochondrial DNA. Numbers above branches correspond to Bayesian posterior probabilities and numbers below branches correspond to bootstrap proportions from uniformly weighted parsimony analysis (proportions < 0.50 not shown).

phylogenies are essentially identical to that inferred in the original combined ML analysis. The only difference is that the phylogeny inferred from the combined data using the protein-coding DNA model parameters places *Eumeces* as the sister taxon to the major clade containing all non-*Sphenomorphus* group lygosomines (if *Acontias* is the root) as in the phylogeny from the protein-coding data alone. All other inferred relationships are identical to those in the original combined ML analysis (Fig. 3). The analysis of the combined data with the structural RNA model did not alter the inferred relationships in Fig. 3. Thus, the use of the compromise model has little impact on the phylogenetic relationships inferred from the combined ML analysis.

4. Discussion

4.1. Strongly supported incongruence between data partitions

Although the combined ML phylogeny (Fig. 3) is the preferred hypothesis of relationships and will be emphasized through the Discussion, the following specific inferred relationships must be viewed with caution (see Section 3: *Incongruence between data partitions*): (1) the rooting of the *Eugongylus* group; (2) the basal *Sphenomorphus* group relationships; (3) the phylogenetic placement of *Notoscincus*; and (4) close relationship between *G. gracilipes* and *Hemiergis*. Following the

recommendations of Wiens (1998), the above relationships inferred in the combined analysis are viewed as tentative until the cause of incongruence can be identified and/or new independent data are collected that can corroborate or refute the current results.

4.2. Evolution of the Australian Sphenomorphus group

This study provides the first explicit test of monophyly of the Australian *Sphenomorphus* group. Phylogenetic analysis of mtDNA strongly supports the Australian *Sphenomorphus* group as a clade, to the exclusion of the sampled non-Australian *Sphenomorphus* group taxa. Although only ~10% of the Australian *Sphenomorphus* group species are included, nearly all the generic (and probably phyletic) diversity is represented in this study. Nearly 75% of the Australian *Sphenomorphus* group species belong to two genera (*Ctenotus* and *Lerista*). Only a single Australian genus, the monotypic *Coggeria*, was not included. The limb-reduced *Coggeria naufragus* was only recently described (Couper et al., 1996) and has morphological attributes that suggests its phylogenetic affinities lie with members of the *Ophioscincus* + *Coeranoscincus* + *Saiphos* clade (Reeder, unpubl. morphological data). However, while the phyletic diversity of the Australian *Sphenomorphus* group is well represented, additional non-Australian taxa (especially members of the *fasciatus* species group of *Sphenomorphus*) need to be included in future studies in order to more rigorously test the monophyly of the Australian clade.

Within the Australian *Sphenomorphus* group, there is a basal dichotomy separating *Notoscincus* (2–3 species; Cogger, 2000; Greer, 1989) from the remaining members of the group. Little is know regarding *Notoscincus* biology (Greer, 1989) and previous hypotheses of the phylogenetic affinities of *Notoscincus* are lacking. However, the present evidence strongly indicates this small clade has been evolving independently from all remaining Australian *Sphenomorphus* group taxa for some time.

Based on morphological data, there are only a handful of explicit phylogenetic hypotheses for the interrelationships within the Australian *Sphenomorphus* group and these have generally focused on small subgroups. Some of these previous hypotheses are congruent with the relationships inferred from the mtDNA. Greer (1979b, 1989) postulated that *Eremiascincus* was derived from either an "*Glaphyromorphus*" *isolepis*-like or "*Glaphyromorphus*" *nigricaudis*-like ancestor. The mtDNA data strongly places *Eremiascincus* with "*G.*" *isolepis*. However, additional members of the "*G.*" *isolepis* species group need to be examined to ascertain the specific relationship between this species group and *Eremiascincus*. "*Glaphyromorphus*" *nigricaudis* was not included in the present study, but preliminary morphological (Reeder, unpubl. data) and molecular (Reeder and Richmond, unpubl. data) data suggest "*G.*" *nigricaudis* is only distantly related to the "*G.*" *isolepis* species group.

Choquentot and Greer (1989) suggested *Hemiergis* was most closely related to "*G.*" *gracilipes*. Both taxa are viviparous, have yellow to yellowish-orange ventral coloration (rare among skinks) and occur in southern Australia ("*G.*" *gracilipes* restricted to southwestern Australia; all other "*Glaphyromorphus*" occur in northern and northeastern Australia). The structural RNA and combined data corroborate Choquentot and Greer (1989) by strongly supporting the placement of "*G.*" *gracilipes* with *H. peroni* ($Pc = 1.0$). Although the separate protein-coding data do not support the "*G.*" *gracilipes* + *Hemiergis* clade (with marginally strong support [$Pc = 0.96$] for "*G.*" *gracilipes* being a member of a clade containing *Anomalopus* and *N. ornatus*), the congruence between the morphological and combined mtDNA data lends confidence in the reality of this clade.

During the evolution of scincid lizards, limb reduction has been a common phenomenon, particularly within the Australian *Sphenomorphus* group (Greer, 1991). In the absence of an explicit phylogenetic analysis, Greer and Cogger (1985) postulated that the many similarities shared among the species of *Anomalopus sensu lato* was the result of convergent evolution associated with limb reduction and/or a fossorial life history. Thus, they partitioned *Anomalopus sensu lato* into three genera (*Anomalopus sensu stricto*, *Coeranoscincus*, and *Ophioscincus*). Greer and Cogger (1985) also recognized two subgenera (*Anomalopus* and *Vermiseps*) within *Anomalopus sensu stricto*, each of which are represented in this study (*A. mackayi* and *A. swansoni*, respectively). The results of this phylogenetic study strongly corroborate Greer and Cogger (1985) by demonstrating that *Anomalopus* is only distantly related to *Coeranoscincus* and *Ophioscincus* (Fig. 3). And finally, although the mtDNA data strongly support the two species of *Anomalopus* as a clade, the remaining five *Anomalopus* species need to be evaluated in order to provide a more rigorous test of monophyly of this highly limb-reduced group.

Phylogenetic analysis of the mtDNA data strongly support *Ophioscincus* as the sister taxon of a well-supported *Coeranoscincus reticulatus* + *Saiphos equalis* clade. *Coeranoscincus reticulatus* and *Saiphos* have identical phalangeal formulas (shared only with *Coggeria*), lending further support to a close relationship between these three-toed skinks. Interestingly, previous studies have never proposed a close relationship between *C. reticulatus* and *Saiphos* (and possibly *Coggeria*). Greer (1983) postulated that *Calyptotis* and *Saiphos* were sister taxa and even speculated that *Saiphos* may be nested within *Calyptotis*. A phylogeny with *Saiphos* and

Calyptotis scutirostrum constrained to be sister taxa is rejected in an S–H test (Table 3), indicating the preferred mtDNA phylogeny (Fig. 3) statistically better explains the evolution of the observed mtDNA data. The close relationship between *Calyptotis* and *Saiphos* was hypothesized to be supported by several morphological characters (Greer, 1983). However, these morphological attributes were subjectively defined (e.g., shape of the palatal rami of the pterygoid) and/or are not unique to the proposed clade. Because of its rarity in the Australian *Sphenomorphus* group, a single loreal scale (present only in *Anomalopus brevicollis*, *A. gowi*, *Lerista praepedita*, and *O. cooloolensis*; Reeder, unpubl. data) is the only potentially convincing morphological apomorphy provided by Greer (1983) for a *Calyptotis* + *Saiphos* clade. Ultimately, DNA data from additional species (e.g., *Coeranoscincus frontalis*, *C. naufragus*) need to be obtained in order to better evaluate this conflict involving the placement of *Saiphos equalis*.

The monophyly of "*Glaphyromorphus*" and "*Eulamprus*" was not supported in this phylogenetic analysis. This comes as no surprise given both groups have traditionally been weakly defined. Greer (1989) acknowledged that "*Glaphyromorphus*" could not be diagnosed by any apomorphies and that this taxon was essentially a repository for species that could not be allocated to other more distinctive genera. As previously mentioned, the mtDNA strongly places "*G.*" *gracilipes* with *Hemiergis* and strongly supports "*G.*" *isolepis* as being closely related to *Eremiascincus*. The third "*Glaphyromorphus*" species included in this study ("*G.*" *arnhemicus*) is placed with "*E.*" *quoyii* with only weak statistical support ($Pc = 0.88$).

A single apomorphy (ovoviviparity) is hypothesized to support "*Eulamprus*" (Greer, 1989). However, given that live-birth has evolved multiple times within the *Sphenomorphus* group (Blackburn, 1982; Shine, 1985), Greer (1992) speculated that "*Eulamprus*" might eventually prove to be polyphyletic. The placements of the three included "*Eulamprus*" species ("*E.*" *amplus*, "*E.*" *murrayi*, and "*E.*" *quoyii*) are relatively well supported by the mtDNA. Also, monophyly of "*Eulamprus*" is also strongly rejected by the S–H test (Table 3). In order to have a taxonomy that reflects phylogenetic history, nomenclatural changes are necessary. However, both "*Glaphyromorphus*" and "*Eulamprus*" are speciose groups (with at least 13 and 15 species, respectively). More extensive sampling within both groups is currently underway and a better (and more thorough) understanding of the evolutionary relationships among the major lineages within these polyphyletic assemblages will be available in the future.

Within the Australian *Sphenomorphus* group occur two distinctive monotypic genera, *Gnypetoscincus queenslandiae* of montane rainforests in northeastern Queensland and *Nangura spinosa* of dry rainforest in southeastern Queensland. Both possess strongly keeled scales, which is an unusual feature for scincid lizards. Within the *Sphenomorphus* group, keeled scales are seen elsewhere only in *Tropidophorus* of Southeast Asia, a genus in which *G. queenslandiae* was originally placed (De Vis, 1890). The phylogenetic placement of these two species has been uncertain, but it has most recently been postulated that their affinities lie with "*Eulamprus*" (Covacevich et al., 1993; Greer, 1989). Analysis of the mtDNA suggests that *Gnypetoscincus* is closely related to "*E.*" *amplus* (also restricted to montane rainforests of eastern-northeastern Queensland), with *Nangura* being the sister taxon to this more exclusive clade.

The vast majority of the species diversity (~75%) of the Australian *Sphenomorphus* group can be found within *Ctenotus* and *Lerista* (>90 and >75 species, respectively; Cogger, 2000). Although taxon sampling for these genera is limited in the present study, the mtDNA data strongly support the monophyly of these two genera. The monophyly of *Ctenotus* is further supported by the possession of auricular lobules, a morphological attribute unique within the Australian *Sphenomorphus* group (Greer, 1989; Storr, 1964). The phylogenetic placement of *Ctenotus* with *Lerista* is of potential importance. Because they are sister taxa (albeit weakly supported) and nested well within the Australian *Sphenomorphus* group, this result implies that the vast majority of species diversity within the Australian *Sphenomorphus* group has arisen relatively recently.

Table 3
Results of the Shimodaira–Hasegawa tests used to evaluate alternative hypotheses

Hypotheses tested (see Sections 3 and 4)	Data	*P*
Lygosomine monophyly[a]	Protein-coding	0.3159 n.s.
Anomalopus sensu lato[b]	Combined data	0.0058*
Calyptotis + *Saiphos*	Combined data	0.0259*
Monophyletic "*Eulamprus*"[c]	Combined data	0.0070*
Monophyletic "*Glaphyromorphus*"[c]	Combined data	0.0000*
Tribolonotus + *Mabuya*	Combined data	0.2138 n.s.
Tribolonotus + *Lygosoma* group	Combined data	0.0229*
Tribolonotus + *Eugongylus* group	Combined data	0.0152*
Tribolonotus + *Sphenomorphus* group	Combined data	0.0045*
Tribolonotus + non-*Sphenomorphus* group lygosomines[d]	Combined data	0.0325*
Tribolonotus as basal lygosomine	Combined data	0.0082*
Eugongylus group + *Mabuya* group	Combined data	0.0000*

[a] Optimal ML tree for the protein-coding data did not support the monophyly of lygosomines.

[b] *Anomalopus sensu lato* = *Anomalopus sensu stricto*, *Coeranoscincus*, and *Ophioscincus*.

[c] Optimal ML tree for the combined data did not support the monophyly of "*Eulamprus*" and "*Glaphyromorphus*."

[d] *Tribolonotus* constrained to be the sister taxon of the clade containing all non-*Sphenomorphus* group lygosomine taxa.

However, the radiation of these two groups has taken divergent paths. Whereas *Ctenotus* is primarily heliothermic (except for *C. pantherinus*) and surface dwelling (Greer, 1989), *Lerista* is primarily a fossorial group with the majority of the species exhibiting some level of limb reduction (Greer, 1987, 1990).

4.3. Higher level lygosomine relationships and the placement of Tribolonotus

Although dealing primarily with the diverse Australian scincid fauna, Greer (1979a) provided the first formal subdivision of the Lygosominae. In this morphological study, Greer allocated all Australian skinks to one of three major lygosomine clades (*Egernia*, *Eugongylus*, and *Sphenomorphus* groups). Greer (1979a) also explicitly placed most other non-Australian lygosomines into one of these groups. The only lygosomine taxa that were not included were *Mabuya* and other taxa Greer (1967, 1970b, 1976, 1977) hypothesized to be derived from *Mabuya* (i.e., *Apterygodon*, *Dasia*, *Eumecia*, *Lamprolepis*, *Lygosoma*, and *Macroscincus*). Given that *Mabuya* (and presumed related taxa) was not allocated to any of these new groups and Greer (1979a, 1983) has assumed that *Mabuya* represented the most structurally primitive lygosomine genus implicitly implies that *Mabuya* is a basal lygosomine (i.e., the *Egernia*, *Eugongylus*, and *Sphenomorphus* groups form a clade to the exclusion of *Mabuya* and its relatives). More recently, Greer (1989) implicitly expanded the *Egernia* group and renamed this assemblage the *Mabuya* group, but provided no formal taxon content or character diagnosis for this new expanded taxon. However, Greer (1989) did acknowledge that the *Mabuya* group may not be monophyletic. Despite the lack of support for the monophyly of this group, some subsequent systematists (e.g., Honda et al., 1999a,b, 2000) have recognized the *Mabuya* group and assumed that this taxon encompassed *Mabuya* and its relatives, as well as the former *Egernia* group.

The combined mtDNA data (2185 bp) of this study strongly supports the monophyly of the *Sphenomorphus* group and places this clade as the sister taxon to a strongly supported clade containing all remaining lygosomines (Fig. 3). Such a relationship is consistent with Greer (1979a, 1989), who postulated that the *Eugongylus* and *Mabuya* groups were more closely related to each other than either was to the *Sphenomorphus* group. A recent mtDNA study by Honda et al. (2000)[1] also supported *Sphenomorphus* group monophyly and its placement as the sister clade to the remaining lygosomines. The present study and Honda et al. (2000) are also congruent in providing strong support for *Eugongylus* group monophyly and a paraphyletic *Mabuya* group.

Because of "*Mabuya* group" paraphyly, Honda et al. (2000) recommended dismantling this assemblage into the following smaller demonstrably monophyletic groups: (1) the *Mabuya* group (*sensu stricto*; containing "*Mabuya*,"[2] *Apterygodon*, and *Dasia*); (2) the *Lygosoma* group (containing *Lygosoma* and *Lamprolepis*); and (3) the *Egernia* group (*sensu* Greer, 1979a; containing *Egernia*, *Corucia*, and *Tiliqua*). The monophyly of the *Egernia* and *Lygosoma* groups is strongly corroborated in my analyses. However, even though the two "*Mabuya*" species formed a clade (Fig. 3), the monophyly of the *Mabuya* group *sensu stricto* could not be rigorously tested since *Apterygodon* and *Dasia* were not included in my study. Three additional "*Mabuya* group" *sensu lato* taxa have yet to be included in any explicitly phylogenetic study, but their phylogenetic affinities can be hypothesized based on published morphological data. Greer (1976, 1977) noted morphological similarities of the African *Eumecia* and *Macroscincus* with other African "*Mabuya*" species; thus, these genera may be members of the *Mabuya* group *sensu stricto*. Based on external morphology, the recently described *Vietnascincus* is similar to other arboreal skinks of southeast Asia (*Apterygodon*, *Dasia*, and *Lamprolepis*), but the description given by Darevsky and Orlov (1994) of the condition of the palatal rami of the pterygoids (i.e., medially separated) in *Vietnascincus* suggest a closer affinity with *Lamprolepis* of the *Lygosoma* group.

The combined (and structural RNA) mtDNA data strongly support the placement of *Tribolonotus* within the exclusive clade containing the *Egernia* and *Mabuya* groups (Fig. 3). However, within this exclusive clade, the specific phylogenetic affinity of *Tribolonotus* is less decisive. The structural RNA data marginally strongly supports ($Pc = 0.95$) *Tribolonotus* as the sister taxon of the *Egernia* group (Fig. 1), whereas the protein-coding data weakly places *Tribolonotus* with the *Mabuya* group (Fig. 2). The combined analysis favors the structural RNA hypothesis *Tribolonotus* + *Egernia* group), but the level of support decreases ($Pc = 0.86$; likely due to the conflict between the two separate data partitions) and an alternative placement of *Tribolonotus* as the sister taxon of *Mabuya* is not a statistically worse explanation of the data (Table 3). However, this specific relationship sup-

[1] The Honda et al. (2000) data set consisted of 1249 bp of 12S and 16S rDNA (all but ~300 bp encompassed in the present study) and had comparable taxon sampling, except for the following: (1) Honda et al. (2000) did not include *Tribolonotus* and lacked Australian *Sphenomorphus* group taxa and (2) the present study included only two *Mabuya* species (vs five) and did not include *Apterygodon* and *Dasia*.

[2] Honda et al. (2000) also provided the first explicit support for the paraphyly of "*Mabuya*" (with respect to the arboreal *Apterygodon* and *Dasia*).

ported by the combined data is consistent with Greer (1979a), who hypothesized that *Tribolonotus* was a member of the *Egernia* group. The possible phylogenetic placement of *Tribolonotus* by the mtDNA data with any other lygosomine taxa (outside the *Egernia* and *Mabuya* groups) is rejected by S–H tests (Table 3). Thus, the inclusion of *Tribolonotus* as a member of the *Egernia* group (as advocated by Greer, 1979a) is the relationship favored in this study. Although *Corucia* was not included in the present study, the placement of *Tribolonotus* within a more exclusive clade containing *Corucia*, *Egernia*, and *Tiliqua* is unlikely since *Tribolonotus* apparently lacks the apomorphies (i.e., $\leqslant 8$ premaxillary teeth and viviparity; Greer, 1979a, 1989) of this more exclusive clade (Reeder, unpubl. data).

In this study and that of Honda et al. (2000), the relative relationships between the *Egernia*, *Lygosoma*, and *Mabuya* groups are identical (i.e., *Lygosoma* group (*Egernia* group + *Mabuya* group)), but our studies differ in the exact placement of the *Eugongylus* group among these groups. Honda et al. (2000) places the *Eugongylus* group as the sister taxon of the *Mabuya* group. However, my data strongly support a sister group relationship between the *Eugongylus* and *Lygosoma* groups and strongly exclude the *Eugongylus* group from the more exclusive clade containing the *Egernia* and *Mabuya* groups ($Pc = 1.0$). An S–H test also rejects a *Eugongylus* group + *Mabuya* group clade (Table 3).

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Appendix A

Specimens for which DNA sequence data were obtained. Institutional abbreviations: AMS, Australian Museum, Sydney; CAS, California Academy of Sciences; KU, Natural History Museum, University of Kansas; NTM, Northern Territories Museum, Darwin; QM, Queensland Museum, Brisbane; SAMA, South Australia Museum, Adelaide; SDSU, San Diego State University; TNHC, Texas Natural History Collection, University of Texas at Austin; WAM, Western Australia Museum, Perth.

A.1. Acontinae

Acontias meleagris—photo voucher (D. Hillis, University of Texas at Austin); South Africa.

A.2. "Scincinae"

Eumeces egregius—USA: data from GenBank (Accession AB016606); *Eumeces septentrionalis*—KU 211138; USA: Kansas, Sumner, Sec 15, T35S, R3W.

A.3. Lygosominae

Anomalopus mackayi—NR 6054; Australia: Queensland, Yetman Rd. site. *Anomalopus swansoni*—SAMA R33731; Australia: New South Wales, Denman tip. *Calyptotis scutirostrum*—SAMA R33887; Australia: Queensland, Yarraman. *Carlia* sp.—CAS 192999; Papua New Guinea: Morobe Dist., Somane [Garasa] Valley, vic Bakaia No. 2. *Coeranoscincus reticulatus*—SAMA R37800; Australia: New South Wales, Border Ranges. *Ctenotus leonhardii*—WAM R97180; Australia: Western Australia, 23.3 km SE of Kalli Homestead. *Ctenotus pantherinus*—AMS R130599; Australia: Western Australia, Carnarvon. *Ctenotus robustus*—SAMA R36579; Australia: New South Wales, Esdale. *Egernia whitii*—SAMA R34781; Australia: South Australia, Kangaroo Island, Cape Hart. *Emoia physicae*—CAS 192949; Papua New Guinea: Morobe Dist., Wau Ecology Institute (2.5 mi NW of Wau). *Eremiascincus richardsonii*—SAMA R40946; Australia: South Australia, near Alberga. *Eugongylus rufescens*—AMS R122480; Papua New Guinea: Bobole. *Eulamprus amplus*—AMS field number 32592 (uncatalogued specimen); Australia: Queensland, Finch Hatton National Park. *Eulamprus murrayi*—SAMA R33699; Australia: New South Wales, Whiam Whiam State Forest. *Eulamprus quoyii*—QM J56099; Australia: Queensland, O'Riellys, Lamington National Park. *Glaphyromorphus arnhemicus*—NTM R19119; Australia: Northern Territories, Raragala Island. *Glaphyromorphus gracilipes*—SAMA R23027; Australia: Western Australia, 18 km W Denmark. *Glaphyromorphus isolepis*—SAMA R34105; Australia: Northern Territories, Jabiru. *Gnypetoscincus queenslandiae*—QM J51015; Australia: Queensland, Massey Creek. *Hemiergis peroni*—SAMA R45326; Australia: South Australia, sect 18, Hund of Smith, within Heritage Area. *Lamprolepis smaragdina*—TNHC 55655; no locality data. *Lerista bipes*—QM J48533; Australia: Queensland, 36 km WNW Jackson, Naccowlah. *Lerista bougainvillii*—SAMA R45205; Australia: South Australia, Wirha Dump. *Lygosoma fernandi*—SDSU 3945; no locality data. *Mabuya longicaudata*—SAMA R38916; Malaysia: no other locality data. *Mabuya perroteti*—TWR 426 (uncataloged TNHC specimen); no locality data. *Morethia butleri*—WAM R119739; Australia: Western Australia, Old

Madura. *Nangura spinosa*—QM J57246; Australia: Queensland, Nangur State Forest. *Notoscincus ornatus*—NTM R14923; Australia: Northern Territories, Tanamai Desert. *Ophioscincus ophioscincus*—QM J46126; Australia: Queensland, Mt. Glorious. *Prasinohaema virens*—AMS R129721; Papua New Guinea: Normanby Island, Guleguleu. *Saiphos equalis*—SAMA R33627; Australia: New South Wales, Spring Creek. *Scincella lateralis*—DCC 2842 (uncataloged TNHC specimen); USA: Texas: Sutton; 0.7–1.2 mi W of bridge over I-10, on FM 3130 (~5–6 mi W of Kimble Co. line). *Sphenomorphus muelleri*—AMS R122684; Papua New Guinea: Fau SHP. *Tiliqua adelaidensis*—SAMA R40687; Australia: South Australia, East of Burra. *Tribolonotus gracilis*—AMS R122122; Papua New Guinea: KarKar Island.

References

Allison, A., Greer, A.E., 1986. Egg shells with pustulate surface structures: basis for a new genus of New Guinea skinks (Lacertilia: Scincidae). J. Herpetol. 20, 116–119.

Anderson, S., Bankier, A.T., Barrell, B.G., de Bruijn, M.H.L., Coulson, A.R., Drouin, J., Eperon, I.C., Nierlich, D.P., Roe, B.A., Sanger, F., Schreier, P.H., Smith, A.J.H., Staden, R., Young, I.G., 1981. Sequence and organization of the human mitochondrial genome. Nature 290, 457–465.

Baverstock, P.R., Donnellan, S.C., 1990. Molecular evolution in Australian dragons and skinks: a progress report. Mem. Queensl. Mus. 29, 323–331.

Blackburn, D.G., 1982. Evolutionary origins of viviparity in the Reptilia. 1. Sauria. Amphib.–Reptilia 3, 185–205.

Buckley, T.R., Arensburger, P., Simon, C., Chambers, G.K., 2002. Combined data, Bayesian phylogenetics, and the origin of the New Zealand cicada genera. Syst. Biol. 51, 4–18.

Choquentot, D., Greer, A.E., 1989. Intrapopulational and interspecific variation in digital limb bones and presacral vertebrae of the genus *Hemiergis* (Lacertilia: Scincidae). J. Herpetol. 23, 274–281.

Cogger, H.G., 1972. A new scincid lizard of the genus *Tribolonotus* from Manus Island, New Guinea. Zool. Meded. Leiden 47, 202–210.

Cogger, H.G., 2000. Reptiles and Amphibians of Australia, sixth ed. Ralph Curtis Publishing, Sanibel Island, Florida.

Couper, P.J., Covacevich, J.A., Marsterson, S.P., Shea, G.M., 1996. *Coggeria naufragus* gen. et sp. nov., a sand-swimming skink from Fraser Island, Queensland. Mem. Queensl. Mus. 39, 233–241.

Covacevich, J.A., Couper, P.J., James, C., 1993. A new skink, *Nangura spinosa* gen. Et sp. nov., from a dry rainforest of southeastern Queensland. Mem. Queensl. Mus. 34, 159–167.

Darevsky, I.S., Orlov, N.L., 1994. *Vietnascincus rugosus*, a new genus and species of the *Dasia*-like arboreal skinks (Sauria, Scincidae) from Vietnam. Russ. J. Herpetol. 1, 37–41.

Darevsky, I.S., Orlov, N.L., 1997. A new genus and species of scincid lizards from Vietnam: the first Asiatic skink with double rows of basal subdigital pads. J. Herpetol. 31, 323–326.

De Vis, C.W., 1890. Descriptions of two lizards of genera new to Australian herpetology. Proc. Linn. Soc. N. S. W. 4, 1034–1036.

Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39, 783–791.

Forstner, M.R., Davis, S.K., Arévalo, E., 1995. Support for the hypothesis of Anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. Mol. Phylogenet. Evol. 4, 93–102.

Goldman, N., Anderson, J.P., Rodrigo, A.G., 2000. Likelihood-based tests of topologies in phylogenetics. Syst. Biol. 49, 652–670.

Greer, A.E., 1967. The generic relationships of the African scincid genus *Eumecia*. Breviora 276, 1–9.

Greer, A.E., 1970a. A subfamilial classification of scincid lizards. Bull. Mus. Comp. Zool. 139, 151–184.

Greer, A.E., 1970b. The relationships of the skinks referred to the genus *Dasia*. Breviora 348, 1–30.

Greer, A.E., 1974. The generic relationships of the scincid lizard genus *Leiolopisma* and its relatives. Aust. J. Zool. 31, 1–67.

Greer, A.E., 1976. On the evolution of the Cape Verdes scincid lizard *Macroscincus coctei*. J. Nat. Hist. 10, 691–712.

Greer, A.E., 1977. The systematics and evolutionary relationships of the scincid lizard genus *Lygosoma*. J. Nat. Hist. 11, 515–540.

Greer, A.E., 1979a. A phylogenetic subdivision of Australian skinks. Rec. Aust. Mus. 32, 339–371.

Greer, A.E., 1979b. *Eremiascincus*, a new generic name for some Australian sand swimming skinks (Lacertilia: Scincidae). Rec. Aust. Mus. 32, 321–338.

Greer, A.E., 1983. The Australian scincid lizard genus *Calyptotis* De Vis: resurrection of the name, description of four new species, and discussion of relationships. Rec. Aust. Mus. 35, 29–59.

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., 1989. The Biology and Evolution of Australian Lizards. Surrey Beatty and Sons, Chipping Norton.

Greer, A.E., 1990. Limb reduction in the scincid 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., 1992. Revision of the species previously associated with the Australian scincid lizard *Eulamprus tenuis*. Rec. Aust. Mus. 44, 7–19.

Greer, A.E., 1997. *Leptoseps*: a new genus of scincid lizards from southeast Asia. J. Herpetol. 31, 393–398.

Greer, A.E., Cogger, H.G., 1985. Systematics of the reduced-limbed and limbless skinks currently assigned to the genus *Anomalopus* (Lacertilia: Scincidae). Rec. Aust. Mus. 37, 11–54.

Greer, A.E., Parker, F., 1967. A new scincid lizard from the northern Solomon Islands. Breviora 275, 1–20.

Greer, A.E., Parker, F., 1968. A new species of *Tribolonotus* (Lacertilia: Scincidae) from Bougainville and Buka, Solomon Islands, with comments on the biology of the genus. Breviora 275, 1–23.

Greer, A.E., Parker, F., 1974. The *fasciatus* species group of *Sphenomorphus* (Lacertilia: Scincidae): notes on eight previously described species and description of three new species. Papua New Guin. Sci. Soc. Proc. 25, 31–61.

Greer, A.E., Simon, M., 1982. *Fojia bumui*, an unusual new genus and species of scincid lizard from New Guinea. J. Herpetol. 16, 131–139.

Gutell, R.R., Fox, G.E., 1988. A compilation of large subunit RNA sequences presented in a structural format. Nucleic Acids Res. 16, 175–247.

Hillis, D.M., Bull, J.J., 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Syst. Biol. 42, 182–192.

Hillis, D.M., Mable, B.K., Larson, A., Davis, S.K., Zimmer, E.A., 1996. Nucleic acids IV: sequencing and cloning. In: Hillis, D.M.,

Moritz, C., Mable, B.K. (Eds.), Molecular Systematics, second ed.. Sinauer, Sunderland, MA, pp. 321–381.

Honda, M., Ota, H., Kobayashi, M., Nabhitabhata, J., Yong, H., Hikida, T., 1999a. Evolution of Asian and African lygosomine skinks of the *Mabuya* group (Reptilia: Scincidae): a molecular perspective. Zool. Sci. 16, 979–984.

Honda, M., Ota, H., Kobayashi, M., Hikida, T., 1999b. Phylogenetic relationships of the Australian skinks of the *Mabuya* group (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. Genes Genet. Syst. 74, 135–139.

Honda, M., Ota, H., Kobayashi, M., Nabhitabhata, J., Yong, H., Hikida, T., 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., Bollback, J.P., 2001. Empirical and hierarchical Bayesian estimation of ancestral states. Syst. Biol. 50, 351–366.

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

Huelsenbeck, J.P., Ronquist, F., Nielsen, R., Bollback, J.P., 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294, 2310–2314.

Hutchinson, M.N., 1980. The systematic relationships of the genera *Egernia* and *Tiliqua* (Lacertilia: Scincidae). A review and immunological reassessment. In: Banks, C.B., Martin, A.A. (Eds.), Proceedings of the Melbourne Herpetological Symposium. Zoological Board of Victoria, Melbourne, pp. 176–193.

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

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

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

Parker, H.W., 1940. Undescribed anatomical structures and new species of reptiles and amphibians. Ann. Mag. Nat. Hist. 5, 257–274.

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

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.

Sanderson, M.J., Kim, J., 2000. Parametric phylogenetics? Syst. Biol. 49, 817–829.

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

Shine, R., 1985. The evolution of viviparity in reptiles: an ecological analysis. In: Gans, C. (Ed.), Biology of the Reptilia, vol. 15 B. Wiley, New York, pp. 606–694.

Storr, G.M., 1964. *Ctenotus*, a new generic name for a group of Australian skinks. Western Aust. Nat. 9, 84–85.

Swofford, D.L., 1999. PAUP*: Phylogenetic Analysis Using Parsimony (* and other methods), Vers. 4.0. Sinauer, Sunderland, MA.

Swofford, D.L., Olsen, G.J., Waddell, P.J., Hillis, D.M., 1996. Phylogenetic inference. In: Hillis, D.M., Moritz, C., Mable, B.K. (Eds.), Molecular Systematics, second ed.. Sinauer, Sunderland, MA, pp. 407–514.

Thompson, J.D., Higgins, D.G., Gibson, T.J., 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. Nucleic Acids Res. 22, 4673–4680.

Titus, T.A., Frost, D.R., 1996. Molecular homology assessment and phylogeny in the lizard family Opluridae (Squamata: Iguania). Mol. Phylogenet. Evol. 5, 49–62.

Van de Peer, Y., Van den Broeck, I., De Rijk, P., De Wachter, R., 1994. Database on the structure of small ribosomal subunit. Nucleic Acids Res. 22, 3488–3494.

Wiens, J.J., 1998. Combining data sets with different phylogenetic histories. Syst. Biol. 47, 568–581.

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

Wiens, J.J., Reeder, T.W., Montes de Oca, A.N., 1999. Molecular phylogenetics and evolution of sexual dichromatism among populations of the Yarrow's spiny lizard (*Sceloporus jarrovii*). Evolution 53, 1884–1897.

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

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

Zweifel, R.G., 1966. A new lizard of the genus *Tribolonotus* (Scincidae) from New Britain. Am. Mus. Novitates 2264, 1–12.