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Molecular systematics of social skinks: phylogeny and taxonomy of the *Egernia* group (Reptilia: Scincidae)

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The lizards of the *Egernia* group of Australia and Melanesia include some of the most distinctive members of the family Scincidae in morphology (including giant size, spinose scalation), ecology and behaviour. Social behaviour, including long-term recognition of individuals and kin, mate fidelity and home site fidelity, is amongst the most complex known in squamate reptiles and is the subject of an expanding number of studies. Lack of a sound phylogeny for the *Egernia* group has limited our ability to understand the evolution and patterns of variation in social behaviour within this group, and evidence for the monophyly of the largest genus, *Egernia* (64% of the species), has been lacking. We present data derived from nucleotide sequences that establish a phylogenetic framework for the *Egernia* group. We used two mitochondrial sequences, the protein-encoding *ND4* gene and a ribosomal gene, *12s rRNA*, and two nuclear sequences, the protein-encoding *c-mos*, and non-encoding intron 7 of *β-fibrinogen*. Our phylogenetic analyses show that *Corucia* of the Solomon Islands is the sister group of the rest of the *Egernia* group. The genus *Egernia* is paraphyletic, including four well-supported monophyletic units, one of which is the sister lineage of the *Tiliqua* lineage (*Tiliqua* plus *Cyclodomorphus*). We suggest a revised taxonomic scheme that recognizes the major monophyletic lineages in *Egernia* (*s.l.*) as distinct genera.

ADDITIONAL KEYWORDS: intron – lizards – mtDNA – nuclear gene – Scincidae.

INTRODUCTION

The advent of molecular systematics has had a revolutionary effect on the classification of organisms. Taking a molecular evolutionary perspective has resolved long-lasting problems and identified surprising new anomalies concerning relationships. A frequent outcome of molecular studies has been the resolution of evolutionary relationships within taxa where conservatism in their evolution, at least with respect to characters that had been classically employed for systematic study, hindered previous attempts. Such taxa have frequently been exposed as paraphyletic grades rather than clades, and are found in most animal groups. Among the squamates, examples of such paraphyletic taxa that have been resolved using a molecular approach include the formerly cosmopolitan skink genera *Eumeces* (Schmitz, Mausfeld & Embert, 2004), *Leiolopisma* (Hutchinson *et al.*, 1990) and *Mabuya* (Mausfeld *et al.*, 2002). The purpose of the present paper is to report on the dissection of another such suspected grade, the scincid lizard genus *Egernia* Gray, 1832.

The Australian region is rich in diversity for a number of squamate groups including the skinks where more than 400 species are recorded, around a quarter of the world's diversity for this group (Pough

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et al., 2004). A distinctive lineage of Australian region skinks is the *Egernia* group (Greer, 1979), which includes some 47 species in four genera, *Corucia* (one species), *Cyclodomorphus* (nine species), *Egernia* (30 species) and *Tiliqua* (seven species). The group ranges in body size from 70 to 350 mm and includes the world's largest living skinks. The ecology of the group is similarly varied including, besides an array of conventional smaller insectivores, an obligate folivore (*Corucia*; Kinghorn, 1928; Parker, 1983), a specialized mollusc eater (*Cyclodomorphus gerrardii*; Estes & Williams, 1984) and large omnivores (*Egernia, Tiliqua*; Barwick, 1965; Brown, 1991). The group includes diurnal, crepuscular and nocturnal foragers, and arboreal climbers, rock-dwellers, grass-swimmers (Wiens, Brandley & Reeder, 2006) and burrowers. A number of species of the genus *Egernia* show a tendency to form stable social aggregations or family groups (Gardner *et al.*, 2001; Chapple, 2003; O'Connor & Shine, 2003; Fuller *et al.*, 2005) while in contrast some species of *Tiliqua* lead relatively solitary lives (Koenig, Shine & Shea, 2002; Milne, Bull & Hutchinson, 2002). A number of species of *Egernia* and *Tiliqua* have monogamous mating systems (Bull, 1988; Gardner *et al.*, 2001). This variation in ecology and social and reproductive behaviour has led to substantial evolutionary ecological research on the group, especially *Egernia* (e.g. Klingenbock, Osterwalder & Shine, 2000; Stow *et al.*, 2001; Lanham & Bull, 2004; O'Connor & Shine, 2004; Chapple & Keogh, 2005). However, with the exception of the *E. whitii* species group (Chapple & Keogh, 2004; Chapple, Keogh & Hutchinson, 2004), the evolutionary relationships among members of the group at any level of evolutionary divergence are barely documented. There is an immediate need for a phylogeny of the group to interpret the evolution of this rich array of adaptive variation.

Much effort has been expended over the past two decades with the exclusive use of mitochondrial nucleotide sequence data for the reconstruction of evolutionary relationships at intermediate levels of divergence, e.g. within a family. Although robust phylogenies are often recovered with mitochondrial nucleotide sequence data, a paucity of suitable nuclear sequences has limited the ability of these studies to identify 'species tree' relationships (Saint *et al.*, 1998). Intrafamilial-level problems are often too recent for the relatively small nuclear coding region datasets available currently to provide sufficient informative sites. The information content of length-variable non-coding regions such as introns is often compromised by problems with sequence alignment especially between the outgroup and ingroup taxa. However, there have been few direct assessments of the utility of the three classes of markers (i.e. mitochondrial, nuclear coding and non-coding genes) in any single group of squamates to date (e.g. Whiting, Bauer & Sites, 2003). In the present study, we use nucleotide sequence data from mitochondrial protein-encoding, ribosomal and tRNA loci, and nuclear protein-encoding and non-coding regions (intron) to recover the phylogenetic relationships among members of the *Egernia* group. All of these loci have been used either independently (e.g. Giannasi, Malhotra & Thorpe, 2001) or in some combination (e.g. Donnellan, Hutchinson & Saint, 1999; Georges *et al.*, 1999) in other reptile groups, but we utilize them together for the first time to recover relationships among con-familial and congeneric taxa.

The *Egernia* group is well defined morphologically via distinctive attributes of palate morphology (Hutchinson, 1981), and earlier molecular genetic phylogenetic work by several authors (Honda *et al.*, 2000; Whiting *et al.*, 2003; Brandley, Schmitz & Reeder, 2005) supports the monophyly of the group. Possible sister lineages of the group have been suggested. Horton (1972) and Greer (1979, 1989) identified south-east Asian '*Mabuya*' (now *Eutropis*, Mausfeld *et al.*, 2002; but see also Whiting *et al.*, 2003) as morphologically similar, while molecular genetic studies suggest that the enigmatic 'crocodile skinks' of the genus *Tribolonotus* are also possible relatives (Hutchinson, 1981; Saint *et al.*, 1998; Reeder, 2003). Three of the genera in the *Egernia* group, *Corucia*, *Cyclodomorphus* and *Tiliqua*, are highly distinctive in morphology and are readily defined (e.g. Shea, 1990). However, the largest genus, *Egernia*, remains without a clear definition, other than comprising those species that lack the anatomical specializations of the other three genera. There is considerable heterogeneity within *Egernia*, and several morphotypic species groups have been long recognized (Storr, 1968, 1978; Horton, 1972) (Table 1).

Table 1. Currently recognized species groups of *Egernia* (Horton, 1972; Storr, 1978)

Species group	Species
cunninghami	*E. cunninghami*, *E. depressa*, *E. hosmeri*, *E. stokesii*
kingii	*E. kingii*
luctuosa	*E. coventryi*, *E. luctuosa*
major	*E. frerei*, *E. major*, *E. obiri*, *E. rugosa*
striolata	*E. douglasi*, *E. formosa*, *E. mcpheei*, *E. napoleonis*, *E. pilbarensis*, *E. richardi*, *E. saxatilis*, *E. striolata*,
whitii	*E. guthega*, *E. inornata*, *E. kintorei*, *E. margaretae*, *E. modesta*, *E. montana*, *E. multiscutata*, *E. pulchra*, *E. slateri*, *E. striata*, *E. whitii*

Our study aimed to use a multiple gene phylogenetic approach to: (1) determine whether *Egernia* as currently conceived is indeed a single monophyletic unit, or whether it is a paraphyletic assemblage; (2) test if the *Egernia* species groups are also monophyletic units; and (3) identify the sister group of the highly specialized *Tiliqua* lineage.

MATERIAL AND METHODS

Species selection and specimens used

A total of 26 species comprising at least one species from each *Egernia* species group and a minimum of two species of each of the polytypic species groups of *Egernia* (Appendix S1) and each of the other polytypic *Egernia* group genera *Cyclodomorphus* and *Tiliqua* and the monotypic *Corucia* were sequenced. One species of each of the genera *Eutropis* and *Tribolonotus* were included as a series of increasingly divergent outgroups. See Appendix S1 for details of specimens examined.

DNA extraction, PCR amplification and nucleotide sequencing

Total cellular DNA was extracted from either liver or scales with a salting-out procedure (Miller Dykes & Polesky, 1988). The mtDNA of one sample of each of nine species (see Appendix S1 for details) was purified by ultracentrifugation through a CeCl gradient following the method of Dowling *et al.* (1996). Aliquots of 50–100 ng DNA were added to a 50-μL reaction mixture containing 4 mM $MgCl_2$, 1 × reaction buffer, 0.8 mM dNTPs, 0.4 mM primers, 1 unit of Biotech *Tth* plus DNA polymerase and the remaining volume of dH_2O. The primers used for amplification and sequencing are listed in Appendix S2. Amplifications were carried out on a Corbett FTS-320 Thermal Sequencer and comprised a single cycle of 3 min at 94 °C, 45 s at 55 °C and 1 min at 72 °C, followed by 29 cycles of 45 s at 94 °C, 45 s at 55 °C and 1 min at 72 °C, ending with a single step of 6 min at 72 °C. PCR products were purified for sequencing using a Bresa-Clean DNA Purification Kit (Bresatec), following the manufacturer's protocol for DNA extraction from solutions. Both strands of each PCR product were directly cycle-sequenced on a Corbett FTS-1 Thermal Sequencer using the Applied Biosystems PRISM Ready Reaction DyeDeoxy Terminator Cycle sequencing kit, following the manufacturer's instructions. The sequencing programme consisted of 25 cycles of 30 s at 94 °C, 15 s at 50 °C and 4 min at 60 °C. Cycle-sequenced product was electrophoresed and viewed on an Applied Biosystems Model 373A Sequencing System.

We carried out steps to limit the possibility of amplifying NUMTs (nuclear mitochondrial DNA sequences) by using templates prepared by ultracentrifugation as outlined above. The enriched mtDNA template from nine species from the genera *Egernia*, *Tiliqua* and *Tribolonotus* was then used in a series of titration experiments designed to determine whether the PCR primers for mitochondrial genes preferentially amplified NUMTs from total cellular DNA templates following the protocols of Donnellan *et al.* (1999). Protein encoding sequences were also translated to check for the presence of premature stop codons.

Sequence alignment

Sequences of *ND4* and *c-mos* were aligned initially with ClustalX (Thompson *et al.*, 1997) and adjusted manually where necessary. The *β-fibrinogen intron 7* sequences were aligned manually. For the tRNAs and *12S rRNA* regions, alignments followed the method of Kjer (1995) in which conserved elements of secondary structure are used as a guide to the assignment of homology. Potential stem and loop structures were identified and aligned by comparison with the secondary structure models of tRNAs (Macey & Verma, 1997) and *12S rRNA* (Springer & Douzery, 1996). Remaining sites were aligned to maximize nucleotide identity. Alignments were made by eye, optimizing the match between our sequences and conserved structural elements identified in the appropriate secondary structure model. For instance, possible stems were invariably present in the squamate sequences, as Hickson *et al.* (1996) have shown for the domain III section of this molecule. For the *12S rRNA* and tRNAs, regions of uncertain homology were not included in the analyses.

Phylogenetic analyses

For the maximum parsimony (MP) analysis we treated gaps according to the recommendations of Simmons & Ochoterena (2000). All single gap positions and gaps of more than one site in length that shared a common 3′ or 5′ terminus were treated as binary characters. The multisite gap sequence positions were excluded from the analysis and the single site gap positions were included after gaps were recoded as missing.

Phylogenetic tree-building algorithms were based on the MP criterion of optimality implemented in PAUP* version 4b10, and Bayesian inference implemented in MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). For MP, characters were weighted equally and heuristic searches, with the ACCTRAN option, TBR branch

Table 2. A, molecular data partitions and model of nucleotide substitution applied. Pi = parsimony informative. B, evaluation of partition strategy by BIC. BIC calculated using MCMC mean lnL. n, number of patterns in data; K, number of estimated parameters. The lower the BIC score the better the fit, the best strategy has rank = 1. C, models of nucleotide substitution selected from Modeltest analysis of final partition selection

A.

Gene region	Aligned length	Included sites	Pi sites
ND4	706	706	311
tRNAs	174	155	52
12S rRNA	316	305	85
c-mos	374	374	14
β-fibrinogen intron 7	1534	788	86
gaps	–	–	8
Total	–	2336	556

B.

Partition strategy	Parts	K	n	BIC	BIC rank
All	1	16	1049	35 553.6	10
mtDNA, nuclear	2	33	1086	34 545.3	7
mtDNA, intron, *c-mos*	3	49	1105	34 559.7	8
mtDNA, intron, *c-mos* 1st+2nd, *c-mos* 3rd	4	65	1119	34 572.7	9
nuclear, rDNA, *ND4*	3	49	1099	34 437.6	6
nuclear, rDNA, *ND4* 1st+2nd, *ND4* 3rd	4	65	1103	33 933.8	5
nuclear, rDNA, *ND4* 1st, *ND4* 2nd, *ND4* 3rd	5	81	1118	33 863.4	3
nuclear, *ND4* 1st, *ND4* 2nd, *ND4* 3rd, *12S rRNA*, tRNA	6	97	1127	33 897.9	4
Nuclear, *ND4* 1st, *ND4* 2nd, *ND4* 3rd, stems, loops	6	97	1129	33 828.0	2
Final 6 partition/model combination	6	94	1129	33 823.5	1

C.

Partition	Model selected
ND4 1st codon position	GTR+Γ+I
ND4 2nd codon position	TVM+Γ+I
ND4 3rd codon position	TIM+Γ
RNA stems	SYM+Γ+I
RNA loops	TrN+Γ+I
c-mos/β-fibrinogen intron 7	TrN+Γ

swapping algorithm and MulTrees option in effect, were used with 100 randomized taxon input orders. MP trees were tested for their robustness using non-parametric bootstrapping with 2000 pseudoreplicates.

To simplify the task of choosing among a very large number of possible combinations of partitions and models, we used a two-stage strategy: first determine the optimal set of data partitions, and then the best model for each of those partitions.

We considered 11 partitions, giving a total of 77 possible partition strategies. Rather than examine all 77, we took a stepwise approach assuming that testing support for a particular partition would be largely independent of possible partitions in other parts of the data and selected a subset of nine (see Table 2B). These were run in MrBayes using the most general model (GTR+Γ+I) for each partition (Lemmon & Moriarty, 2004; Lee & Hugall, 2006). The Bayesian Information Criterion (BIC) was then calculated using the MCMC equilibrium average lnL (Posada & Buckley, 2004; Lee & Hugall, 2006). BIC is very similar to the Akaikie Information Criterion (AIC) but also takes account of the amount of information; in this case we use the number of patterns in the data (Lee & Hugall, 2006). The results (summarized in Table 2B) show that BIC supports splitting the data into mtDNA and nuclear, the mtDNA data into genes and further into codon positions, and RNA into stems and loops but not into tRNA and *12S rDNA*, and did not support splitting the nuclear data. Therefore, a

six-partition strategy (with branch lengths linked) comprising the three *ND4* codon positions, RNA stems, RNA loops and nuclear DNA was chosen as the best fit.

The model of nucleotide substitution for each partition was selected with hierarchical likelihood ratio tests and the AIC implemented in Modeltest (Posada & Crandall, 2001; Table 2C). The closest appropriate model available in MrBayes was thus GTR+Γ+I for *ND4* 1st and 2nd positions, RNA stems and loops, and GTR+Γ for *ND4* 3rd positions and nuclear DNA (see Lemmon & Moriarty, 2004). MCMC runs confirmed this combination of partition and model actually had the best BIC score of all partition strategies originally tested (Table 2B). However, the gamma shape parameter (Γ) for the nuclear DNA partition was unstable (with variance much greater than the mean), and therefore the final model used GTR+I for the nuclear partition (Lee & Hugall, 2006).

These Bayesian MCMC used 4×2 million step chains (with standard heating T = 0.2, default prior settings, branch lengths were linked), 1 : 100 sampling, and a 50% burn-in (leaving 10 000 sampled trees). These indicated acceptable chain swapping rates, and that MCMC lnL equilibrium and posterior probability (PP) convergence (for both nucleotides and amino acids) were attained by 1 million steps. Therefore, the full analysis employed two independent runs of 4×10 million step chains with 1 : 100 sampling, with the first 20 000 sampled trees discarded as burn-in (leaving 80 000 samples for analysis). The two runs returned PPs within 0.01 of each other across all nodes, with no PP differing in significance at the 0.95 level. All parameters had an effective sample size (ESS) > 1000, indicating accurate posterior topology and branch length estimation (Beiko *et al.*, 2006).

If a bipartition's PP was > 95%, it was considered to be significantly supported. The interpretation of Bayesian PPs for branches in a phylogenetic analysis is well defined; they represent the probability that the corresponding clade is present in the true tree, given the data examined, the likelihood model and the specified priors (Larget & Simon, 1999; Huelsenbeck & Rannala, 2004). In contrast, there is no clear or widely accepted interpretation of other commonly used measures of phylogenetic support, such as non-parametric bootstrap proportions or decay indices, and their use in the context of statistical testing is not straightforward (e.g. see Hillis & Bull, 1993; Wilcox *et al.*, 2002; Huelsenbeck & Rannala, 2004). However, Bayesian PPs may be over-estimates of support (Suzuki, Glazko & Nei, 2002; Douady *et al.*, 2003), and so we interpret nodal support through a combination of Bayesian PP, non-parametric bootstraps and decay indices.

Hypothesis testing

We use the approximately unbiased (AU) test and a range of likelihood-based tree selection tests to assess the ability of our data to distinguish between alternative phylogenetic hypotheses (Shimodaira, 2002). Because these tests require likelihoods for each nucleotide site, we used the ML criterion of optimality implemented in PAUP* to obtain site likelihoods. Because the current implementation of ML in PAUP* does not allow partitioning of data sets, we applied the GTR+Γ+I model to the entire dataset and jointly estimated all parameters of the model along with the tree topology using a single heuristic search. The model parameter estimates were then used as fixed values when finding the best ML tree under each topological constraint representing alternative phylogenetic hypotheses. Tree selection was carried out in CONSEL version 0.1 (Shimodaira & Hasegawa, 2001).

RESULTS

Comparisons of sequences of the mitochondrial genes that were sequenced from both total genomic DNA and titrated extractions revealed no differences in the nine individuals tested. In addition, none of the *ND4* protein coding sequences contained unexpected stop codons, indicating that it is unlikely that any NUMTs were amplified with the primers used. A total of 2336 bp comprised the final dataset after large overlapping indels in the *β-fibrinogen intron* and regions of uncertain homology in the *β-fibrinogen intron*, *12S rRNA* and tRNAs were excluded. A total of 556 parsimony-informative sites were present in the final dataset (Table 2A).

The six-partition strategy was substantially better than strategies with one to four partitions (Table 2B). However, as the AU tests (Table 3) were only implementable in PAUP*, which only supports a single partition model, we note any topological variation in trees derived from these partition strategies. Strategies with five and more partitions all gave very similar results, i.e. the same topology with similar PP for each node (Fig. 1B). Models with one to four partitions differed in having non-significant support (i.e. PP < 0.95) for the grouping of *E. napoleonis* and *E. richardi*, but significant support (i.e. PP > 0.95) for the *E. depressa–E. kingii–E. hosmeri–E. stokesii–E. napoleonis–E. richardi* clade and higher ($0.90 <$ PP < 0.94) but not significant support for the placement of *E. formosa* as the sister lineage to the *E. cunninghami–E. saxatilis–E. striolata* clade.

The strict consensus of the six equally most parsimonious trees found (Fig. 1A) and the tree resulting from the Bayesian analysis (Fig. 1B) agree in recog-

Table 3. Approximately unbiased tests (AU) of alternative tree topologies

Tree	lnL	obs	np	au	bp	kh	sh	wkh	wsh
Globally best tree	–16 168.7867	–8.0	0.920	0.786	0.777	0.870	0.993	0.870	0.998
AH 1	–16 182.5544	13.8	0.101	0.109	0.050	0.117	0.318	0.117	0.301
AH 2	–16 182.559	8.0	0.140	0.114	0.113	0.130	0.510	0.130	0.283
AH 3	–16 235.5117	66.7	>> 0.001	>> 0.001	0	>> 0.001	0.001	>> 0.001	>> 0.001
AH 4	–16 176.7819	13.8	0.114	0.101	0.110	0.113	0.318	0.113	0.207

Alternativee hypotheses: AH 1, reciprocal monophyly of *Egernia s.l.* and *Cyclodomorphus/Tiliqua*; AH 2, monophyly of *Egernia s.l.*; AH 3, monophyly of *Cyclodomorphus* and *Tiliqua*; AH 4, monophyly of the *Egernia cunninghami* species group. Np, bootstrap probability of the selection; au, *P*-value of the approximately unbiased test; bp, as np, but calculated directly from the replicates; kh, sh, wkh, wsh, *P*-values of the KH, SH and weighted KH and SH tests, respectively [see Shimodaira & Hasegawa (2001) for an explanation of these tests].

nizing the same major clades within the ingroup. In both there is strong support for *Corucia* as the sister lineage to the remaining members of the *Egernia* group. Both also find that members of the genus *Egernia* do not form a single monophyletic sister group to the *Tiliqua* lineage. Instead, the species of the *Egernia* group form a series of clades, in which the species content is consistent across analyses, but the branching order is sensitive to the analysis used. These clades are outlined below:

1. *luctuosa* clade (*coventryi* and *luctuosa*). This pairing branches early, either as the sister lineage of other Australian members of the group (parsimony) or as the sister lineage of the *whitii* group.
2. *major* clade (*frerei* and *major*). These two species form a pair with uncertain relationships to the other lineages. In the parsimony analysis the major group is the sister lineage of the *whitii* clade, while the Bayesian analysis places it as the sister of the *Tiliqua* lineage plus the *striolata* and *cunninghami* species groups.
3. *whitii* clade (*inornata*, *kintorei*, *margaretae*, *striata* and *whitii*). Both analyses agree on the content and substructure of this clade. It consistently splits into two sublineages, one including the desert-adapted species of Storr's *inornata* species group (*inornata*, *kintorei* and *striata*), the other the more temperate-adapted species of the *whitii* group (*whitii*, *margaretae*).
4. remaining *Egernia* clades. The remaining species of *Egernia* that were sampled cluster into two lineages although the composition and branching order are not fully concordant in the MP and Bayesian analyses. Unlike the other clades, in which morphotypic species groups were consonant with phylogenetic lineages, the two clades are both composite, comprising members of the *cunninghami*, *striolata* and *kingii* species groups. The first lineage ('Eastern *Egernia*') comprises the type species of *Egernia*, *E. cunninghami*, and the two eastern members of the *striolata* species group that we sampled, *saxatilis* and *striolata*. The second lineage ('Western *Egernia*') comprises the rest of the *cunninghami* species group (*depressa*, *hosmeri* and *stokesii*), western species of the *striolata* species group (*napoleonis* and *richardi*) and *E. kingii*. One species, *E. formosa*, possibly represents a third lineage as its affinities are uncertain. It is placed as the sister of the Eastern *Egernia* clade in the Bayesian analysis but is a member of the Western *Egernia* clade in the MP analysis. In the MP analysis the Eastern *Egernia* clade is the sister of the *Tiliqua* clade, and the Western *Egernia* clade is the sister of the Eastern *Egernia* plus *Tiliqua*. In the Bayesian analysis, the Eastern and Western *Egernia* clades are sisters, the two together being the sister clade of the *Tiliqua* lineage plus the *major* clade. In both analyses, a monophyletic *cunninghami* group is not supported, with *cunninghami* consistently not falling with the other three spiny-scaled species. Relationships among the western *cunninghami*-group species are not fully concordant in the two analyses, although neither finds the three western spiny-scaled species to be monophyletic; *E. depressa* is consistently separate from *hosmeri* + *stokesii*.
5. *Tiliqua* (*s.l.*). The final clade comprises the species treated recently as two sister genera, *Cyclodomorphus* and *Tiliqua*. The MP analysis supports this dichotomy, but the Bayesian analysis shows a paraphyletic *Tiliqua*, with *Cyclodomorphus* nested within.

Hypothesis testing (Table 3) to force a monophyletic *cunninghami* species group found that this arrangement was not supported by our data ($P < 2 \times 10^{-6}$). Other forced topologies were the taxonomic status quo, i.e. reciprocal monophyly of *Egernia s.l.* and the *Tiliqua* lineage, monophyly of *Egernia s.l.* only, and

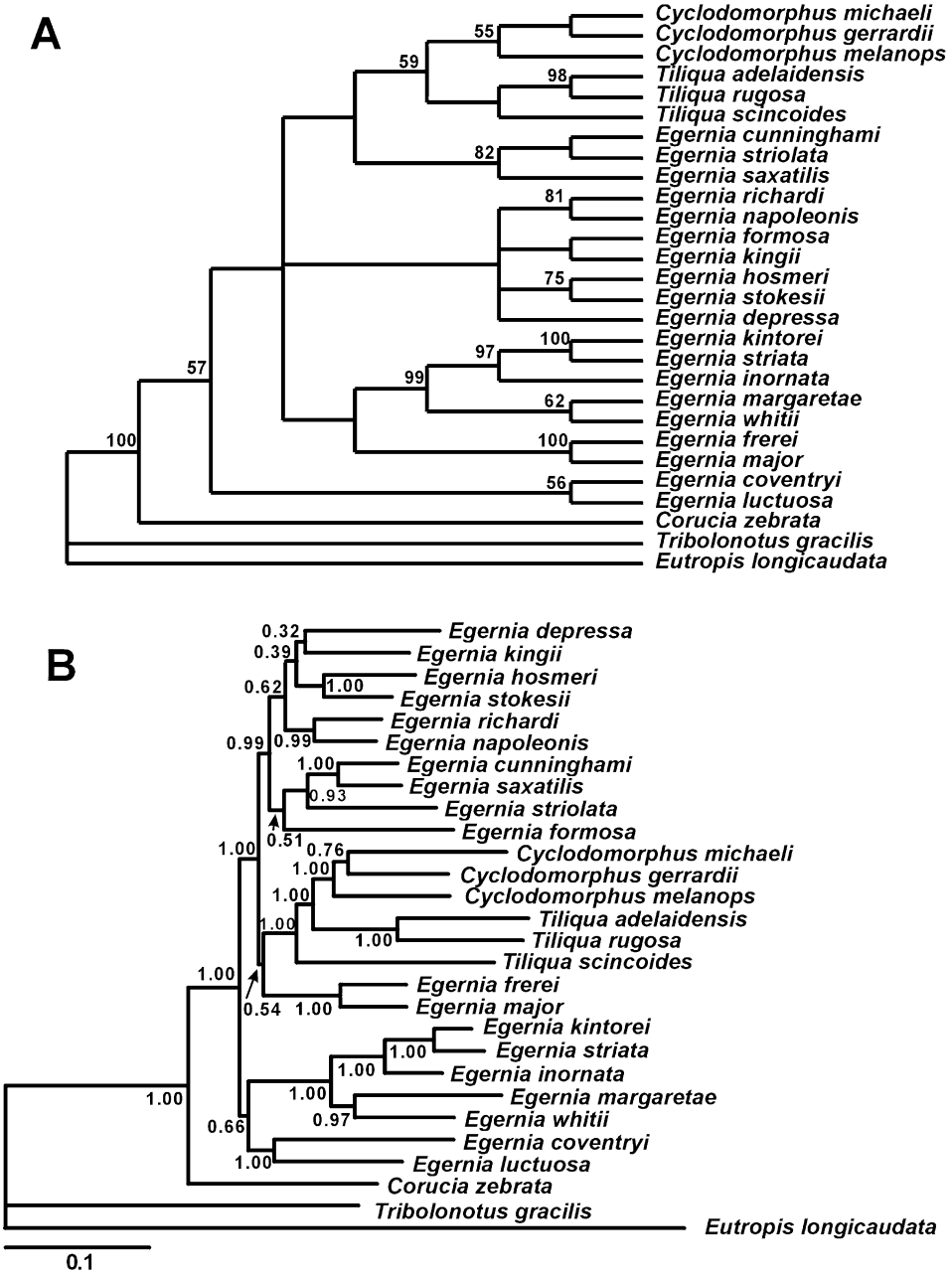

Figure 1. A, the strict consensus of the six equally most parsimonious trees (each of length 3021 steps), with bootstrap proportions > 50% shown. B, Bayesian tree. Posterior probability values are shown at relevant nodes.

reciprocal monophyly of *Tiliqua* and *Cyclodomorphus*. While these three were worse than the Bayesian majority rule consensus tree, the difference was not statistically significant. Currently it is not possible to use the six-partition model in the AU likelihood ratio test but instead we report the proportion of MCMC sampled trees in the six-partition Bayesian analysis that are consistent with each hypothesis (= PP of that hypothesis). In all cases, no sampled trees were compatible with any of the hypotheses.

DISCUSSION

Our data give strong support to the long-held suspicion that the species long grouped as the genus *Egernia* are best viewed as a grade and not a mono-

phyletic lineage. Following a split with the lineage that is now represented by the Solomon Islands endemic, *Corucia*, evolutionary diversification within Australia has produced several lineages of morphologically cohesive species. By far the most morphologically distinctive lineage is the *Tiliqua* lineage (Shea, 1990), and its numerous synapomorphic morphological specializations have led to the remaining *Egernia*-group species being placed by default in a single genus, defined only by the contrast with the *Tiliqua* lineage. Beyond the taxonomic implications, our findings suggest a number of interesting revisions of the way in which evolution within this important group of skinks has proceeded.

Although early workers (e.g. Horton, 1972) saw *Egernia* (*s.l.*) as a very recent (Plio-Pleistocene) offshoot from the Asian *Mabuya* (*s.l.*), it is now clear that the *Mabuya* group is only distantly related to *Egernia* (Honda *et al.*, 2000; Whiting *et al.*, 2003; Brandley *et al.*, 2005). Fossils attributable to *Egernia* (*s.l.*) date to the Late Oligocene to early–middle Miocene (Hutchinson, 1992; Shea & Hutchinson, 1992; Martin *et al.*, 2004). mtDNA divergences are reasonably high: the average pairwise difference in ND4 between *Corucia zebrata* and Australian taxa is 0.18, equating to a GTR+Γ+I divergence estimate of 0.46. Considering the commonly cited range of rates of 1–2% Mya^{-1} (see Chapple & Keogh, 2005) this indicates that the extant diversification probably predates the Pliocene. Together these suggest a relatively long (mid-Tertiary, if not older) history of the *Egernia* (*s.l.*) group within Australia.

The reason for the assumed relationship between *Mabuya* Group and *Egernia* Group skinks is that plesiomorphic members of each lineage are remarkably similar in general body form, although these similarities are largely symplesiomorphies. Plesiomorphic features retained in the *Egernia* group, including pterygoid teeth in *Corucia* (Greer, 1976), separated palatines in most *Egernia s.l.* (Mitchell, 1950; Hutchinson, 1981) and post-embryonic finalization of the fusion of the frontal bones (Littlejohn & Rawlinson, 1971), all tend to mark this lineage as stemming from skinks that are transitional between base grade 'scincine' and crown group 'lygosomine' skinks. The closed palate of the *Tiliqua* lineage appears to be derived within the *Egernia* group, possibly an adaptive change to strengthen the palate associated with evolution of jaws and dentition specialized for crushing hard-shelled prey (Edmund, 1969; Estes & Williams, 1984).

One outcome of our study is the recognition that the morphotype represented by the *Egernia striolata* species group (Horton, 1972; Storr, 1978) seems likely to represent the plesiomorphic morphology that gave rise to two of the most distinctive skink morphologies, the spiny skinks of the *Egernia cunninghami* species group, and possibly also the robust blue-tongues (*Tiliqua s.s.*). Moreover, there is strong support for the idea that the spiny morphology evolved twice, independently in *E. cunninghami* of the Great Dividing Range in eastern Australia (sister species include *striolata* and *saxatilis*), and in the shorter-tailed trio of *E. depressa*, *E. hosmeri* and *E. stokesii*, in inland Australia (sister species include *napoleonis* and *richardi*). This parallelism points to independent evolution in eastern and western Australia during the Tertiary, suggesting that there were barriers to free interchange. The relatively giant species, *E. kingii*, is placed as another specialized offshoot of the western members of this grade.

Patterns of evolutionary diversification within the *E. whitii* species group have been discussed by Chapple and co-workers (Chapple & Keogh, 2004; Chapple *et al.*, 2004) and this more detailed analysis is mirrored in our trees. These show a basal separation between the primarily saxicoline and temperate species of the *E. whitii* subgroup, represented here by *E. whitii* and *E. margaretae*, and the strictly burrowing and arid-adapted members of the *E. inornata* subgroup, represented by *E. inornata*, *E. kintorei* and *E. striata*.

The evolution of sociality within the *Egernia* group can be reviewed in the light of the cladistic structure revealed by this study. Reports of sociality in *Corucia* (Hauschild & Gassner, 1999) indicate its presence is plesiomorphic for the *Egernia* group, so that those species apparently leading solitary lives appear to have given up sociality, possibly an unusual situation in the animal kingdom and one that might yield interesting tests for theories that aim to explain how sociality evolves. One notable consequence of uncovering the cladistic patterns within *Egernia* in its old, all-inclusive sense, is that it becomes clear that most of the larger studies that have been directed at sociality have focused unevenly on the groups we have informally referred to the Eastern *Egernia* and Western *Egernia*, in particular on the species *E. stokesii* (Bull *et al.*, 2000, 2001; Gardner *et al.*, 2001; Duffield & Bull, 2002; Gardner, Bull & Cooper, 2002), *E. cunninghami* (Barwick, 1965; Stow & Sunnucks, 2004a, 2004b) and *E. saxatilis* (O'Connor & Shine, 2003, 2004), the latter two species being the closest relative of each other among the taxa we sampled. Studies of sociality in the *whitii* group are mostly at an initial stage, with only *E. whitii* having been subjected to intensive study (Hickman, 1960; Chapple & Keogh, 2005). Work on the *major* group is beginning (Osterwalder, Klingenbock & Shine, 2004; Fuller *et al.*, 2005), while the *luctuosa* group is yet to be subjected to detailed studies of social systems (Clemann, Chapple & Wainer, 2004).

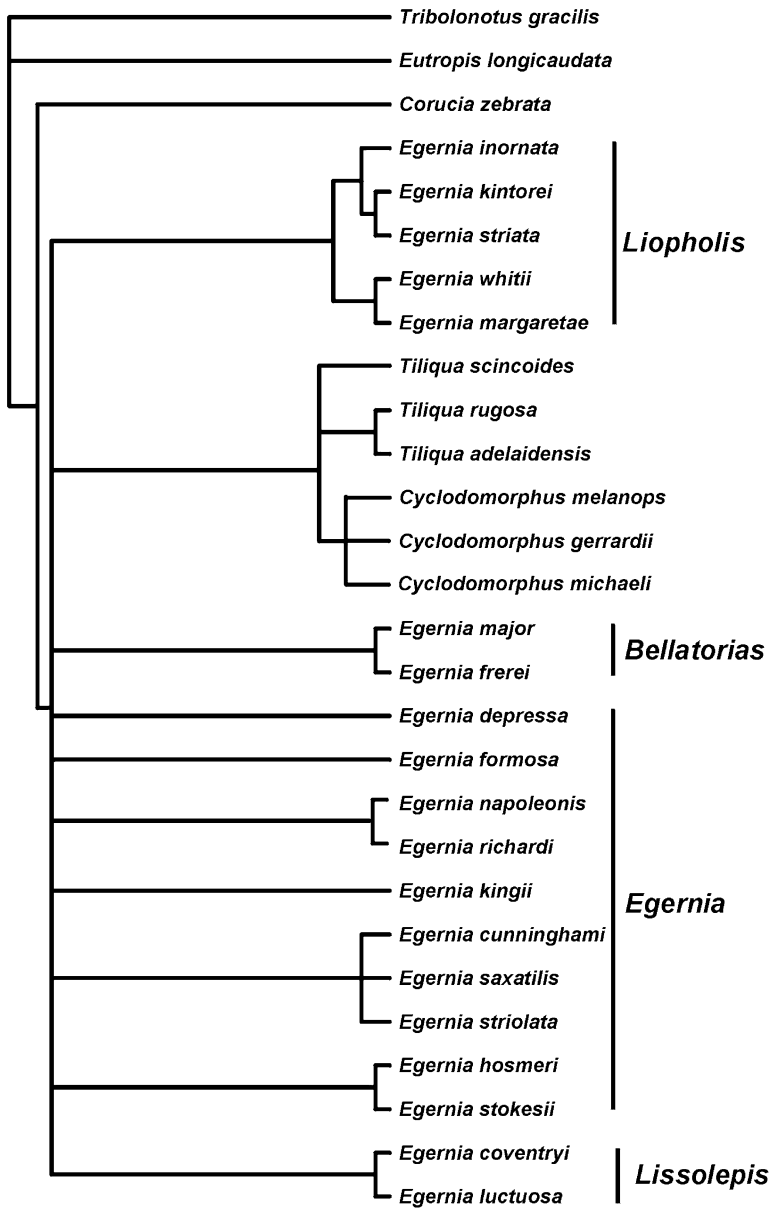

Figure 2. Strict consensus tree of the MP and Bayesian trees, showing suggested generic break up of *Egernia*.

Further work is now in progress aimed at clarifying relationships within this group of lizards. This will be aimed at clarifying relationships within our restricted genus *Egernia*, further exploring relationships within the *Tiliqua* lineage and attempting an estimation of the divergence dates for the major evolutionary events within the lineage.

TAXONOMY

Our data strongly support the paraphyly of traditional *Egernia*, from which we conclude that this traditional concept of the genus should not continue. The resolved major lineages within *Egernia* can be used to establish a revised generic arrangement for the *Egernia* group (Fig. 2).

The *luctuosa*, *major* and *whitii* groups all consistently form clades distinct from one another and from the remainder of the species in the traditional genus *Egernia* (members of the *cunninghami*, *kingii* and *striolata* groups). These three major clades, that we name separately from *Egernia*, are likely to be monophyletic, historical units, so that continuing work on the relationships and evolution within these lizards will be better based if these three clades are treated as independent entities from each other and from the

three species groups that remain in *Egernia s.s.* Names are available for these lineages, *Lissolepis*, *Bellatorias*, and *Liopholis*, which are revalidated below.

Our proposal of four genera to replace the previous one makes use of the morphological features that have been used to define some of the species groups in traditional *Egernia*. The species groups were arrived at intuitively (Horton, 1972; Storr, 1978), by a subjective visual assessment of obvious external features, shape and size, with the aim of making a large and varied group more taxonomically manageable. The set of features subsequently used to define the species groups (Storr, 1978) was not derived as a result of phylogenetic analysis. These features have never been seriously considered as phylogenetically useful because the characters in question are relatively few, some are at least partly continuous and therefore difficult to codify, and most show polymorphism and homoplasy not only within and between species of the *Egernia* Group but also among other skink lineages, making determination of evolutionary polarity difficult.

Nevertheless, these essentially subjective and difficult to characterize features summarize an overall within-group similarity that our molecular data now reveal as representing real historical units and not just conveniences for the construction of identification keys. The existence of distinctive morphologies for the clades corroborates the taxonomic partitioning of *Egernia*, but without the molecular framework, there would not have been enough evidence for this based on the morphology alone.

We accept that this new generic arrangement is still incomplete in some respects. The more narrowly defined *Egernia* is paraphyletic with the *Tiliqua* lineage in the MP analyses, and may not comprise a single lineage. Thus, conservatively the members of the *cunninghami*, *kingii* and *striolata* groups remain in *Egernia s.s.* until resolution of their relationships is attained. Our study suggests that relationships within the *Tiliqua* lineage should be evaluated further, as our data give only inconsistent support for reciprocal monophyly of *Cyclodomorphus* and *Tiliqua*.

Synonymies are abbreviated to primary synonyms. Citations and spelling lapses and emendations for older names are given in Cogger, Cameron & Cogger (1983).

Egernia *Group*

A clade of scincid lizards characterized by the following suite of character states: frontal bones fused in adults, although fusion often incomplete anteriorly in juveniles; palatal rami of the palatines separated medially (contacting in *Cyclodomorphus* and *Tiliqua*); vomers paired, elongate, projecting posteriorly between the palatines and partially dividing the choanal passages; Meckelian groove obliterated by dentary overgrowth; lateral dentition highly variable in number and morphology; pterygoid teeth present in *Corucia* but otherwise absent; presacral vertebrae 26 in most included lineages but elevated in the *Tiliqua* clade (31 or more); frontoparietals paired; interparietal relatively large, separating the parietals; supranasals absent, but partial postnasals defined by a postnarial groove in some species; prefrontals present; four or fewer supraoculars, the first two in contact with the frontal; lower eyelid scaly, moveable; iris of eye typically paler than pupil, which is round in most species; ear opening obvious, usually fringed anteriorly by one or more enlarged lobular scales; multiple rows of supradigital scales; preanal scales scarcely larger than adjacent ventrals; tail cylindrical, tapering to a point in most species, but highly modified in some; caudal autotomy planes divide the transverse process, lost in a few species; karyotype $2n = 32$ (King, 1973; Donnellan, 1991). All species viviparous, litter size interspecifically variable.

Cogger *et al.* (1983) provide all reference citations for generic synonymies apart from names published subsequently by Wells & Wellington (1984, 1985).

Egernia *Gray, 1838*

Type species *Tiliqua cunninghami* Gray, 1832. Type locality 'eastern Australia in latitude 29 S'.

Tropidolopisma Duméril & Bibron, 1839. Type species *Tropidolopisma dumerilii* Duméril & Bibron, 1839 (= *Egernia kingii* [Gray, 1838]).

Silubosaurus Gray, 1845. Type species *Silubosaurus stokesii* Gray, 1845.

Contundo Wells & Wellington, 1984. Type species *Tiliqua napoleonis* Gray, 1838.

Sivascincus Wells & Wellington, 1985. Type species *Egernia pilbarensis* Storr, 1978.

Storrisaurus Wells & Wellington, 1985. Type species *Storrisaurus husbandi* Wells & Wellington, 1985 (= *Egernia rugosa* De Vis, 1888).

Definition: The clade comprising *Egernia cunninghami* Gray, 1838, and all species that share a more recent common ancestor with *Egernia cunninghami* than with *Tiliqua scincoides*, *Liopholis whitii*, *Lissolepis luctuosa* or *Bellatorias major*.

Description: A genus of *Egernia* Group skinks, medium sized to large lizards [adult snout–vent length (SVL) 100–240 mm]; body squarish in the two larger species (*kingii* and *rugosa*) but head and body more or less dorsoventrally compressed in most; midbody scales in 24–46 rows, dorsals varying between species, from smooth, to striate to multi-keeled to spinose; nasal scale with postnarial groove running to the first

supralabial; subocular scale row incomplete; eyes relatively small, the eyelids similarly coloured to the adjacent scales.

Included species: *cunninghami* Gray, 1832, *depressa* (Günther, 1875), *douglasi* Glauert, 1956, *formosa* Fry, 1914, *hosmeri* Kinghorn, 1955, *kingii* (Gray, 1838), *mcpheei* Wells & Wellington, 1984, *napoleonis* (Gray, 1838), *pilbarensis* Storr, 1978, *richardi* (Peters, 1869), *rugosa* De Vis, 1888, *saxatilis* Cogger, 1960, *stokesii* (Gray, 1845), *striolata* (Peters, 1870).

Egernia rugosa has tended to be placed with the *major* group by earlier workers, due seemingly to its large size. Its multicarinate scalation and small eye appear to place it with the restricted genus *Egernia*, but establishing the precise affinities of this poorly known species will require molecular data.

Liopholis *Fitzinger, 1843*

Type species *Lygosoma moniligera* Duméril & Bibron, 1839 (= *Scincus whitii* Lacépède, 1804). Type locality Australia and Kangaroo Island, South Australia.

Flamoscincus Wells & Wellington, 1984. Type species *Egernia kintorei* Stirling & Zietz, 1893.

Definition: The clade comprising *Liopholis whitii* (Lacépède, 1804), and all organisms or species that share a more recent common ancestor with *Liopholis whitii* than with *Tiliqua scincoides*, *Egernia cunninghami, Lissolepis luctuosa* or *Bellatorias major*.

Description: A genus of *Egernia* Group skinks, relatively small to medium-sized lizards (adult SVL 75–200 mm); head and body squarish in cross-section; midbody scales in 34–52 rows, the dorsals smooth (keeled in *L. pulchra*); nasal scale without postnarial groove; subocular scale row incomplete; eyes relatively large, the eyelids usually with distinct cream margins, easily differentiated from adjacent scales.

Included species: *inornata* (Rosén, 1905), *guthega* (Donnellan, Hutchinson, Dempsey & Osborne, 2002), *kintorei* (Stirling & Zietz, 1893), *margaretae* (Storr, 1968), *modesta* (Storr, 1968), *montana* (Donnellan, Hutchinson, Dempsey & Osborne, 2002), *multiscutata* (Mitchell & Behrndt, 1949), *pulchra* (Werner, 1910), *slateri* (Storr, 1968), *striata* (Sternfeld, 1919), *whitii* (Lacépède, 1804).

Lissolepis *Peters, 1872*

Type species *Cyclodus* (*Omolepida*) *luctuosus* Peters, 1866. Type locality King George's Sound, Western Australia.

Definition: The clade comprising *Lissolepis luctuosa* (Peters, 1866), and all organisms or species that share a more recent common ancestor with *Lissolepis luctuosa* than with *Tiliqua scincoides*, *Egernia cunninghami*, *Liopholis whitii* or *Bellatorias major*.

Description: A genus of *Egernia* Group skinks; medium-sized lizards (adult SVL 100–130 mm); head and body squarish in cross-section; dorsal scales smooth, in 20–28 rows; nasal scale with a long (*coventryi*) to short (*luctuosa*) postnarial groove; complete subocular scale row; eyes relatively small, the eyelids similarly coloured to the adjacent scales.

Included species: *coventryi* Storr, 1978, *luctuosus* (Peters, 1866).

Bellatorias *Wells & Wellington, 1984*

Type species *Tropidolepisma major* Gray, 1845. Type locality 'Australia', restricted to Sydney and Rockhampton by Günther (1875).

Hortonia Wells & Wellington, 1984. Type species *Hortonia obiri* Wells & Wellington, 1985).

Definition: The clade consisting of *Bellatorias major* (Gray, 1845), and all organisms or species that share a more recent common ancestor with *Bellatorias major* than with *Tiliqua scincoides*, *Egernia cunninghami*, *Liopholis whitii* or *Lissolepis luctuosa*.

Description: A genus of *Egernia* Group skinks, large to very large lizards (adult SVL 160–310 mm); head and body squarish in cross-section; midbody scales in 26–36 rows, dorsals smooth to weakly keeled; nasal scale with postnarial groove running to the first supralabial; subocular scale row incomplete; eyes relatively large, the eyelids usually with distinct cream margins, easily differentiated from adjacent scales.

Included species: *frerei* (Günther, 1897), *major* (Gray, 1845), *obiri* Wells & Wellington, 1985.

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SUPPORTING INFORMATION

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

Appendix S1. Specimens examined.
Appendix S2. Primers used for PCR amplification and nucleotide sequencing.

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