

A molecular phylogeny of the Australian skink genera *Eulamprus*, *Gnypetoscincus* and *Nangura*

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Abstract

Skinks from the genera *Eulamprus*, *Gnypetoscincus* and *Nangura* are a prominent component of the reptile fauna of the mesic forests of the east coast of Australia and have been the subject of numerous ecological studies. Highly conserved morphology and the retention of ancestral traits have limited our understanding of the relationships within and among these genera beyond an initial identification of species groups within *Eulamprus*. To address this deficit and to explore the relationships between *Eulamprus* and the monotypic genera *Nangura* and *Gnypetoscincus*, sections of two mitochondrial genes (ND4 and 16S rRNA) were sequenced and subjected to Bayesian phylogenetic analysis. This phylogenetic analysis supports recognition of the three species groups proposed for *Eulamprus* (*murrayi*, *quoyii* and *tenuis*) and indicates that this genus is paraphyletic, with *Gnypetoscincus* and *Nangura* being proximal to basal lineages of the *tenuis* group. To resolve these and broader problems of paraphyly, we suggest that each of the species groups from '*Eulamprus*' should be recognised as a distinct genus. The phylogenetically and ecologically distinct water skinks of the *quoyii* group would be retained within *Eulamprus* and the diverse species of the *tenuis* group allocated to *Concinnia*. We suggest placing the monophyletic *murrayi* group, endemic to the rainforests of central eastern Australia, in a new genus (yet to be formally described). The sequencing data also revealed the existence of a genetically divergent but morphologically cryptic lineage within *E. murrayi* and substantial diversity within *E. quoyii*. There is evidence for two major habitat shifts from rainforest towards drier habitats, one leading to the *quoyii* group and the second defining a clade of three species within the *tenuis* complex. These ecological transitions may represent adaptations to general drying across eastern Australia during the late Miocene–Pliocene. Each of the major areas of east coast tropical or subtropical rainforest contains multiple phylogenetically diverse endemic species, reflecting the long-term persistence and high conservation value of wet forest habitats in each area.

Introduction

The Australian genus *Eulamprus* is part of the *Sphenomorphus* lineage of lygosomine skinks and its members are characterised by relatively large body size, fully developed limbs and viviparous reproduction (Greer 1989, 1992). Members of the genus occur in mesic habitats along the east coast of Australia and several species, especially those in rainforests, have very restricted distributions (Fig. 1, Table 1). Greer (1989) split the genus into three species groupings based on morphological characters, the *tenuis*, *quoyii* and *murrayi* groups, although the first of these, like the genus as a whole, was not defined by any derived trait and was not proposed to be monophyletic. With subsequent taxonomic revisions (Greer 1992; Hutchinson and Rawlinson 1995; Sadler 1998) seven species are recognised within the *tenuis* complex, three within the *murrayi* complex and five within the *quoyii* group (Table 1). Each group has a broad geographic range across eastern Australia, yet each also includes one or more species with very narrow geographic ranges (Fig. 1).

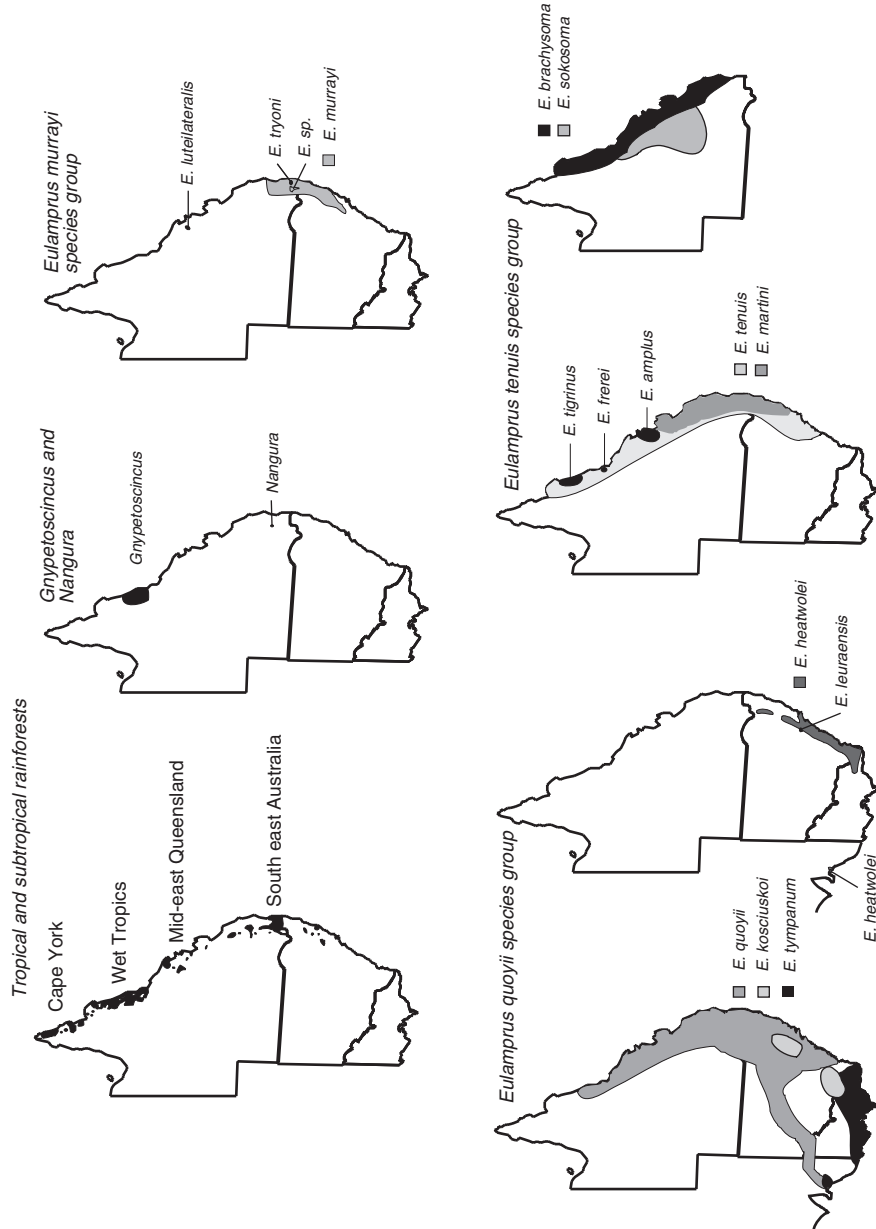


Fig. 1. Map of mainland eastern Australia showing distributions of tropical and subtropical rainforest (adapted from Adam 1992), *Gnypetoscincus*, *Nangura* and each of the *Eulamprus* species groups (from Cogger 2000).

Table 1. Species groupings proposed by Greer (1989) and habitat characteristics of these species as well as *Nangura spinosa* and *Gnyptoscincus queenslandiae* (as per Cogger 2000)

| Species | Habitat |
|--------------------------|---|
| <i>E. tenuis</i> group | |
| <i>E. amplus</i> | Among rocks or at the base of trees beside streams in rainforest |
| <i>E. brachysoma</i> | Rocky areas in rainforest, sclerophyll forests and sub-tropical woodlands |
| <i>E. frerei</i> | Granite tors and boulders in high montane rainforest |
| <i>E. martini</i> | Clearings in rainforests and vine thickets, moister sclerophyll forests and woodlands |
| <i>E. sokosoma</i> | Dry rainforest, vine thickets, moist sclerophyll forests and sub-tropical woodlands |
| <i>E. tenuis</i> | Rock slopes primarily in rainforest and wet and dry sclerophyll forests |
| <i>E. tigrinus</i> | Rainforest |
| <i>E. murrayi</i> group | |
| <i>E. luteilateralis</i> | Litter and logs in montane rainforest |
| <i>E. murrayi</i> | Rainforest and wet sclerophyll forests |
| <i>E. tryoni</i> | Rainforest and wet sclerophyll forests |
| <i>E. sp.</i> | Rainforest and wet sclerophyll forests (pers. obs.) |
| <i>E. quoyii</i> group | |
| <i>E. heatwolei</i> | Open upland forests and grasslands. Swamps, lagoons and creeks |
| <i>E. kosciuskoi</i> | Beside creeks in montane forests and woodlands and in alpine bogs and marshes |
| <i>E. leuraensis</i> | Riparian and swampy areas in montane forests and heaths |
| <i>E. quoyii</i> | Most wet habitats in a wide variety of vegetation types |
| <i>E. tympanum</i> | Rocks and logs along small creeks |
| <i>N. spinosa</i> | Creek banks in seasonally dry rainforest |
| <i>G. queenslandiae</i> | Logs in rainforest |

Due to the paucity of informative morphological variation there has not been any further refinement of phylogenetic relationships among these species.

Not only are the relationships within the genus currently unresolved, but there also remains uncertainty about the relationships of the monotypic genera *Nangura* and *Gnyptoscincus* to each other and to *Eulamprus*. *Gnyptoscincus queenslandiae* may be closely related to *Eulamprus* on the basis of its well developed limbs, viviparity, east coast distribution and chin scalation (Greer 1989). *G. queenslandiae* also has inguinal fat bodies, a character which, within the broader *Sphenomorphus* lineage of skinks, is known only in the *tenuis* group and three species of *Glaphyromorphus*. From morphological analysis, *Nangura spinosa* appears to be a primitive member of the *Sphenomorphus* group but differs significantly in two characters (Covacevich *et al.* 1993). Its karyotype is $2n = 28$ whilst all genera tested within the present *Sphenomorphus* grouping have $2n = 30$. The parietal scales of *N. spinosa* are totally separated by the interparietal, a character state otherwise found only in *Eulamprus quoyii*. However, *N. spinosa* lacks a postorbital bone, a character state present in *Eulamprus*. The species' keeled scales are unusual and resemble those of *G. queenslandiae*. Whilst the current evidence supports *N. spinosa* being placed in the *Sphenomorphus* lineage, it is still uncertain what its relationships are with other members of the group and, given several unique traits, it is possible that the genus represents a relatively ancient divergence.

In order to gain a better understanding of relationships within *Eulamprus* and to explore the phylogenetic affinities of *Nangura* and *Gnyptoscincus*, we have generated mtDNA

sequence data and from these estimated a phylogeny. This is intended to generate a broad framework for interpreting historical biogeography and speciation within the genus and the habitats they occupy (e.g. Moritz *et al.* 2000; Stuart-Fox *et al.* 2001), as well as a template for interpreting differences in ecology and life history (e.g. Daniels *et al.* 1987; Daniels and Heatwole 1990; Schwarzkopf and Shine 1991; Schwarzkopf 1993, 1996, 1998; Shine and Harlow 1993; Doughty and Shine 1997, 1998; Sumner *et al.* 1999, 2001).

Materials and Methods

Where available, two samples of each of the 12 currently recognised *Eulamprus* species were sequenced, covering as broad a geographic range as possible (see Appendix for details). In addition, *Nangura spinosa*, *Gnypetoscincus queenslandiae* and two outgroup species, *Egernia frerei* and *Ctenotus rawlinsoni*, were sequenced. *E. frerei* represented the phylogenetically distinct *Egernia* group and *C. rawlinsoni* a divergent lineage within the *Sphenomorphus* group (Greer 1989). DNA was extracted following a standard chelex/proteinaseK extraction, amplified following standard PCR protocols and sequenced using ABI protocols.

A 540-bp region of the 16S rRNA mitochondrial gene was amplified using the primers 16SaR (5'-CGCCTGTTTATCAAAAACAT-3') and 16SbR (5'-TGCACTAGACTCAAGTCTGGCC-3') (Palumbi 1996). Due to amplification difficulties, the *Eulamprus amplus* 16S rRNA sequence was supplied by T. Reeder. A 954-bp region of the mitochondrial ND4 gene was amplified using the primers ND4 (5'-TGA CTACCAAAGCTCATGTAGAAGC-3'; Bovine 11173–11196, modified from Arevalo *et al.* 1994) and tLEU2 (5'-TTTACTTGGATTGCACCA-3'; Bovine 12086–12105, modified from the Arevalo *et al.* 1994 LEU primer). Of this region, the first 400 bp from the ND4 end was sequenced in all taxa and used to estimate the phylogeny.

Sequences were aligned in ClustalX (Higgins *et al.* 1992). Alignments were manually checked, with reference to reading frames for ND4. The final ND4 alignment was translated to check for stop codons and frameshift mutations.

The aligned sequences were analysed phylogenetically using a combination of methods (likelihood, parsimony) with emphasis on the MCMC-Bayesian approach (Huelsenbeck *et al.* 2001; reviewed in Holder and Lewis 2003) implemented in the program Mr Bayes (Huelsenbeck and Ronquist 2001). For this analysis, the model of sequence evolution (GTR + Γ) was selected using Mr ModelTEST Ver. 3.06 (Posada and Crandall 1998). We conducted two independent analyses to check for consistency of results, each with multiple ($n = 4$) chains, a random starting tree and 2000000 generations, with trees sampled every 100 generations to estimate likelihood and sequence evolution parameters. Inspection of the output files indicated that likelihood and other parameters reached asymptotes well before 100000 generations (1000 trees); accordingly, we base our inference on a consensus of the 19000 trees sampled after this burn-in period. As a complement to the Bayesian analysis, we also conducted parsimony searches with weighting of transversions over transitions (10:1) or exclusion of 3rd codon positions within the ND4 sequence, all with 1000 bootstrap pseudoreplicates. Phylogenetic hypotheses were compared using likelihood ratio tests, specifically the Shimodaira and Hasagawa (SH) test which is appropriate for testing the maximum-likelihood tree against alternatives (Goldman *et al.* 2000). These analyses were performed using PAUP 4.0b8 (Swofford 2001). All sequences have been deposited in GenBank (accession numbers AF530191–AF530264).

Results

Sequence evolution and variation

Of the 400 ND4 sites aligned, 213 were variable and 176 were phylogenetically informative. No stop codons were observed when the sequence was protein translated. For 16S rRNA, 499 sites were aligned with 149 variable sites, of which 106 were parsimony informative. Comparing the base compositions of the taxa revealed them as being adenosine rich with adenosine constituting 33% of the nucleotides. Percentages of cytosine (26%) and thymine (24%) were approximately equal, with guanine (17%) being the least represented. Rates of substitution estimated from the Bayesian analysis indicate an 8–10-fold excess of transitions over transversions. These parameters are typical for mtDNA (Moritz *et al.*

1987). Most nucleotide changes occur at the third codon position (15%, 6.5% and 31.5% of sites variable for 1st, 2nd and 3rd positions respectively) and the Bayesian estimate of the overall shape parameter for the gamma distribution was $\alpha = 0.23$. Levels of DNA sequence divergence (model: GTR + Γ ; $\alpha = 0.23$) between species ranged from 3.3% (ND4 7.1%; 16S 1.0%; between *E. sokosoma* and *E. brachysoma*) to >20% in most pairwise comparisons (Table 2). Between the *quoyii* and *tenuis* species groupings, as defined by Greer (1989) (see Table 1), the average level of divergence was 26.6% (ND4 55.4%; 16S 17.5%). This compares with 13.6% (ND4 40.0%; 16S 6.2%) within the *tenuis* group, 12.2% (ND4 44.9%; 16S 5.8%) within the *murrayi* group and 13.0% (ND4 28.4%; 16S 9.2%) within the *quoyii* group. *G. queenslandiae* and *N. spinosa* differed from *Eulamprus* species by a minimum of 13.3% (ND4 36.8%; 16S 6.7%; *E. murrayi*) and 13.0% (ND4 40.3%; 16S 5.6%; *E. tenuis*), respectively. Two species were found to include individuals with highly divergent mtDNAs. Samples from Cambridge Plateau in north-eastern New South Wales identified as *E. murrayi* in the field were 10.5% (ND4 23.0%; 16S 4.3%) divergent from *E. murrayi* and 15% (ND4 55.5%; 16S 4.2%) from *E. tryoni*. This contrasts markedly with otherwise low sequence divergence across the range of *E. murrayi* (average of 1.3% for ND4 and cytochrome *b* combined, unpublished data). Here we refer to this population as *Eulamprus* spp. pending formal description. The second example concerns the northern-most sample of *E. quoyii* that was >20% divergent from other samples of this species, again suggesting the possibility of cryptic lineages within this widespread taxon.

Phylogenetic analyses

The majority-rule consensus across the 19000 trees sampled from the Bayesian analysis (subsequent to the burn-in period) revealed several strongly supported clades (Fig. 2). Two major species groupings suggested by Greer (1989), the *quoyii* and *murrayi* clades, are clearly defined in the present molecular analysis (100% and 99%, respectively). The *quoyii* clade forms a sister group to the remaining species in the analysis, the closer relationship between the *murrayi* and *tenuis* groups being firmly inferred from the data (97%). Within the *quoyii* clade the analysis indicates close affinity between *E. kosciuskoi* and *E. leuraensis*, and of *E. quoyii* to these; otherwise, the relationships among species within this group remain obscure. Within the *murrayi* clade, the new taxon from Richmond Range (*Eulamprus* sp.) and *E. murrayi* are identified as sister taxa and there is some indication (83%) that *E. tryoni*, the third species endemic to this region, is more closely related to these than is *E. luteilateralis*. Each of the relationships described above, except for (*quoyii* (*kosciuskoi*, *leuraensis*)), were also present in the parsimony analyses, though often with lower support levels, as indicated by bootstrapping.

The remaining species – all members of Greer's *tenuis* group along with the monotypic genera *Gnypetoscincus* and *Nangura* – form a single clade, though with slightly less (91%) support. Within this third clade, there is strong support (98%) for grouping of *tigrinus*, *brachysoma*, *sokosoma* and *martini*, and 100% support for a subclade of the last three species. There is reasonable confidence (91–92%) for inclusion of two other members of the *tenuis* complex (*E. tenuis*, *E. amplus*) in this lineage, though because of uncertainty about the position of *E. frerei*, it appears paraphyletic with *Nangura* and possibly *Gnypetoscincus* as well. Overall, there is a tendency for relationships among the more basal elements of this clade (*Gnypetoscincus*, *Nangura*, *E. frerei*, and *E. amplus*) to be less clearly resolved. The same trends are evident in parsimony analyses – the majority-rule consensus supports the topology (*tenuis* (*tigrinus* (*martini* (*sokosoma*, *brachysoma*))), but

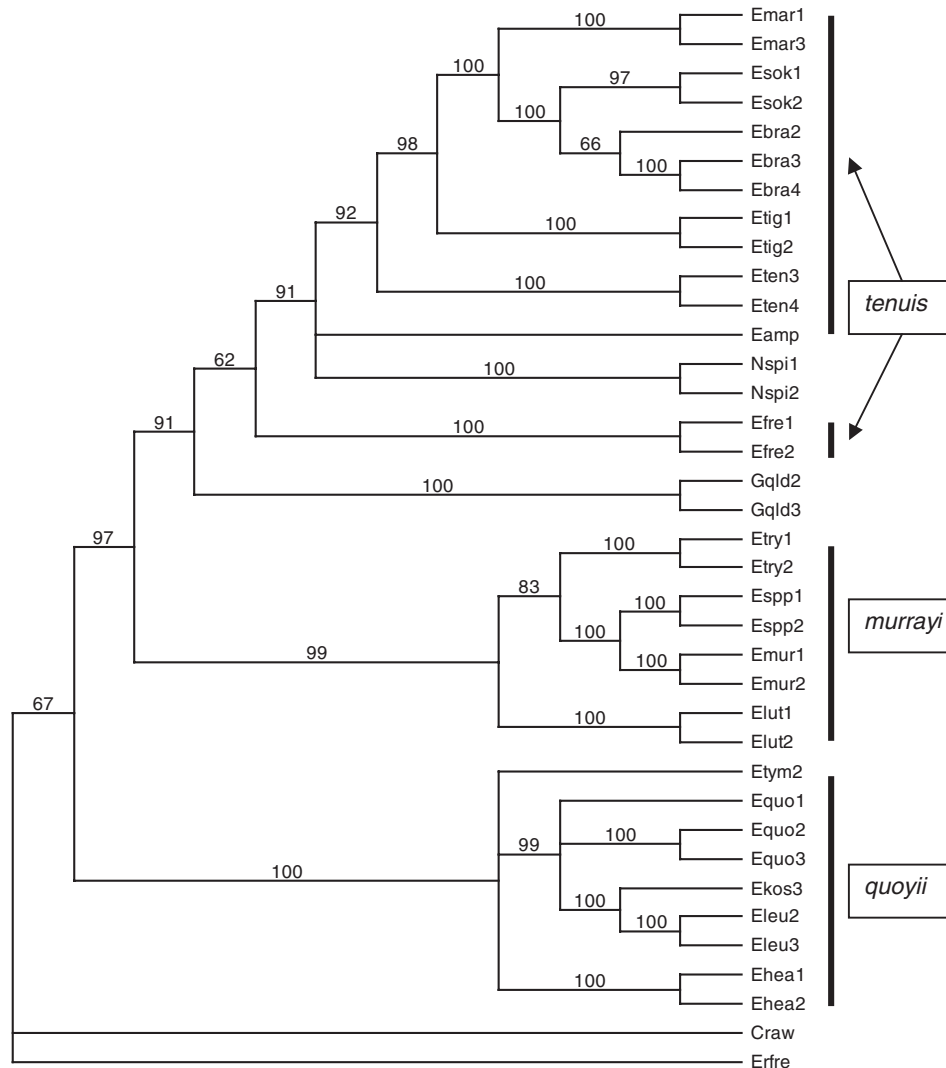


Fig. 2. Phylogenetic hypothesis obtained from the consensus of 19000 trees sampled from a Bayesian search of tree space. The three major species groups suggested by Greer (1989) are indicated on the right. Numbers above the branches indicate the proportion of trees in which the clade to the right was present and can be interpreted as the level of statistical confidence.

relationships of the other two *tenuis* group species (*E. amplus* and *E. frerei*), *G. queenslandiae* and *N. spinosa* are unresolved.

To investigate further the ambiguity regarding the placement of *G. queenslandiae* and *N. spinosa*, in particular, we tested alternative hypotheses using likelihood. The consensus from the Bayesian analysis (Fig. 2) has a likelihood (using the same values for sequence evolution parameters) of $\ln L = -6710.7$. Alternative topologies in which *G. queenslandiae* and *N. spinosa* form a polytomy that is either (i) immediately basal to the *tenuis* group, (ii) basal to both the *tenuis* and *murrayi* groups, or (iii) outside of all *Eulamprus*, have likelihoods of $\ln L = -6716.4$, -6721.8 and -6731.8 , respectively. The Shimodaira and

Hasagawa test (using 1000 bootstraps with full-optimisation option) indicated that the first alternative is not significantly worse than the best tree (one-tailed SH tests, $P = 0.36$). However alternative (ii) is marginally rejected ($P = 0.075$) and alternative (iii) more clearly so ($P = 0.02$). Thus, from the molecular data alone, we can be confident that *Eulamprus* is paraphyletic with respect to the monotypic genera *Gnypetoscincus* and *Nangura* and we suggest, but cannot demonstrate conclusively, that they are most closely related to, and perhaps within, the *tenuis* species group. In addition, we also tested the inter-group relationships proposed by Greer (1989) in which the *tenuis* group represents a basal grade and the *quoyii* and *murrayi* groups are sisters – this had a substantially and significantly lower likelihood ($\ln L = -7596.85$, SH test, $P < 0.001$) and can be confidently rejected in favour of the topology with the *quoyii* group basal and *murrayi* and *tenuis* groups as sister clades.

Discussion

Phylogeny and implications for taxonomy

The mitochondrial sequence data support and refine the broad species groups within *Eulamprus* as hypothesised by Greer (1989), but also suggest a different interpretation of relationships among these groups and parphyly of the genus in relation to *Gnypetoscincus* and *Nangura*. Before considering the biogeographic and evolutionary implications of the new hypothesis of relationships, we first explore consistency of key morphological changes considered by Greer with the new phylogenetic hypothesis (Fig. 3) and indicate changes to taxonomy that could follow.

As before, the monophyly of the *quoyii* group is supported by two derived character states – grooved subdigital lamellae and the distal dorsal scales being in a single row. Likewise, the species within the *murrayi* group are united by having the postmental in contact with one infralabial. More at issue is interpretation of two other characters previously used as evidence for monophyly of the *quoyii* + *murrayi* species groups. According to Greer (1989), members of the *tenuis* group together with *Gnypetoscincus* (and three species of *Glaphyromorphus*) are unusual among *Sphenomorphus* group of lygosomine skinks in having inguinal fat bodies, a trait also widespread within the *Eugongylus* group. These fat bodies are also present within *Nangura* (P. Couper, personal communication) and we suggest that this represents a synapomorphy for the clade (*tenuis* group + *Gnypetoscincus* + *Nangura*) rather than the ancestral condition, as proposed by Greer (1989). The second proposed synapomorphy for the clade of (*quoyii* + *murrayi* groups) was the presence of 5 scales separating the 3rd pair of enlarged chin scales, rather than the 3 scales seen in all other Australian representatives of the *Sphenomorphus* group skinks. Again, the new phylogenetic hypothesis reverses the polarity, suggesting that the presence of 5 scales as a synapomorphy for the genus (and *Gnypetoscincus* and *Nangura*) with a reversal to 3 scales in the *tenuis* group. A corollary of this interpretation is that *Gnypetoscincus* and *Nangura* are supported as a sister taxa to the species of the *tenuis* group. This hypothesis (Fig. 3) differs from the molecular tree in the placement of *E. frerei* relative to *Nangura*, but is not rejected relative to the Bayesian tree (Fig. 2) in a likelihood test ($\ln L = -6715$, SH RELL bootstrap test $P = 0.20$). We take this reconciliation of morphological and molecular traits as our working hypothesis of relationships for the group.

The strong support from the molecular analysis (and some morphological traits) for parphyly of *Eulamprus* relative to *Gnypetoscincus* and *Nangura* raises the question of whether the former genus should be split or whether *Gnypetoscincus* and *Nangura* should

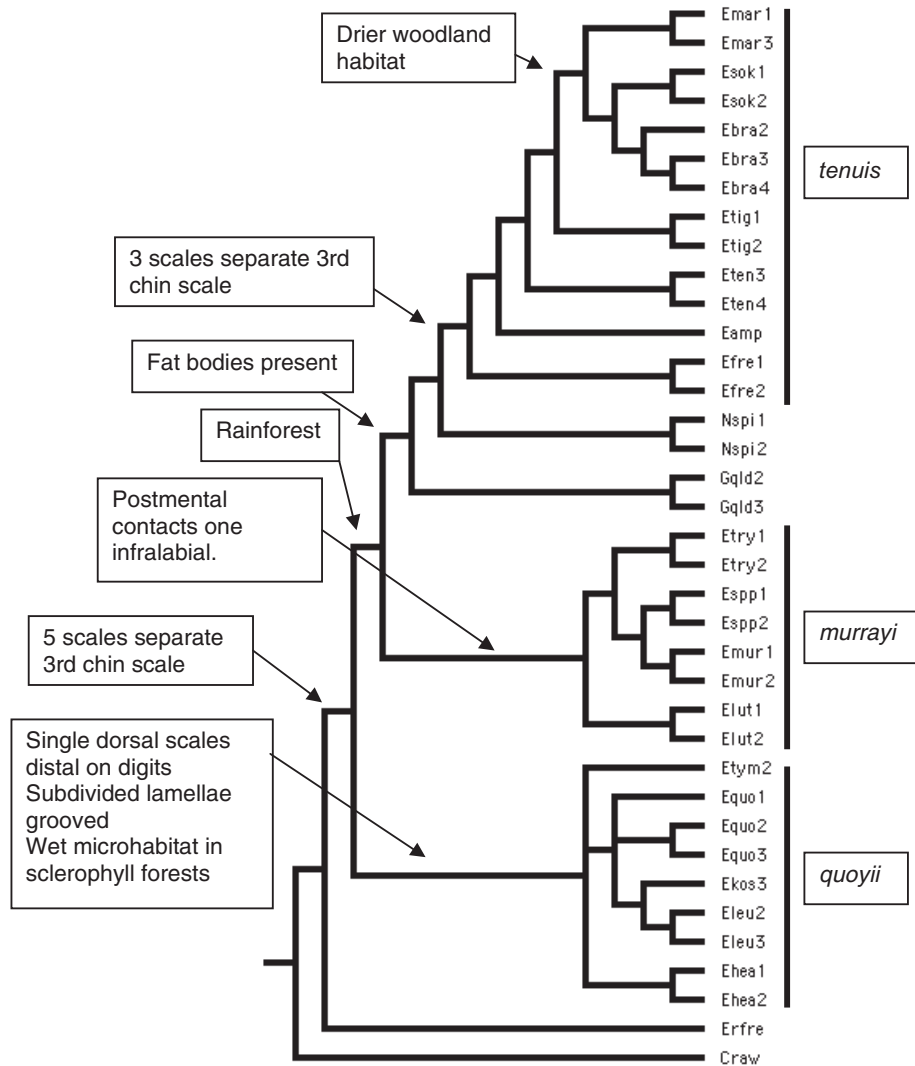


Fig. 3. Mapping of key morphological traits and habitat shifts on the phylogeny modified from Fig. 2 (see text).

be subsumed within *Eulamprus*. Greer (1989) notes that the only trait uniting *Eulamprus* is ovoviviparity, a condition also shared with *Gnyptoscincus* and a taxonomically broader mtDNA phylogenetic analysis, including one species from each of the three *Eulamprus* species groups, shows the genus to be polyphyletic relative to other genera of Australian skinks of the *Sphenomorphus* group (Reeder 2003). The *quoyii* group is shown here to be phylogenetically cohesive and highly divergent from the remaining species. In contrast to the other clades, this group occurs primarily in south-eastern Australia and also is somewhat ecologically distinct, being more strongly heliothermic and occurring in association with water in drier forests – hence the colloquial name ‘water skinks’ (Greer 1989). Considering the concordance across the phylogenetic, ecological and biogeographic evidence, we suggest that the *quoyii* group be considered as a separate genus from the

remainder. As the type species for the genus is *E. quoyii* (Fitzinger 1843), the *quoyii* group must remain within *Eulamprus*.

The phylogenetic hypothesis (Fig. 3) indicates that the remaining species of *Eulamprus* are paraphyletic with respect to *Gnyptoscincus* and *Nangura*, a result supported and extended in the broader analysis of *Sphenomorphus* group relationships (Reeder 2003). Accordingly, we suggest that the *tenuis* and *murrayi* groups, each of which appears to be monophyletic, should be placed into separate genera. The species of the former could be allocated to *Concinnia*, a genus proposed by Wells and Wellington (1983), *E. tenuis* being the type species. In addition to *tenuis* group species, *Concinnia*, as proposed by Wells and Wellington also contains species from *Glaphyromorphus* (*fuscaudis* and *mjobergi*), for which there is no evidence of monophyly with the *tenuis* group, as well as members of the *murrayi* group. Further research is therefore necessary to determine the appropriate limits for *Concinnia* and which, if any, species from genera other than *Eulamprus* should be included (see also Reeder 2003). Until this is completed we propose that only species from the *tenuis* group be assigned to *Concinnia*. There is no existing generic name applicable to the species of the *murrayi* group and a formal description of this genus is underway. We expect that this proposed arrangement will be stable, but clearly there is a need for further phylogenetic analysis of relationships among species of the *Sphenomorphus* group (Greer 1989; Hutchinson 1993; Reeder 2003).

The current molecular analysis has also revealed substantial diversity and possible cryptic species within some currently recognised species. Intraspecific phylogeography has previously been studied intensively within three of the species examined here: *G. queenslandiae* (Moritz *et al.* 1993; Schneider *et al.* 1998), '*E.*' *amplus* (Stuart-Fox *et al.* 2001) and '*E.*' *murrayi* (O'Connor, Mousalli and Moritz, unpublished). The highest level of divergence observed was between two parapatric lineages within the Wet Tropics endemic, *G. queenslandiae*, corresponding to 6% divergence across the gene segments examined here. This is substantial, but is still much less than the >10% divergence observed between the individuals of '*E.*' *murrayi* from Cambridge Plateau and surrounding populations. The aberrant population, here referred to as '*E.*' sp. probably represents a narrowly endemic cryptic species and is being investigated further. Even more dramatic is the divergence of >20% between the Wet Tropics sample of *E. quoyii* and others (Border Ranges, south-east Queensland and Sydney, New South Wales) from this widely distributed species. An ongoing analysis of phylogeography within *E. quoyii*, as currently recognised, has confirmed the presence of multiple distinct lineages and some cryptic species (I. Scott, personal communication).

Implications for historical biogeography and ecology

The mesic forest environments occupied by most of these species have been present on the east coast, with varying patchiness and extent, for millions of years and probably covered much of the continent prior to the general drying from the mid-late Miocene to the present (Adam 1992; Hope 1994; Kershaw *et al.* 1994). The deep molecular divergence within and between major clades of *Eulamprus* (*sensu lato*) is consistent with diversification of these skinks within these habitats over this long history, with the major lineages probably separating well back into the Miocene. Further support for the long history of *Eulamprus* comes from the recent finding (Mackness and Hutchinson 2000) of an early Pliocene fossil attributable to the *quoyii* group from northern Queensland.

The current phylogeny suggests two major shifts in habitat among the lineages studied here. The more ancient divergence was that between the moist forest species and the mainly

saxicoline and creek-dwelling water skinks. Within the clade consisting of the *tenuis* and *murrayi* groups, plus *Gnypetoscincus* and *Nangura*, the basal lineages are rainforest specialists (though *Nangura* is found in drier vine thickets) with the more recently derived clade in the *tenuis* group consisting of '*E. martini*', '*E. brachysoma*' and '*E. sokosoma*' representing a shift back towards rocky or creekline habitats within drier and more open woodlands. Australia has an extremely rich reptile fauna with a large number of habitat generalists occurring in rainforests, but relatively few rainforest endemics (reviewed in Williams *et al.* 1996). For both flora and fauna, rainforest contractions since the mid-Miocene may have caused the extinction of rainforest specialists (Heatwole and Taylor 1987; Busby and Brown 1991; Hope 1994; Archer *et al.* 1994) or, for species persisting in now drier forests, promoted ecological shifts towards mesic microhabitats. The shifts towards such habitat preferences in both the *quoyii* and *martini/sokosoma/brachysoma* lineages (Fig. 3) may reflect this trend.

In broad terms, the coastal wet forests occupied by most of these species can be split into four biogeographic regions (from north to south): the Wet Tropics, mid-east Queensland, a region incorporating south-east Queensland and north-east New South Wales, and south of the Hunter Valley (e.g. Keast 1981; Adam 1992). Each of the three major clades revealed here spans multiple regions but has its diversity focused in one or two (Fig. 1). The *quoyii* clade is primarily a southern radiation, although *E. quoyii* itself (as currently recognised) is widely distributed. Three of the four species in the *murrayi* clade are from the rainforests of south-east Queensland and north-east NSW, the fourth being endemic to the mid-east Queensland rainforest. Finally, the clade consisting of the *tenuis* group plus *Gnypetoscincus* and *Nangura* includes three endemic species from the Wet Tropics rainforests, one from mid-east Queensland rainforests and one from south-east Queensland as well as the three drier forest taxa distributed from mid-east to south-eastern Queensland. Collectively, these relationships indicate deep historical connections between the now isolated rainforests of mid-east Queensland and the Wet Tropics, on one hand, and south-eastern Queensland, on the other. Whether the phylogenetic affinities of the mid-east Queensland rainforests are primarily to the north or south requires phylogenetic analysis of additional groups with multiple, narrowly endemic species (e.g. snails: Hugall *et al.* in press; plants: Crisp *et al.* 2001). Whatever the general pattern of biogeography, the considerable divergence (>15%) between each *Eulamprus* endemic to mid-east Queensland and their nearest relatives, together with recent evidence for substantial local endemism and genetic diversity within this region (e.g. Couper *et al.* 2000; Stuart-Fox *et al.* 2001) emphasises the antiquity of this fauna and high conservation value of their rainforest habitats, as well as those of the better known Wet Tropics and the border region of Queensland and New South Wales.

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Appendix. Details of the sequenced specimens of *Eulamprus* species

| Species | Genetic code | Sample code | Voucher specimen | Location |
|----------------------------|--------------|-------------|------------------|--|
| <i>E. amplus</i> | E. amp1 | CJS 673 | | Mt Blackwood, Qld |
| <i>E. amplus</i> | E. amp2 | CJS 740 | | Finch Hatton Gorge, Qld |
| <i>E. brachysoma</i> | E. bra2 | CJS 645 | | Boulder Ck, Eungella, Qld |
| <i>E. brachysoma</i> | E. bra3 | DOC 61 | | Chillagoe Caves, Qld |
| <i>E. brachysoma</i> | E. bra4 | DOC 10 | | Chillagoe Caves, Qld |
| <i>E. frerei</i> | E. fre1 | Q1037 | | Mt Bartle Frere, Qld |
| <i>E. frerei</i> | E. fre2 | CON | | Mt Bartle Frere, Qld |
| <i>E. heatwolei</i> | E. hea1 | NR88L | AMS R133188 | 15 km N of Kanangra Walls, NSW |
| <i>E. heatwolei</i> | E. hea2 | NR92 | AMS R133191 | 15 km N of Kanangra Walls, NSW |
| <i>E. kosciuskoi</i> | E. kos3 | 94 | | Cathedral Rock, New England NP, NSW |
| <i>E. leuraensis</i> | E. leu2 | NR 3875 | | Blue Mtns, NSW |
| <i>E. leuraensis</i> | E. leu3 | NR 3876 | | Blue Mtns, NSW |
| <i>E. luteilateralis</i> | E. lut1 | CJS 754 | | Dalrymple Rd, Eungella, Qld |
| <i>E. luteilateralis</i> | E. lut2 | A35 | | Eungella, Qld |
| <i>E. martini</i> | E. mar1 | D5 | | Gambubal SF, Qld |
| <i>E. martini</i> | E. mar3 | DOC 39 | | Lamington NP, Qld |
| <i>E. murrayi</i> | E. mur1 | DOC 718 | | Nightcap NP, NSW |
| <i>E. murrayi</i> | E. mur2 | DOC 717 | | Pt Lookout, NSW |
| <i>E. quoyii</i> | E. quo1 | T81 | QM J47602 | Charmillon Ck, Qld |
| <i>E. quoyii</i> | E. quo2 | Q910 | | Lamington NP, Qld |
| <i>E. quoyii</i> | E. quo3 | 1142 | | Oxford Falls, Sydney, NSW |
| <i>E. sokosoma</i> | E. sok1 | DHR1 | | Hervey Range, Townsville, Qld |
| <i>E. sokosoma</i> | E. sok2 | DHR4 | | Hervey Range, Townsville, Qld |
| <i>E. tenuis</i> | E. ten3 | DOC 106 | | Bulburin SF, Qld |
| <i>E. tenuis</i> | E. ten4 | CHDD 230 | | Mt Nebo, D'Aguilar Range, Qld |
| <i>E. tigrinus</i> | E. tig1 | CJS 869 | | Lake Eacham, Qld |
| <i>E. tigrinus</i> | E. tig2 | CJS 799 | | Massey Ck, Atherton Tbl, Qld |
| <i>E. tryoni</i> | E. try1 | DOC 760 | | Lamington NP, Qld |
| <i>E. tryoni</i> | E. try2 | DOC 751 | | Lamington NP, Qld |
| <i>E. tympanum</i> | E. tym2 | NR 3950 | AMS R148525 | Kosciusko NP, NSW |
| <i>E. sp.</i> | E. spp1 | BP 121 | | 1.5 km N of Cambridge Plateau, Richmond Range, NSW |
| <i>E. sp.</i> | E. spp2 | BP 131 | | 1.5 km N of Cambridge Plateau, Richmond Range, NSW |
| <i>G. queenslandiae</i> | G. qld 2 | JJ 136 | | Massey Ck, Atherton Tbl, Qld |
| <i>G. queenslandiae</i> | G. qld 3 | Q 193 | | Mt Lewis, Qld |
| <i>N. spinosa</i> | N. spi 1 | N. spi | | Oakview SF, Qld |
| <i>N. spinosa</i> | N. spi 2 | Q925 | QM 7247 | Nangur SF, Qld |
| <i>Egernia frerei</i> | Er. fre | CJS 676 | | Mt Blackwood |
| <i>Ctenotus rawlinsoni</i> | C. raw | N29869 | | Cape Flattery |