Phylogenetic Relationships of Australian Skinks of the *Mabuya* Group (Reptilia: Scincidae) Inferred from Mitochondrial DNA Sequences

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(Received 25 June 1999, accepted 14 September 1999)

Portions of two mitochondrial genes (12S and 16S ribosomal RNAs) were sequenced to analyze the phylogenetic relationships of the *Mabuya* group from the Australian region (*Corucia*, *Egernia* and *Tiliqua*). Results indicated the monophyly of these genera and their divergence from Asian and African members of this group. This suggests that the diversity of the *Mabuya* group in the Australian region has increased through an endemic radiation, not through multiple colonizations from outside. Among the genera from this region, *Corucia* and *Tiliqua* were closest to each other. This result contradicts with those of the previous hypotheses on the basis of morphological and immunological data that, respectively, suggested closest affinities between *Corucia* and *Egernia*, and *Egernia* and *Tiliqua*. We suppose that the morphological characters exclusively joining *Corucia* and *Egernia* are actually in plesiomorphic state.

INTRODUCTION

Australia is noted for its unique fauna (e.g., Darlington, 1957). A number of systematists and biogeographers have attempted to reveal the origins and diversification processes of vertebrate lineages occurring in this region. Despite enthusiastic efforts and vigorous debates by those researchers, however, little consensus has yet been attained even on the most basic issues relevant to the history of each lineage: Gondwanaland origin or Laurasian origin; current diversity as a consequence of multiple colonization or *in situ* radiation (e.g., compare corresponding accounts by Cracraft [1974], Tyler [1979], and Cogger and Heatwole [1981]).

Recently a few molecular phylogenetic studies elucidated relationships of Australian and non-Australian taxa in particular lineages, giving useful clues to the solution of those problems (e.g., Fuller et al., 1998; Donnellan et al., 1999; Goerges et al., 1999). However, the number of lineages studied from such an approach are yet too few to allow any generalizations.

The scincid subfamily Lygosominae contains over 600 species of lizards distributed in Australia, as well as in temperate and tropical Asia, central and southern Africa, Madagascar and western Indian Ocean islands, southeastern North America, and central and South America includ-

ing the Caribbean islands (Greer, 1970; Matsui, 1992; Zug, 1993). King (1973), on the basis of chromosomal data, recognized three distinct groups among Australian lygosomines. Greer (1979) demonstrated that these groups well correspond to three morphologically defined evolutionary lineages therein referred to as the *Egernia*, *Eugongylus* and *Sphenomorphus* groups. This view has been further confirmed by the subsequent systematic studies using chromosomal, morphological and immunological data for both Australian and non-Australian lygosomines (e.g., Hardy, 1979; Ota et al., 1988, 1991, 1995, 1996; Greer, 1989; Baverstock and Donnellan, 1990; King, 1990; Donnellan, 1991a,b). Most of these works have also revealed that chromosomal and morphological features of the Australian *Egernia* group are quite similar to those of a few non-Australian genera including the broadly distributed and highly diversified genus *Mabuya*. Thus, Greer's (1979) *Egernia* group is currently referred to as the *Mabuya* group together with *Mabuya* and other non-Australian relatives of this genus (Greer, 1989; but see Hutchinson [1981] for a different view as below).

The *Mabuya* group has a geographic range almost equal to that of the entire subfamily (Boulenger, 1887; Greer, 1970; Nussbaum and Raxworthy, 1994). Greer (1979) supposed that, within the Australian lygosomines, the *Mabuya* (= *Egernia*: see above) group was closer to the *Eugongylus* group than to the *Sphenomorphus* group. Such a relationship was confirmed by Hutchinson (1981)

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on the basis of immunological data, although he went so far as to even assume a sister relationship of the Australian members of the *Mabuya* group with the *Eugongylus* group, not with Asian *Mabuya*. With respect to the non-Australian components of the *Mabuya* group, Honda et al. (1999b) recognized two distinct lineages for the Asian and African genera (i.e., *Lygosoma* and *Mabuya* subgroups) on the basis of molecular data. They, however, did not examine their relationships with the Australian genera of this group.

The *Mabuya* group from Australia (including Papua New Guinea and adjacent islands) consists of three genera, *Corucia*, *Egernia* and *Tiliqua* sensu lato (Greer, 1979). Their phylogenetic relationships are still controversial. Greer (1970), on the basis of morphological characters, argued for the closer affinity between *Corucia* and *Egernia*. On the other hand, results of immunodistance analysis by Hutchinson (1981) suggested the closest relationship between *Egernia* and *Tiliqua*.

We partially sequenced mitochondrial DNA for representatives of the *Mabuya* group from Australian region and analyzed resultant data together with sequence data for non-Australian members of this group phylogenetically. Our purposes are to elucidate the relationships among the Australian genera, and their affinity with non-Australian members of the *Mabuya* group. We then discuss the source of diversity of this group in Australia accordingly.

MATERIALS AND METHODS

Five lygosomine species were used. Voucher specimens are deposited in the herpetological collection of the Department of Zoology, Kyoto University (KUZ). Of these, four specimens (*Corucia zebrata*: KUZ 46906; *Egernia frerei*: KUZ 45196; *Tiliqua gigas*: KUZ 46926; and *T. nigrolutea*: KUZ 50018), representing the three Australian genera of the *Mabuya* group, were obtained from pet dealers in life or in fresh dead state, and the other (*Carlia fusca*: Guam, Mariana Islands, KUZ 27794) of the *Eugongylus* group were sampled in the field. Published sequences for representatives of the three putative lineages of the Asian/African *Mabuya* group (Honda et al., 1999b: i.e., *Lamprolepis smaragdina* and *Lygosoma bowringii* of the *Lygosoma* subgroup; *M. longicaudata* of the Asian *Mabuya* subgroup; and *M. quiquetaeniata* of the African *Mabuya* subgroup) were also incorporated into the analysis. We selected *Eumeces latiscutatus* of the subfamily Scincinae, a possible closest relative of Lygosominae (Greer, 1970), as an outgroup to root the resultant dendrograms.

Recently, *Cyclodomorphus* (accommodating *branchialis*, *casuarinae* and *maxima*), *Hemisphaeriodon* (monotypic with *gerrardii*) and *Trachydosaurus* (monotypic with *rugosus*), once regarded as synonyms of *Tiliqua*, have been revalidated (Cogger, 1994). However, since immunologi-

cal and morphological data indicate both monophyly and high genetic similarity of the above four genera (Hutchinson, 1981; Greer, 1989), designation of *T. gigas* and *T. nigrolutea* as the representatives of all four genera should involve any substantial error in the results of the analyses. Greer (1979) stated that *Tribolonotus* might belong to the *Mabuya* group. However, this genus is obviously a member of the *Sphenomorphus* group (Hutchinson, 1981).

DNA extraction, amplification and sequencing are described in detail elsewhere (Honda et al., 1999a,b). A part of mitochondrial 12S and 16S ribosomal RNA (rRNA) genes consisting of approximately 830 base pairs (bp) were amplified using the polymerase chain reaction (PCR; Saiki et al., 1988) with primers L1091, H1478, L2606, and H3056 (Kocher et al., 1989; Hedges et al., 1993).

Alignments for DNA sequences were determined based on maximum nucleotide similarity. We prepared a pairwise matrix of distance by Kimura's (1980) two-parameter model. The neighbor-joining (NJ) method (Saitou and Nei, 1987) was applied to infer relationships among taxa on the basis of the distance matrix. Degrees of supports for internal branches of each tree were assessed by 1,000 bootstrap replications (Felsenstein, 1985). These analyses were performed by use of Clustal W 1.4 (Thompson et al., 1994). Maximum parsimony analysis (MP) was also performed using PAUP 3.1.1 with heuristic option (Swofford, 1993). No frequency bias was assumed for transition and transversion. The confidence was assessed by 1,000 bootstrap resamplings (Felsenstein, 1985). In both analyses, gap sites were excluded.

RESULTS

Aligned sequences from two mitochondrial genes are presented in Fig. 1. The 12S rRNA fragment consisted of 389 total sites, 159 of which were variable. For the 16S rRNA fragment, there were 437 total aligned sites, 145 of which were variable. Intergeneric nucleotide replacements within Lygosominae varied from 63 bp (*Corucia* vs. *Tiliqua nigrolutea*) to 150 bp (*Lamprolepis* or *Lygosoma* vs. *Mabuya longicaudata*). Nucleotide replacements within the Australian *Mabuya* group were observed from 63 bp to 74 bp (*Egernia* vs. *T. gigas*). Interspecific nucleotide replacements involved 44 bp and 118 bp in *Tiliqua* and *Mabuya*, respectively.

The NJ dendrogram derived from mitochondrial DNA distance matrix (not given) is shown in Fig. 2A. The ingroup portion of this dendrogram showed tetrachotomous clusters. First cluster was monotypic with *Carlia*. The second with 85% bootstrap support was composed of the Asian and African *Mabuya*, whereas the third, supported in all bootstrap iterations (100%), consisted of the *Lygosoma* subgroup (as represented by *Lamprolepis* and *Lygosoma*). The four Australian representatives

<i>Eumeces latiscutatus</i>	1	GCTCAGCCATAAAGTATGGTAGTACAA-TCACAACACTACCGCCAGAGAACTACAAGTAAAACTTAAACCTCAAGGACTTGGCGGTGCTCCACATCAACCTAGAGAGCGCTGCTTATAATCGATAATCCACGTTCCACGCTACCA	150
<i>Carlia fusca</i>		...T...G...A.AAAG...T...AC...CGTT...A...C...CACT...C...C...A...T...TC...	
<i>Corucia zebrata</i>		...T...G...ACA.A...AC.CA...A...TT...C...G...G...A...GT...C...T...TC...	
<i>Egernia frerei</i>		...T...C...ACA.AC...TA.CA...A...T...C...G...G...T...T...C...CC...T...T...T...	
<i>Lamprolepis smaragdina</i>		...C...A...T...ATA.AC.AC.AT...TGT.GT...G...C...T...A...C...C...G...CC...TT...A...C	
<i>Lygosoma bowringii</i>		...CT.A...C...ATA.AC.C...CC...G.TG.GT...G.AC...GT...A...T...A.C.A...TC.G...G...C...C...A...C...	
<i>Mabuya quinquetaeniata</i>		...T...C.TC.A.AAA...AC.TAA...C...TT...T...C...T...A...G...A...T...GC...CC...AA...T...	
<i>Mabuya quinquetaeniata</i>		...T...C.T...ATA.AC...A...CA...T...GT...C...G...A...A...T...GG...CC...T...T...G	
<i>Tiliqua gigas</i>		...T...C...ACA.A.G.TA.TA...A...C.TT...C...G...G...A...T...C...CC...T...T...C...	
<i>Tiliqua nigrolutea</i>		...T...C...ATA.A.G.TA.CA...A...C.TT...C...G...G...A...T...C...CC...T...T...C...	
<i>Eumeces latiscutatus</i>	151	CCCTTCGCC—CTCAGCCTATATACCGCGCTCGTAAGCTACCTTCTGAAAGAGTACA-GTAAGCAAAACGATTATTAACTAGCACGTCAGTCAAGGTGTAGCACATGAGGTGAAGAGATGGGCTACATTTCTGCCACAGAAAAC-	300
<i>Carlia fusca</i>		G.CA.T.TA.A...C...A...CC.A...T...T...AA...C...G...C...C...AAGCT...G...	
<i>Corucia zebrata</i>		...T...T...A.AT...C...A...A...C...G...A...AC...G...A...A...G...A...A...T...T	
<i>Egernia frerei</i>		...CC.T.TA.A.C...C...C...G...A...A...G...A...AC...AT...T...G...C...ATT...C	
<i>Lamprolepis smaragdina</i>		...CC.T...A.T.C...CC...C...A...C...A...G...T...T...C...AT...A...G...C...AAGCT...T	
<i>Lygosoma bowringii</i>		...CC.T...A.AT...C...A...G...A...G...G...A...AT...A...G...C...AAGCT...T	
<i>Mabuya quinquetaeniata</i>		...TT...T.AAAC...C...C...A...G...A...A...G...T...CC.GC...A...A...C...AA...T	
<i>Mabuya quinquetaeniata</i>		...CC.A...C...C...C...A...GTC.A...G...AC...AA...T...G...C...C...A...C...T	
<i>Tiliqua gigas</i>		T.C.T...A.A.G...C...T...G...AC.A...G...A...TAC...A...G...AGAA...AT	
<i>Tiliqua nigrolutea</i>		T.C.T...A.A.GT...C...T...G...AC.A...G...A...TAC...A...A...A...AT	
<i>Eumeces latiscutatus</i>	301	ACGAACAGCCTAATGAACTTAGGCCAAAAGCGGATTAGCAGTAAGACAAGCAAGAACCCCTGTCTTAAACCGCTCTGGAGCGCGCTGTCTTAAATAGAGACAGTATGAACGGCTAAATGAGGACAAACCTGTCTTGCACACC	450
<i>Carlia fusca</i>		...T...A...TACT...TT...AT...G.GTT...AA...C...T...A...G...A...G...A...AT...G.A	
<i>Corucia zebrata</i>		...AG.TA...A.TCA.CG...A...T...AT...T.A...GA...C...A...T...T...A...G...S.T	
<i>Egernia frerei</i>		...AG...A...T.C.C...T...T...AT...T.A...G...C...A...T...C...A...T...A...G.T	
<i>Lamprolepis smaragdina</i>		...TA...T...AC.TA.C...T...T...GA.GA...T...A...A...G...T...C...A...T...A...A	
<i>Lygosoma bowringii</i>		...G...A...TACGT...C...T...A.GA...T...A...A...G...T...C...A...T...C...A.TG...	
<i>Mabuya quinquetaeniata</i>		...AC.C...CCGT...TTG...T...A...A...CTTGT...T...C...C...A...T...T...T	
<i>Mabuya quinquetaeniata</i>		...ACT...ACCGT...TC...T...AA...GTT...C...G...C...T...CC...G...AT...T	
<i>Tiliqua gigas</i>		...AG.TG.G...AC.CA.C...A...A...T...AT...GT.TT.A...T...T...C...A...T...A...G...T	
<i>Tiliqua nigrolutea</i>		...AG.TA...A.CA.C...T...A...AT...G...TT...TT...T...C...A...T...A...A...G...	
<i>Eumeces latiscutatus</i>	451	AATCAGTGAACGTATCTCCCGTCCAAAAGCGGAATAACCCCAATAGACAGAGAACCGTGTGAGCTTAAACAAGCTACTA-TGCACCACACAA-GCTGCACTAGTAAGTATTAAAGTTGGGGCGACTCGGAACCAAAAAA	600
<i>Carlia fusca</i>		...C...A...A...TT.G...A...T...A...T...CT.TAGA.TG.CGC...C...A...C...A...C...	
<i>Corucia zebrata</i>		...TAT...A...A...T...A...C...A...A...AA...AC.CAT.AAG...A...C...CTTA...G...A...C...	
<i>Egernia frerei</i>		...TT.A...A...T...A...A...C...A...G...ACAA...AC.CAT-AG...T...C...CTTA...C...G...	
<i>Lamprolepis smaragdina</i>		...T...T...A...G...T...G...T...A...T...T...A...C...ACA...A...AT...CT.A.AAACC...GCCA...G...T...C...C...	
<i>Lygosoma bowringii</i>		...T...A...G...T...GTG...C...C...AT...A...C...AAGC...TAA...A...C...C...	
<i>Mabuya quinquetaeniata</i>		...A...A...A...T...T...TTGA...G...TCG...TAC...AC...G...TA...C...A...C...G...	
<i>Mabuya quinquetaeniata</i>		...A...A...T...G...C.A.A...C...A...C...C...TT...ACC...G...GTACT...G...TAC...C...	
<i>Tiliqua gigas</i>		...T...A...A...TA.G...ATA...A...C...A...AAG.AT...TT-AA...CC...CCA...A...C...-	
<i>Tiliqua nigrolutea</i>		...T...A...A...T...ATA...A...CG...ACAAG.ACT...AA...TC...CCCAA...A...C...-	
<i>Eumeces latiscutatus</i>	601	ACTTCGAGCAGACAGCA-CCCACTCTTACCAAGACCAACAGTCAAG—CCCAAAACGACCAAGTAAC—ACTGATCAACGACCAAGTTACCCAGGGAATACAGCGCATCTTCTCAAGAGTTTATGACAGAGAGTTT	750
<i>Carlia fusca</i>		...ATT...T...A...AA...T...T...CTT...A...C...C...C...C...C...C...C...	
<i>Corucia zebrata</i>		...ACT...C...G...T...C...TAT...T...C...C...T...C...C...C...C...	
<i>Egernia frerei</i>		...C...A...ATT...C...T...G...TAT...T...C...T...C...C...C...C...	
<i>Lamprolepis smaragdina</i>		...C...T...A...GG...AGAC...T...CT...C...CATA...C...C...T...T...C...C...	
<i>Lygosoma bowringii</i>		...A...G...CAAAC...CCCTT...G...C...T...ACAAA...C...T...T...C...C...	
<i>Mabuya quinquetaeniata</i>		...TG...T...AAC...C...G...T...C...TGCTT...TCCT...G...C...TGGTG...C...C...	
<i>Mabuya quinquetaeniata</i>		...T...AGTT...A...G...G...C...T...TA-T...C...G...CCCA...CG...C...C...	
<i>Tiliqua gigas</i>		...ACT...C...G...C...TAA...G-C...C...T...C...C...C...C...	
<i>Tiliqua nigrolutea</i>		...AGT...C...G...T...C...TAT...C...C...T...C...C...C...	
<i>Eumeces latiscutatus</i>	751	ACGACCTCGATGTTGGATCAGCAGACCCCAATGGTGCAGCCGCTATTAAAGSTTGGTTGTTCACGATTAAACAGT	
<i>Carlia fusca</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Corucia zebrata</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Egernia frerei</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Lamprolepis smaragdina</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Lygosoma bowringii</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Mabuya quinquetaeniata</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Mabuya quinquetaeniata</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Tiliqua gigas</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	
<i>Tiliqua nigrolutea</i>		...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...A...	

Fig. 1. Aligned sequences of a 826 bp segment of the 12S and 16S rRNA genes. The initial 389 bp in each row correspond to 12S rRNA gene sequence. The 16S rRNA gene sequence begins at the asterisk. Dot indicates an identity with the first sequence; dash denotes a gap.

Fig. 2. (A) Neighbor-joining (NJ) dendrogram deriving from distance matrix from 12S and 16S rRNA sequence data. Numbers at branch indicate bootstrap proportions in 1,000 bootstrap pseudoreplications. Branches without BP values were not supported in $\geq 50\%$ of the replicates. Bar equals 0.1 Kimura's two-parameter distance. (B) Maximum parsimony (MP) cladogram using heuristic option (618 steps, 176 bp informative under the condition of parsimony, consistency index = 0.58). Branches without BP values were not supported in $\geq 50\%$ of the 1,000 bootstrap replicates.

were exclusively close to each other to constitute the fourth cluster with 86% support. Within this cluster, *Egernia* was located outside of the *Corucia-Tiliqua* subcluster (91%). Congeneric samples of *Tiliqua* exclusively constituted lowest clusters (93%).

Resultant cladogram of MP (Fig. 2B) showed no substantial inconsistency with the NJ dendrogram in terms of branching topology at the level more than 70% bootstrap iterations.

DISCUSSION

A few previous authors assumed the Australian members of the *Mabuya* group (= *Egernia* group) to be monophyletic on the basis of morphological and immunological data (Greer, 1979; Hutchinson, 1981). With respect to the Asian members of this group, Greer (1977) presumed that four phylogenetic lineages were independently derived from an Asian *Mabuya*-like ancestor. However, this view was negated by Honda et al. (1999b), who demonstrated the presence of two distinct lineages, the *Lygosoma* and *Mabuya* subgroups, within the Asian and African members of this group by the analysis of DNA sequence data. Phylogenetic relationships revealed in the present study indicate not only the monophyly of the Australian genera of the *Mabuya* group, but also their constituting the third major evolutionary lineage in this group, which may be referred to as the *Egernia* subgroup.

A number of morphological and karyological studies demonstrated a considerable similarity between the *Egernia* subgroup and non-Australian members of the *Mabuya* group (see above). On the other hand, within the Australian lygosomines, the *Egernia* subgroup and the *Eugongylus* group are supposed to be closer to each other than to the *Sphenomorphus* group (Greer, 1979; Hutchinson, 1981). Hutchinson (1981) further argued for the closer affinities of the former two sub/groups with each other against the non-Australian *Mabuya* group, whereas Greer's (1979) view on this regard remained equivocal. Unfortunately, we failed to obtain explicit evidence for this point, and this seems to reflect the almost concurrent radiation of all lineages involved (Fig. 2).

Greer (1970) surmised that *Corucia* and *Egernia* were exclusively closely related because both of these genera differ from other lygosomines in having palatine bones slightly separated along the midline of the secondary palate (palatine bones contacting medially in others). On the other hand, immunological data suggested a closer *Egernia-Tiliqua* affinity against *Corucia* (Hutchinson, 1981). Relationships proposed with high bootstrap values in the present results (i.e., closest relationship between *Corucia* and *Tiliqua*) support neither of those previous hypotheses. The widely separated palatines exhibited by most scincine genera is likely to represent a primitive character state in Scincidae, because Scincinae

is obviously a basal group of this family (Greer, 1970, 1979). On the other hand, the extensive secondary palate formed by the close apposition of palatines is considered to be a synapomorphy of Lygosominae (Greer, 1986). Our results thus suggest that the common ancestor of the *Egernia* subgroup had slightly separated palatines, and that the medial contact of palatines in *Tiliqua*, apparently similar to the state in many other lygosomines, have independently evolved from the slightly separated state in *Corucia*. Hutchinson's (1981) analysis by micro-immunoelectrophoresis seems to suffer technically, because it at least partially depends on a subjective estimate of the intensity of precipitin arcs (Greer, 1986).

Distributions of *Egernia* and *Tiliqua* are largely confined to Australia, New Guinea and adjacent islands, except for *T. gigas* which ranges from New Guinea west to Sumatra (e.g., de Rooij, 1915; Cogger, 1994). According to the phylogenetic relationships inferred above, the three genera seem to have been derived from the common ancestor of the *Egernia* subgroup through endemic Australian radiation, rather than from multiple colonizations from outside, such as Southeast Asia, as is assumed for the Australian varanids (Fuller et al., 1998). Populations of *T. gigas* in the Sunda Archipelago of Indonesia and *C. zebrata* in the Solomons (McCoy, 1980) are thus considered as representing secondary dispersals.

We would like to thank A. E. Greer for detailed information of his work and useful suggestions, to Y. Yasukawa for the arrangement to obtain fresh dead material from pet dealers for free of charge, to M. Hasegawa for providing specimens of *Carlia*, and to K. Ishida and N. Takada for the laboratory assistance. Special thanks are due N. Satoh and members of his laboratory for a continuous support to our laboratory experiments. Experiments were also carried out using the facility of the Kyoto University Museum.

Our research was partially supported by Grants-in-Aid from the Japan Ministry of Education, Science, Sports and Culture (Basic Researches C-09839024 to H. Ota and C-10836010 to T. Hikida).

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