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# Evolution of Asian and African Lygosomine Skinks of the *Mabuya* Group (Reptilia: Scincidae): A Molecular Perspective

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**ABSTRACT**—Phylogenetic relationships among Asian and African lygosomine skinks of the *Mabuya* group were inferred from 825 base pairs of DNA sequences of mitochondrial 12S and 16S rRNA genes. Results indicated the presence of two distinct lineages within this group, of which one consisted of *Lamprolepis* and *Lygosoma*, and the other of *Apterygodon*, *Dasia*, and Asian and African *Mabuya*. Within the latter, African species of *Mabuya* first diverged from the remainder, leaving the Asian congeners together with the *Apterygodon–Dasia* clade. Our results, while suggesting the non-monophyly of the genus *Mabuya*, do not support the currently prevailing phylogeographical hypothesis which assumes the independent origins of *Lamprolepis* and *Lygosoma* from the Asian *Mabuya*-like stock. On the other hand, our results suggest that morphological and karyological similarities between the *Apterygodon–Dasia* clade and *Lamprolepis* are attributable to symplesiomorphy, while their ecological similarity to convergence. Morphological and karyological and karyological similarity by *Dasia*.

# INTRODUCTION

The subfamily Lygosominae contains over 600 species (Greer, 1970a; Matsui, 1992; Zug, 1993). Within this subfamily, three evolutionary lineages (i.e., *Eugongylus, Mabuya* and *Sphenomorphus* groups) are recognized on the morphological, karyological and immunogenetic grounds (e.g., King, 1973, 1990; Greer, 1979, 1989; Hardy, 1979; Baverstock and Donnellan, 1990; Donnellan, 1991a, b; Ota *et al.*, 1988, 1991, 1995, 1996). Of these, the *Mabuya* group is mainly distributed in temperate and tropical Asia, central and southern Africa, and Australia. *Mabuya*, the largest genus of this group with broadest range, also occurs in Madagascar and South America including the West Indian Islands, but is not distributed in Australia (Boulenger, 1887; Matsui, 1992; Nussbaum and Raxworthy, 1994).

Three arboreal genera (*Apterygodon*, *Dasia* [sensu stricto] and *Lamprolepis*) and one terrestrial or semi-fossorial genus (*Lygosoma* [sensu Greer, 1977]) have been assigned to the *Mabuya* group together with *Mabuya* and a few other African

\* Corresponding author: Tel. +81-75-753-4091; FAX. +81-75-753-4114. and Australian genera. Of these, the former three taxa had been grouped together as the genus Dasia sensu lato (Smith, 1937; Mittleman, 1952), when Greer (1970b) proposed the current generic arrangements on the basis of morphological characters. He also argued that the Apterygodon-Dasia lineage and the Lamprolepis lineage had evolved independently from a Mabuya-like stock in Southeast Asia. With an extension of this view, Greer (1977) considered that, besides the genus Mabuya, those two arboreal lineages, Lygosoma, Australian members of the Mabuya group, the Eugongylus group, and the Sphenomorphus group constitute six phylogenetic lineages independently derived from the Asian Mabuya-like stock (he argued for the subsequent derivations of the African endemic genera of the Mabuya group from the Mabuya-like stock within this continent). However, the chronological order of these divergences was not hypothesized in that work. Later, Australian members of the Mabuya group, the Eugongylus group and the Sphenomorphus group were attributed to divergences earlier than that in Asian and African members of the Mabuya group (Greer, 1979, 1989). The remaining three lineages, Apterygodon–Dasia, Lamprolepis and Lygosoma, as well as Mabuya, are still considered as derived from the Mabuya-like stock in Asia (Greer, 1977), although their detailed relationships remain uncertain.

The genus *Mabuya* seems to have first emerged in South or Southeast Asia and then dispersed through Africa onto Madagascar and South America, because a few species from South and Southeast Asia exhibit most primitive states of characters among the extant *Mabuya* species (Greer, 1977). Although some authors (e.g., Greer, 1977) pointed out the possible non-monophyly of this genus due to its wide distribution and great morphological diversity, no comprehensive phylogenetic analyses have ever been made for the genus and its relatives to verify this prediction.

There have been a number of debates regarding the phylogenetic relationships and classification of lygosomine skinks, and most of relevant arguments have depended on morphological evidence (e.g., Mittleman, 1952; Greer, 1970a, 1974, 1979; Horton, 1972, 1973). However, due to the scarcity of informative characters, it is not easy to formulate a sufficiently reliable phylogenetic hypothesis for this group solely on the morphological ground. Phylogenetic analyses on the basis of molecular data are, therefore, expected to much contribute to the solution of this problem.

We sequenced a part of mitochondrial DNA for representatives of Asian and African *Mabuya*, and the three other lineages supposedly derived from the *Mabuya*-like stock in Asia (see above), and analyzed resultant data phylogenetically. The purpose of this study is to reveal the pattern and process in the early evolution of the widespread and apparently substantially diverged *Mabuya* group in Asia and Africa.

#### MATERIALS AND METHODS

Tissues were obtained from eight Southeast Asian species belonging to five genera of the *Mabuya* group (*Apterygodon vittatus*, *Dasia gricea*, *D. olivacea*, *Lamprolepis smaragdina*, *Lygosoma bowringii*, *Mabuya longicaudata*, *M. multifasciata* and *M. rudis*), and two African *Mabuya* (*M. quiquetaeniata* and *M. striata*) (Table 1, see Appendix for further detail). We selected *Eumeces latiscutatus* of the subfamily Scincinae, a possible closest relative of Lygosominae (Greer, 1970a), as an outgroup for which tissues were available to us.

Small amounts of livers, removed from anesthetized or dead specimens and stocked at  $-80^{\circ}$ C, were homogenized in extraction buffer [150 mM NaCl, 10 mM Tris-HCl (pH 8.0), 10 mM EDTA, 1% sodium dodecyl sulfate]. After digesting samples with Proteinase K (100 µg/ml) at 50°C for three hours, DNA was extracted with phenol (three times) and 25:24:1 of phenol/chloroform/isoamyl-alcohol (once), and was precipitated in ethanol with one-tenth volume of 3.0 M sodium acetate (pH 5.2). Samples resuspended in TE buffer were

further purified by RNase digestion (20  $\mu$ g/ml) at 37°C for one hour, followed by ethanol precipitation. DNA amplification and sequencing are described in detail elsewhere (Honda *et al.*, 1999). A part of mitochondrial 12S and 16S rRNA genes was amplified by the polymerase chain reaction (PCR) using primer L1091 (5'-AAACTGGGAT-TAGATACCCCACTAT-3') and H1478 (5'-GAGGGTGACGGGC-GGTGTGT-3'), and L2606 (5'-CTGACCGTGCAAAGGTAGCGTAA-TCACT-3') and H3056 (5'-CTCCGGTCTGAACTCAGATCACGTAGG-3'), respectively (Kocher *et al.*, 1989; Hedges *et al.*, 1993). The numbering system followed that for the human sequence (Anderson *et al.*, 1981).

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. The degree of supports for internal branches of each tree was 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). In this analysis, each nucleotide base was regarded as a character and four kinds of salt as different character states. 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, 157 of which were variable. In the 16S rRNA fragment, there were 436 total aligned sites, 144 of which were variable. Intergeneric nucleotide replacements between five lygosomine genera varied from 70 base pairs (bp) (Apterygodon vittatus vs Dasia gricea) to 152 bp (Lamprolepis smaragdina vs Mabuya longicaudata). Nucleotide replacements between congeneric species of Dasia and Mabuya were observed in 73 and 74 bp (D. grecea vs D. olivacea from Borneo and Malay Peninsula, respectively), and from 82 bp (M. multifasciata vs M. rudis) to 121 bp (M. longicaudata vs M. quiquetaeniata or M. striata), respectively. Intraspecific nucleotide replacements of D. olivacea involved 18 bp (Malay Peninsula vs Borneo), whereas there were no replacements between two samples of *L. smaragdina* (Guam vs Saipan).

The NJ dendrogram derived from mitochondrial DNA distance matrix (not given) is shown in Fig. 2A. The ingroup portion of this dendrogram was divided into two major clusters, of which one, consisting of *Lamprolepis* and *Lygosoma*, was completely supported in bootstrap iterations (100%). The other

**Table 1**. Distribution of the genera of the *Mabuya* group. Asterisk (\*) indicates taxonomic and/or geographic groups studied in the present analysis. (a) including western Oceanian islands; (b) including Madagascar; (c) including West Indies Islands. See Appendix for detailed localities.

Genus	South Asia	Southeast Asia	Africa	South America
Apterygodon		+*		
Dasia	+	+*		
Lamprolepis		+ <sup>*, a</sup>		
Lygosoma		+*		
Mabuya	+	+*	+ <sup>*, b</sup>	+ <sup>c</sup>

#### Phylogeny of the Mabuya Group

								150
Lumeces latiscutatus	GCTCAGCCATAAACTATGGTAGTACAATCACAAC	ACTACCCGCCAGAGAACTAC/	AAGIGAAAAACIIAAAA	CICCAAGGACIIGGCG	GIGCICCACAICAACCI.	AGAGGAGCCIGICCIAIAAIC	GATAATCCACGTTCCACCCTA	CCAC
Apterygouon vittatus		CT	AG		тсс	••••••	СС	····¦
D olivaçea (Malay Pen.)	TC C T ATACAC - G AT C	с стт	۸۵		тсс.	• • • • • • • • • • • • • • • • • • • •		••••
D. olivacea (Malay Fell.)	T C T ATAAAC $- G$ AT	C GTT	A0		тсс	••••••	С САА ТС	
Lamprolepis smaragdina	C. A T ATA. AC. AC. AT T	GT. GT	G C	Т	A. C C. G		CC	
l vaosoma bowringii	. CT. A. C ATA. AC C CC G. T	G GT	G. AC GT	A T	A. C. A TC. G		CC.AC.	
Mabuva longicaudata					TGC		CCAAT	T
M. multifasciata		GGT					CCATG.	T
M. quinquetaeniata		GT	AG	A			C	G.
M. rudis	TGC. TATACC. ATCATT	GGC	C	T			CAAT	Т
M. striata		T	AG	т			CTTTC.	Т
	151							300
Eumeces latiscutatus	CTTTCGCCCTCAGCCTATATACCGCCGTCGTA	AGCCTACCTTCTGAAAGAA-	GIACAGIAAGCAAAACA	GITAT-TAACTAGCAC	GICAGGICAAGGIGIAG	CACA I GAGG I GGAAGAGA I GG	GCTACATTITCTGCCACAGAA	AA-C
Apterygodon vittatus	II.A.CC	CG	AC. A. A G	AA		A. AA	AA.C	!
Dasia gricea	II. IA. CC	·····G······	. C. A. A G		• • • • • • • • • • • • • • • • • • • •		· · · · · · · · · · · · · · · · · · ·	C. I .
D. olivacea (Ivialay Pen.)	101A.C	····I·······	A A. A		• • • • • • • • • • • • • • • • • • • •	A.A	A. [	
D. olivacea (Borneo)	1I.A.C		AA. A. A		•••••	A.A	A. CT	
Lamprolepis smaragolna	CA T A AT		. C. A G I I .	A.CAI			AA	
Lygosoma bowningii Mahuwa langiaaudata	Т. Т. АААС	AIG	A A	A.CAI	•••••		AAGC	
M multifacciata	Т. Т. ААС		AA.AG	TC A		A. AA	۸ TT	ı
M. mulliasciala	CC A C C	A	TC A G	A C AA	•••••	т. с. с	с с л	ст
M. quinquetaernata M. rudie	т т атс с	Δ	AC A G			ΔΔΔ Τ	Δ ΤΟΤ	CT
M etriata		Δ	TC A G T	C 44		ΤΔ ΔΔ	C AT T	C. T
W. Strata	100.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1		10.7					
	301				*			450
Eumocos latiscutatus		GATTTAGCAGTAAGACAAGC	AAGAAACCCTGTCTTAA		GOTGTOTTGTAAATAGA	GACCAGTATGAACGGCTAAAT	GAGGACAAACCTGTCTCTTGC	.700.
Antervoodon vittatus			G C	CTA	C A	T	G	G. T
Dasia gricea		Δ Τ Δ	ττ Δ Δ	ΓΔ	с A	т	G AT	G
D olivaçea (Malay Pen.)	T AGC G C GCC TG	Δ	ΔΤ C	с	C A		Δ Δ	G.T.
D. olivacea (Borneo)	T AGC G C GCC TG	Δ	ΔΤ C	с	С. А		ΑΑ	G. TT
Lamprolenis smaraddina		T GA GA	Τ ΔC	Δ G T	с A	т	Δ	
Lamprolepis smaragama	G AC TACGT C	Τ GΔ	Τ Δ Δ	GT AGT	C A	т.	C	G
Mabuva longicaudata	AC C CCGT TTG	Т. А. А.	CTIGIT	C			T.	T
M multifasciata	T. AC. TACGT. A.G. T.		A TGTT A	С. Т	A.	T	AA	G T
M. quinquetaeniata			GTTCG	С. Т	G		A1	T
M. rudis	AG CATAC. G C. GTA. A. G T.		GTT	C	A.		A	т
M. striata			ATT. AC G	т	A.	T	TTA.	T
	451							600
Eumeces latiscutatus	451 AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAG	AAGACCCTGTGGAGCTT	AAAACAAGCTACTATO	CACCACACAAGCT-GCA	ACTAGTAAGTAGTTTTAAGTT	GGGGCGACTTCGGAACCAAAA	600 AAAA
Eumeces latiscutatus Apterygodon vittatus	451 AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAG	GAAGACCCTGTGGAGCTT	AAAACAAGCTACTATO	CACCACACAAGCT-GCA	ACTAGTAAGTAGTTTTAAGTT	GGGGCGACTTCGGAACCAAAA	600 AAAA 'G
Eumeces latiscutatus Apterygodon vittatus Dasia gricea	451 AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG TTAGT. AAT.	GAATAACCCCATAAGACGAG CT.A	AAGACCCTGTGGAGCTT	AAAACAAGCTACTATO	CACCACACAAGCT-GCA AC.ATAAC	ACTAGTAAGTAGTTTTAAGTT GTAATC .GTGCAAT	GGGGCGACTTCGGAACCAAAA	600 AAAA :G
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.)	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG TT. A. GT. 	GAATAACCCCATAAGACGAG CT.A .GG.A AT.T	AAGACCCTGTGGAGCTT	AAAACAAGCTACTATG A.CAC A.CCA	CACCACACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT GTAATC .GTGCAAT .GCAAT	GGGGCGACTTCGGAACCAAAA	600 AAAA 
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo)	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG 	GAATAACCCCATAAGACGAG CT. A. .GG. A. AT. T. AGT.	SAAGACCCTGTGGAGCTT	AAAACAAGCTACTATG A.CAC A.CCA A.CCA A.CCA	CACCACACAAGCT-GCA AC.ATA	ACTAGTAAGTAGTTTTAAGTT GTAATC GTGCAAT GCAAT GTAAT	GGGGCGACTTCGGAACCAAAA A. GC A. C	600 AAAA G
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG 	GAATAACCCCATAAGACGAG C.A	SAAGACCCTGTGGAGCTT	AAAACAAGCTACTATC A.CAC A.CCA A.CCA A.CCA TT.A.CAC	CACCACACAAGCT-GCA AC.ATA	ACTAGTAAGTAGTTTTAAGTT GTGCAAT.C GTGCAAT GCAAT. GTAAT. CGGCAG.	GGGGCGACTTCGGAACCAAAA A. GC A. C A. C A. C A. C	600 VAAAA 2G 
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG 	GAATAACCCCATAAGACGAG CT.A. .GG.A. AT.T. AGT. .G.T.A.T. 	AAGACCCTGTGGAGCTT	AAAACAAGCTACTATG A.CAC A.CCA A.CCA A.CCA TT.A.CAC CC.AT	CACCACACAAGCT-GCA AC.ATA	ACTAGTAAGTAGTTTTAAGTT GT. GCAAT. G. CAAT. G. TAAT. G. TAAT. C. GGCA. G. C. TAA.	GGGGCGACTTCGGAACCAAAA 	600 VAAAA CG
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG TA.GT. A.AT. T.A.A.T. T.A.A.T. T.A.A.T. T.A.G.T. A.A.T.	GAATAACCCCATAAGACGAG CT. A. .GG. A. AT. T. AGT. A. T. .G. T. A. T. GTG.	SAAGACCCTGTGGAGCTT	AAAACAAGCTACTATG A.CC/ A.CC/ A.CC/ A.CC/ TT.A.CAC CC.AT G.TCGAT	САССАСАСААGCT-GCA .AC. ATAAC .C A	ACTAGTAAGTAGTTTTAAGTT GTAATC GGCAAT GTAAT CGGCAG CGCAG CGCAG CGCAG	GGGGCGACTTCGGAACCAAAA A. GC A. C A. C A. C A. C A. C A. C A. C A.	600 VAAAA XG XG XG XG XG
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. mulifasciata	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG 	GAATAACCCCATAAGACGAG CT.A AT.T. AGT.T. G. T.A.T G. T.A.T GTG. T.TITGA T. T.T.A	BAAGACCCTGTGGAGCTT	AAAACAAGCTACTATC 	CACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGT GTAAT. C. GTAAT. C. G. CAAT. G. CAAT. C. GGCA. C. GCA. C. TAA. 	GGGGCGACTTCGGAACCAAA A. C A C A C A C A C A C A C A C A C	600 AAAA CG C.C.C C.C.C
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. quinquetaeniata	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG 	GAATAACCCCATAAGACGAG CT.A	BAAGACCCTGTGGAGCTT	AAAACAAGCTACTATC A.CAC A.CC/ A.CC/ TT.A.CAC CC.AT G.TCG.AT A.CCC	САССАСАААВСТ-GCA AC. ATA	ACTAGTAAGTAGTTTTTAAGTT GTCAAT GCAAT GTAAT CGGCAG CGCACAA CGTAA CGTACT CG.GTACTG	GGGGCGACTTCGGAACCAAAA 	600 AAAAA XG X.C.C X.C.C X.G.L
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringli Mabuya longicaudata M. multifasciata M. quinquetaeniata M. rudis	451 AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG 	GAATAACCCCATAAGACGAG CT.A	BAAGACCCTGTGGAGCTT	AAAACAAGCTACTATC A.CCA A.CCA A.CCA A.CCA C.AT G.TCGAI A.CCA C.AT A.CCA A.CCA A.CCA	САССАСАСААGСТ-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT GTAATC GCAAT GTAAT CGGCAG CTAA G.TAC CGTACTG TTCTC.G	GGGGCGACTTCGGAACCAAAA A. G A. C A. C A. C A. C A. C A. C A. C A. C	600 VAAAA XG X.C.C X.C.C X.C.
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. multifasciata M. rudis M. striata	451 AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG 	GAATAACCCCATAAGACGAC CT.A. GG.A. AT.T. AGT.A. G.T.A.T.  G.T.A.T.  T.TITGA. .T. TITGA. .T. T.T.A. .G. C.A.A. .T. AGA.	BAAGACCCTGTGGAGCTT	AAAACAAGCTACTATG 	CACCACCAAGACT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGT GCAAT GCAAT CGGCAG. CTAA 	GGGGCGACTTCGGAACCAAAA AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC	600 VAAAA CG C.C.C C C.C.
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Malay Pen.) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. mulitiasciata M. mulitiasciata M. quinquetaeniata M. rudis M. striata	451 AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG TT.A.GT. A.A.T. TT.A.A.T. T.A.A.T. T.A.A.T. T.A.A.T. T.A.A.T. A.A.T. A.A.T. A.A.T. A.A.T. A.A.T. A.A.T. A.A.T.	GAATAACCCCATAAGACGAC CT.A	BAAGACCCTGTGGAGCTT	AAAACAAGCTACTATG 	САССАССАСААGСТ-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA A C A C A C A C A C A C A C A C A C TAC GTA C	600 AAAAA G 2. C. C 2. C. C 2. C. C 3. C. C
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. quinquetaeniata M. quinquetaeniata M. quinguest M. striata	451     AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A GG.A AT.T GG.T.A.T .GTG. .T. ITTGA .G.C.A.A .TA.A .T. AGA	BAAGACCCTGTGGAGCTT	AAAACAAGCTACTATG 	CACCACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA 	600 AAAAA CG C.C.C C.C. C.C. C.C. C.C. C
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. multifasciata M. rudis M. striata	451       AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A. C.A. G. G.A. G. T.A.T. GG. .T. ATTGA. .T. TTGA. .T. TTGA. .T. AGA. .T. AGA. T. AGA.	AAGACCCTGTGGAGCTT	AAAACAAGCTACTATT A. C A. C C( A. C C( T T. A. C C( T T. A. C A( C C. AT G. T. CG A1 A. C CA A. C A( T. GA. A AC AACAACTGATCAACGAA	CACCACCACAAGCT-GCA AC.ATA AC AC.ATA CC GC.TATGCCAT ACA.A.TCCTACAAAC A.CCAA ACA A.CCAA CAT.AG A.C TT AC A.AC.TT AC A.ACTT AC A.AC AC ACACAAGTTACCCCAGGG	ACTAGTAAGTAGTTTTAAGT 	GGGGCGACTTCGGAACCAAAA A. G A. G A. C A. C A. C A. C A. C A. C A. C A. C	600 AAAAA CG C.C.C C.C. C.C. C.C. C.C. C
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Malay Pen.) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. muitiasciata M. muitiasciata M. nutis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea	451       AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATG A.CCC A.CCC A.CCC C.ACA.CCC CC.ATA.CCC C.ATA.CCC A.CCC A.CCA A.CCA C.ACAC T.GA.AAC	CACCACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGT GTAAT. C. GTAAT. C. G. CAAT. G. CAAT. G. CAAT. G. TAAT. C. GCA. G. C. TAA. C. GTACT. C. GTACT. C. G. GTACT. C. G. GTACT. C. G. GTACT. MICL. GTA. TA. G. CAC T. C. G. GTACT. T. C. G. GTACT. T. C. G. GTACT. T. C. G. GTACT. T. C. G. GTACT. T. C. G. GTACT. T. T. T. T. T. T. T.	GGGGCGACTTCGGAACCAAAA A	600 AAAAA CG 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. quinquetaeniata M. quinquetaeniata M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivgoca (Malay Pen.)	451     AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATG       A. C	CACCACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA 	600 AAAAA CG 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. multifasciata M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Boango) D. olivacea (Boango)	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A. C.A. G. G.A. G. T.A. G. T.A. G. T.A. G. T.A. 	XAAGACCCTGTGGAGCTT 	AAAACAAGCTACTATT A. C A. C	CACCACCAAGAGCT-GCA AC.ATA	ACTAGTAAGTAGTTTTAAGT 	GGGGCGACTTCGGAACCAAAA 	600 AAAAA 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Malay Pen.) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. mutitasciata M. mutitasciata M. nutitasciata M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Bomeo) Lamprolepis emaradrina	451     AATCAGTGAAACTGATCTCCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A	CCAAAAACGACCCAGT	AAAACAAGCTACTATG A.CCC A.CCC A.CCC A.CCC GA.CCC GA.CCC A.CCC A.CCC A.CCC A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA A.CCA CA. CA. CA. CA. CCA CA. CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CA. CCA CCA CA. CCA CCA CCA CCA CCA CCA CCA CCA CCA CCA CCA CCA CA. CCA CCA CCA CCA CCA CCA CCA CCA CCA CA. CCA CA. CCA CA. CCA 	CACCACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGT GTAAT. C. GTAAT. C. G. CAAT. G. CAAT. G. CAAT. G. TAAT. C. GGCA. G. C. TAA. C. GTACT. C. GTACT. C. G. GTACT. C. G. GTACT. MICT. C. G. GTA. TA. G. MICT. C. G. MICT. C. G. TCT. C. G. TCT. C. G. T. T. T. T. T. T. T. T. T.	GGGGCGACTTCGGAACCAAAA A	600 AAAAA CG C.C.C C.C.C C.C. C.C. C.C.
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. nutlifasci	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATG	CACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA 	600 AAAAA CG C.C.C C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C. C.C.
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nudis M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mahuwa homicaudata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC     CT.A.     G.G.G.A.     AT.T.     AG.T.T.     G.T.A.T.    G.G.A.    G.TA.T.    G.C.A.A.    T.TAGA.    T.AGA.    T.AGA.    T.AGA.    T.AGA.	XAAGACCCTGTGGAGCTT 	AAAACAAGCTACTATT A.CA.CCC A.CCC TT.A.CCC TT.A.CCC TT.A.CCA CCAT G.T.CGAT A.CCA A.CCA T.GA.AAC AACACTGATCAACGA C.G.C.AA C.G.C.AA CT.G.C.AA CT.G.C.A T.GC.C.A T.G.C.C.AC CT.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.A T.G.C.C.C.A T.G.C.C.C.A T.G.C.C.C.A T.G.C.C.C.A T.G.C.C.C.A T.G.C.C.C.C.C.C.C.C.C.C.C.C.C.C.C.C.C.C.	CACCACCAAGACT-GCA AC. ATAAC I.C AC I.G TA. TGCAT I.G TA. TGCAT ACA A CCTACAAAC 	ACTAGTAAGTAGTTTTAAGT 	GGGGCGACTTCGGAACCAAAA 	600 CG C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C C
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Malay Pen.) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. rudis M. rudis M. rudis M. striata Eumeces latiscutatus Apterygodon vitatus Dasia gricea D. olivacea (Bomeo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A	CCAAAAACGACCCAGT	AAAACAAGCTACTATA 	CACCACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGT GTAAT. C. GTAAT. C. G. CAAT. G. CAAT. G. CAAT. G. TAAT. C. GGCA. G. C. TAA. C. GTACT. C. GTACT. C. GTACT. C. GTACT. C. GTACT. TTCT. C. G. GTA. TA. T. T. T. T. T. T. T. T. T. T	GGGGCGACTTCGGAACCAAAA A	6000 MAAAA SG 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. quinquetaeniata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC    CT.A	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATG       A. C	CACCACAAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA A	6000 MAAAA 3G 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. nudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. quinquetaeniata M. rudis	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC     CT.A.     G.G.G.A.     AT.T.     AGG.T.T.     G.T.A.T.    G.G.A.    G.TA.T.    G.C.A.A.    T.AGA.    T.AGA.    T.AGA.    T.AGA.    T.AGA.     G.C.A.A.    T.AGA.    T.AGA.     G.C.C.A.A.    T.AGA.    T.AGA.     G.C.CA.A.     GC.A.A.    T.AGA.    T.AGA.     G.C.C.C.A.A.    T.AGA.     G.C.C.C.A.A.     G.C.C.C.A.A.     G.C.C.C.A.A.     G.C.C.C.A.A.     G.C.C.C.A.A.     G.C.C.C.A.A.     G.C.C.C.A.A.     G.C.T.C.A.A.     G.TC.A.A.     G.CC.A.A.     G.CCA.A.     G.CCA.A.	аладассстатадаастт 	AAAACAAGCTACTATT A. C	CACCACCAAGACT-GCA AC. ATAAC I.C AC IGC TA. TGCAT ACA A. TCCTACAAAC A CCCTACAAAC A CCCTACAAAC 	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA 	6000 MAAAA 2G 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. rudis M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multi'asciata M. guinquetaeniata M. guinquetaeniata M. striata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A. GG.A. AT.T. AGT.T. 	аладассстатадаастт сс	AAAACAAGCTACTATC A.CCA A.CCA A.CCA A.CCA G. TCGAI G. TCGAI A.CCC A.CCC A.CCA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CAA CCAA CC	CACCACCAAGAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGT GTAAT. C. GTAAT. C. G. CAAT. G. CAAT. G. TAAT. C. GGCA. C. C. GCA. C. C. GTACT. C. GTACT. C. GTACT. C. GTACT. C. GTACT. C. GTACT. T. T. T. T. T. T. T. T. T.	GGGGCGACTTCGGAACCAAAA 	6000 MAAAA SG 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringi Mabuya longicaudata M. multifasciata M. quinquetaeniata M. rudis M. striata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC     CT. A.     G G. A.     A T. T.     AG T. A. T.	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATG     A. C	CACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA A	6000 MAAAA 3G 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nudis M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. quinquetaeniata M. rudis M. striata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC     CT.A.     G.G.G.A.     AT.T.     AGG.T.     C.T.A.T.     G.T.A.T.     G.T.A.T.    GCA.A.     T.TTTGA.    T.AGA.     T.A.T.     G.C.A.A.     T.A.AA.     T.A.AA.     T.A.GA.     G.C.A.A.     A.A.     T.A.GA.     G.C.C.     G.C.C.     G.C.     G.T.     C.C.     GC.     G.T.	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATT A. C A. C AC A. C	CACCACAAGCT_GCA AC. ATAAC AC. ATAC GC. TA. TGC AT ACA A. TCCTACAAAC A. C AC CAT. AG A. C TT AC A. C TT AG A. A. C. CTGT A. C ATGC ACCAAGTTACCCCAGGG	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA 	6000 MAAAA G S C.C. S.C. S.C. S.C. S.C. S.C.
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Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. nutlifasciata M. quinquetaeniata M. rudis M. striata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC     CT. A.     G C. A.     AG T. T.     AG T. A. T.	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATG A.CAC A.CCC A.CCC A.CCC C.AT A.CCC A.CCC A.CCA A.CC.AC A.CCA A.CCA A.CAA AC C.AA AC C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.C.G.C.AA C.T.G.C.AA C.T.C.C.AA C.T.C.C.AA C.T.C.AA C.AA C.AA C.AA C.G.C.AA C.AA C.G.C.AA C.AA C.AA C.AA C.G.C.AA C.AA C.AA C.AA C.G.C.AA C.AA C.AA C.G.C.AA C.AA C.AA C.G.C.AA C.AA C.AA C.AA C.G.C.AA C.AA 	CACCACAAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC AC C CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC CC	6000 MAAAA 3G 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nudis M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. guinguetaeniata M. rudis M. striata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC     CT.A.     G.G.G.A.     AT.T.     AGG.T.A.     C.T.A.     G.T.A.T.    G.G.A.     T.T.TTGA.    T.T.A.     G.C.A.A.    T.AGA.    T.AGA.    T.AGA.     SACCAACAAGTCAAAG-C(G.TCA     GC.A.A.    T.AGA.     G.C.C.C.     G.C.C.     G.C.C.     G.T.C.     G.T.C.     G.T.C.     G.T.C.     G.T.     G.T. </td <td>AAGACCCTGTGGAGCTT </td> <td>AAAACAAGCTACTATT A. C A. C (C  A. C (C T T. A. C (A T T. A. C (A C C AT</td> <td>CACCACAAGCT_GCA AC. ATAAC I.C A C I.G TA. TGC AT ACA A. TCCTACAAAC  A C AA ACA A. C AC . CAT. AG A. C </td> <td>ACTAGTAAGTAGTTTTAAGTT </td> <td>GGGGCGACTTCGGAACCAAAA , A., G , A., C , C., C., C., C., C., C., C., C., C.,</td> <td>6000 MAAAA 2G 2 2 2 2 2 2</td>	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATT A. C A. C (C A. C (C T T. A. C (A T T. A. C (A C C AT	CACCACAAGCT_GCA AC. ATAAC I.C A C I.G TA. TGC AT ACA A. TCCTACAAAC A C AA ACA A. C AC . CAT. AG A. C 	ACTAGTAAGTAGTTTTAAGTT 	GGGGCGACTTCGGAACCAAAA , A., G , A., C , C., C., C., C., C., C., C., C., C.,	6000 MAAAA 2G 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. rudis M. rudis M. striata Eumeces latiscutatus Apterygodon vitatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. multifasciata M. guinquetaeniata M. rudis M. striata	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A. GG.A. AT.T. AGT.T. GG. 	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATE A.CAC A.CCC A.CCC A.CCC A.CCC G.TCGAT A.CCA A.CCC A.CCC A.CCA T.GA.AAC -AACACTGATCAACGA. CG.CAA CC.G.C.AA CC.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.G.C.AA C.T C.T C.T C.T C.T ACAGT 	CACCACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT GTAAT GTGCAAT GCAAT GTAAT CGGCAG CGTAC CGTACTG GTA.T.AG GTA.TAG GTA.TAG TT T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T T	GGGGCGACTTCGGAACCAAAA 	600 MAAAA 30 2 2 2 2 2 2 2
Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. nutlifasciata M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Borneo) Lamprolepis smaragdina Lygosoma bowringii Mabuya longicaudata M. nutlifasciata M. nutlifasciata M. quinquetaeniata M. nutlifasciata M. quinquetaeniata M. nutlifasciata M. quinquetaeniata M. rudis M. striata Eumeces latiscutatus Apterygodon vittatus Dasia gricea D. olivacea (Malay Pen.) D. olivacea (Malay Pen.) D. olivacea (Malay Pen.)	451     AATCAGTGAAACTGATCTCCCGGTCCAAAAGCCG	GAATAACCCCATAAGACGAC CT.A	AAGACCCTGTGGAGCTT 	AAAACAAGCTACTATG A.CAC A.CCA C.AC C.AC C.AT C.AC C.AT C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.C.AC C.C.AC C.G.C.AC C.G.C.AC C.AC C.G.C.AC C.AC C.AC C.AC C.AC C.C.AC C.C.C.AC C.G.C.AC C.C.C.C.C.C.C C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.C.AC C.AC C.C.C.AC C.C.C.C.C.C C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC C.AC 	CACCACAAGCT-GCA AC. ATA	ACTAGTAAGTAGTTTTAAGTT 	GGGGGGACTTCGGAACCAAAA AC AC AC AC AC AC AC AC AC AC C GTAC GTAC C C.C. C.C. C.C. C.C. C.C. C.C.	6000
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Fig. 1. Aligned sequences of a 825 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.

major cluster, supported in 94% of bootstrap iterations, contained *Apterygodon*, *Dasia* and *Mabuya*. The latter cluster was further split into two subclusters consisting of African *Mabuya* (99%), and Asian *Mabuya*, *Apterygodon* and *Dasia* (71%), respectively. Within the latter, *Apterygodon* and *Dasia* (86%), and three Asian *Mabuya* examined (93%) constituted lower subclusters. Conspecific samples exclusively constituted lowest clusters in all iterations (100%).

Resultant cladogram of MP (Fig. 2B) showed no substantial inconsistency with the NJ dendrogram in terms of branching topology, although *Apterygodon*, *Dasia* and the Asian members of *Mabuya* did not constituted an exclusive cluster.



**Fig. 2.** (A) Neighbor-joining (NJ) dendrogram derived 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. "Asia" includes the western Oceanian islands. (B) Maximum parsimony (MP) cladogram using heuristic bootstrapping analysis (691 steps, 211 bp informative under the condition of parsimony, consistency index=0.56). Branches without BP values were not supported in  $\geq$ 50% of the replicates.

#### DISCUSSION

On the basis of differences in skull and external morphology, Greer (1970b) thought that Apterygodon and Dasia (sensu stricto) are monophyletic among the three arboreal genera formally assigned to Dasia (sensu lato), whereas Lamprolepis emerged independently from the Asian Mabuya-like stock. Later, he emphasized this view by arguing that the Apterygodon-Dasia lineage, Lamprolepis, and the terrestrial/ semi-fossorial Lygosoma constitute the three distinct phylogenetic lines independently derived from the Asian Mabuyalike stock (Greer, 1977). Karyological data (Ota et al., 1996) also offered a circumstantial support to Greer's (1977) view by indicating closer chromosomal similarities of the three arboreal genera with Asian species of Mabuya than with African congeners or other lygosomine groups. However, phylogenetic relationships inferred from DNA sequences in the present study do not support Greer's (1977) view with respect to the independent origins of Lamprolepis and Lygosoma, because these two genera exclusively constituted a cluster. Moreover, our results strongly suggest that the collective divergence of these two genera have occurred prior to the separation between the African Mabuya and the Asian *Mabuya–Apterygodon–Dasia* clade. These may contradict with Greer's (1977) view, which seemingly assumed that *Lamprolepis* and *Lygosoma* have derived from the *Mabuya*-like stock within Asia.

Based on the morphological character, Greer (1976, 1977) assumed that the African endemic genera of the *Mabuya* group and African species of *Mabuya* were derived from the *Mabuya*-like stock through *in situ* continental radiation rather than from multiple colonizations from outside. Relationships depicted in Fig. 2A and 2B do not contradict with the postulated monophyly of African members of the *Mabuya* group, although the number and size of samples examined are too small to draw any definite conclusion by this result alone.

Considering our results, the Asian and African members of the *Mabuya* group are likely to constitute two major evolutionary lineages, which may be referred to as the *Lygosoma* and *Mabuya* subgroups. Ecological similarity, involving morphological specialization to arboreal habits (e.g., Greer, 1970b), between the *Apterygodon–Dasia* clade of the *Mabuya* subgroup and *Lamprolepis* of the *Lygosoma* subgroup thus seem to be attributable to the convergence rather than to the recent common ancestry. Morphological and karyological similarities among the *Apterygodon–Dasia* clade, *Lamprolepis*, *Lygosoma* and Asian species of *Mabuya* (Greer, 1970b, Ota *et al.*, 1996) are supposed to be symplesiomorphy, although a few species of *Lygosoma* seems to have differentiated karyotypes (de Smet, 1981).

Greer (1970b, 1977) thought that *Apterygodon* and *Dasia* sensu stricto are monophyletic, constituting one of the distinct phylogenetic lineages derived from the Asian *Mabuya*like stock. This view was confirmed by the present results. *Apterygodon* differs from *Dasia* and *Mabuya* in having an ectopterygoid process and a karyotype of 2N=28 format, and in lacking pterygoid teeth: both of the latter have basically 2N=32 format karyotypes and pterygoid teeth, and lack the ectopterygoid process (Greer, 1970b; Ota *et al.*, 1996). Relationships illustrated by our analysis also favor views of the previous authors that those character states unique to *Apterygodon* have evolved from states of corresponding characters in *Dasia* (Greer, 1970b; Ota *et al.*, 1996).

The nucleotide replacements between species of *Mabuya* were larger than those between some combinations of different genera. Moreover, Asian *Mabuya* were not exclusively clustered with African congeners in NJ analysis (Fig. 2A), although this relationship was not support in enough bootstrap proportion in MP analysis (Fig. 2B). These suggest the genetic heterogeneity and the non-monophyly of the genus. Further analysis for more species of *Mabuya*, including those from Madagascar and South America, are strongly desired to revise its systematics.

Recently *Vietnascinsus* was described from Vietnam as another genus of arboreal skinks monotypic with *V. rugosus* (Darevsky and Orlov, 1994). We have had no chance to directly examine this skink, but judging from the original description, it may be closest to *Lamprolepis* because both genera share a medial separation of palatal rami of pterygoids (Greer, 1970b; Darevsky and Orlov, 1994). We thus suspect that *Vietnascinsus* belongs to the *Lygosoma* subgroup of the *Mabuya* group. This view definitely needs further verifications.

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Appendix. Localities and catalogue numbers of specimens examined in this study. These specimens were deposited in the herpetological collection of the Department of Zoology, Kyoto University (KUZ). *Apterygodon vittatus*: Matang, Borneo, KUZ 27168. *Dasia gricea*: Gombak, Peninsular Malaysia, 22014. *D. olivacea*: Kaki Bukit, Peninsular Malaysia, 22142; Matang, Borneo, 27228. *Lamprolepis smaragdina*: Guam, Mariana Islands, 27775; Saipan, Mariana Islands, 35004. *Lygosoma bowringii*: Khao Chong, Thailand, 37884. *Mabuya longicaudata*: Lanyu, Taiwan, 35015. *M. multifasciata*: Mae Hon Son, Thailand, 32896. *M. quiquetaeniata*: Africa (detailed localities unknown), 45890. *M. rudis*: Dumoga-Bone, Sulawesi, 18572. *M. striata*: Kasenga, Zambia, 38944. *Eumeces latiscutatus*: Kyoto City, Japan, 46592.