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Vedda rock art at Hulanuge
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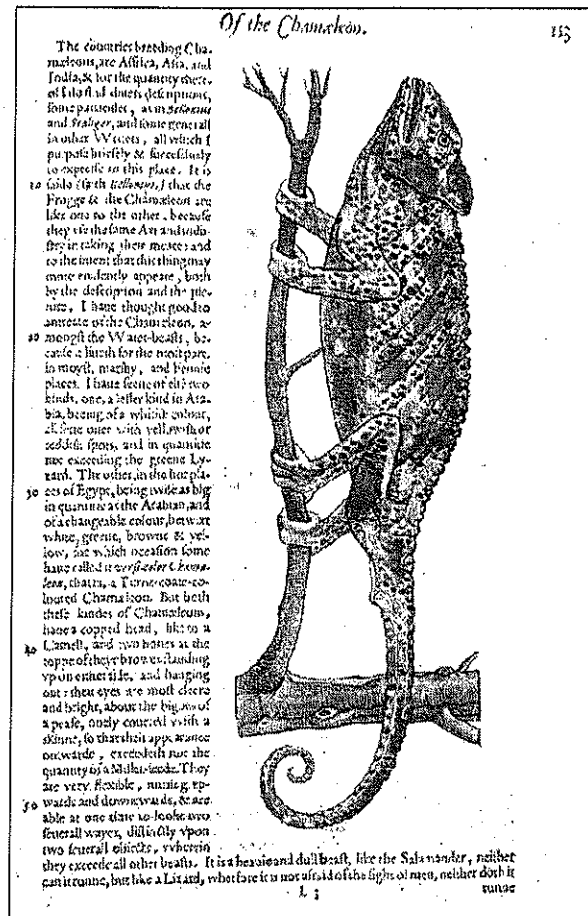
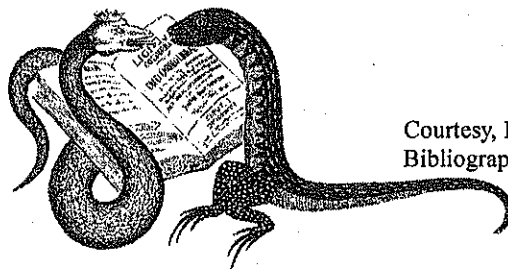


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HIGHER-LEVEL MOLECULAR PHYLOGENETIC RELATIONSHIPS OF THE ENDEMIC GENUS *LANKASCINCUS* FROM SRI LANKA BASED ON NUCLEAR DNA SEQUENCES

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Abstract

The island of Sri Lanka, located off the tip of the Indian peninsula, has an amazingly diverse and highly endemic herpetofaunal assemblage despite its close proximity to the mainland. *Lankascincus*, a scincid genus endemic to the island of Sri Lanka, is one of the most common skinks found on the island. Nonetheless, many aspects of its biology and systematics are poorly understood. *Lankascincus* is a lygosomine scincid but it has an uncertain phylogenetic affinity within this major lineage of skinks. It is unclear if *Lankascincus* belongs within the *Sphenomorphus*-group or *Eugongylus*-group, two of four major lineages of lygosomines. We take a molecular DNA sequence approach to resolve the placement of *Lankascincus* within the larger lygosomine radiation. We find that *Lankascincus* represents an independent lineage separate from the *Eugongylus*-, *Mabuya*-, *Egernia*-, or *Sphenomorphus*-groups.

Introduction

The genus *Lankascincus* was recently described by Greer (1991), for six species of scincid lizards (*deignanai*, *deraniyagalae*, *gansi*, *fallax*, *taprobanensis*, and *taylori*) that are endemic to Sri Lanka (Plate 1, Figs. 1,2,3,4 & 5). The relationship of *Lankascincus* to other members of the lygosomine subfamily of skinks, however, remains unclear. Before 1991, the three previously described species

were placed in the catch-all genus *Sphenomorphus*, and assumed to belong to the larger *Sphenomorphus*-group of lygosomine skinks. When Greer (1991) placed these three species along with three newly described species into the genus *Lankascincus*, he suggested that *Lankascincus* was actually more closely allied to the *Eugongylus*-group of lygosomine lizards. This assessment was based on the fact that *Lankascincus* possesses

three of the *Eugongylus*-group characters (dorsal surface of digits primarily covered with a single row of scales, premaxillary teeth $e'' 11$, and the inner preanals are overlapped by the outer preanals) and none of the *Sphenomorphus*-group characters. In addition, *Lankascincus* possesses a colored iris representing a fourth *Eugongylus*-group character (CCA personal observation, Greer, 1989).

Lankascincus is arguably the most abundant scincid lizards found in Sri Lanka. Members of the genus range throughout the entire island from such diverse habitats as humid rainforest, arid scrubforest, vicinity of human settlements, and moist montane forests (up to at least 1700m). Despite the broad range and abundance of this group of skinks, there is virtually no information available on the ecology, life-history, or systematics of this group.

Here we introduce DNA sequence data from the nuclear genome for the *c-mos* gene to provide phylogenetic evidence for the higher order relationships of the genus *Lankascincus*. Understanding where *Lankascincus* fits into the larger lygosomine radiation will allow researchers to better assess the biogeography and systematics of the diverse Asian and Pacific lygosomine scincid radiation.

Materials and Methods

Specimens—DNA sequences for the *c-mos* locus were aligned from three species of *Lankascincus*, five *Mabuya*-

group species representing three genera, five *Eugongylus*-group species representing four genera, three *Egernia*-group species representing three genera, and eight *Sphenomorphus*-group species, representing five different genera. In addition, four different outgroup species were used representing four different families (Table 1). For specimens used in this study, muscle and liver tissue samples were dissected from freshly sacrificed specimens, and stored either at -80°C , or in 70% Ethanol. All specimens included in the phylogenetic analyses are listed in Table 1.

DNA Isolation, Amplification, and Sequencing—For new samples (see Table 1) DNA was isolated from either muscle or liver tissues following the protocols of Hillis *et al.* (1990). Tissues (~100 - 200 mg) were digested with proteinase K for three hours.

Polymerase chain reaction (PCR) was used to amplify a three hundred and fifty seven base-pair region of the nuclear *c-mos* gene (Saint *et al.*, 1998). The primers used were: forward SAM(G73) 5'GCG GTA AAG CAG GTG AAG AAA3' and reverse SAM(G74) 5'TGA GCA TCC AAA GTC TCC AAT C3' (Saint *et al.*, 1998).

The protocols of Hillis *et al.* (1990) were followed to amplify double-stranded PCR products. The specific thermal cycle used is as follows: (a) one cycle at 94°C X 3 minutes, 47°C X 1 minute, and 72°C X 1 minute; (b) thirty four cycles at 94°C X 45 seconds, 47°C X

45 seconds, and 72°C X 1 minute; (c) one cycle at 72°C X 6 minutes. PCR products were sequenced using an ABI Big Dye v.3 terminator cycle sequencing kit and run on an ABI 3100 automated DNA sequencer at the University of North Dakota.

Phylogenetic Analysis— In order to assess the phylogenetic affinities of the genus *Lankascincus* within the larger lygosomine scincid radiation we chose 21 species from the four major lygosomine lineages (*Sphenomorphus*-group, *Eugongylus*-group, *Mabuya*-group [see discussion with regard to the paraphyly of *Mabuya*], and the *Egernia*-group). These combined with tissue samples from three species of *Lankascincus* (*L. gansi*, *L. fallax*, and *L. taprobanensis*) represent the in-group taxa (24 species from 16 genera in all). The out-group taxa chosen represent a representative of the Scincine subfamily (*Brachymeles*), *Xantusia* (Family Xantusiidae, the likely sister taxa to skinks (Harris, 1999)), and *Cordylus* (Family Cordylidae, the likely sister taxa to Scincidae + Xantusiidae (Harris, 1999)). Data from *Sphenodon*, *Cordylus*, *Xantusia*, *Lipinia*, *Corucia*, *Tiliqua*, and *Egernia* were taken from the genbank (Harris, 1999; Saint et al., 1998).

Three hundred and fifty seven base-pairs from 28 individuals were aligned using Clustal X (Thompson et al., 1994). Maximum parsimony and maximum likelihood were the two optimality criteria used to assess

phylogenetic relationships (Edwards, 1972; Felsenstein, 1981). All phylogenetic analysis was done using PAUP* 4.0d64, written by David Swofford. The presence of a bias in the type of base substitutions for DNA sequences has been well documented (Brown et al., 1982; Edwards et al., 1991; Knight and Mindell, 1993; Thorpe et al., 1994; Vigilant et al., 1989; Wakeley, 1996). Base substitutions are often partitioned into two distinct classes: transitions and transversions. Transitions generally occur at a much higher frequency than transversions; for recently divergent populations almost all base substitutions are transitions (Vigilant et al., 1989; Wakeley, 1996). Maximum likelihood was used to estimate transition:transversion ratio using PAUP* 4.0d64, and this estimate is used for all analyses (ti/tv = 2.6). The two parameter Hasegawa-Kishino-Yano (1985) likelihood model was implemented using nucleotide frequencies estimated from the data. All searches were done using the heuristic search options in PAUP* with 20 random addition sequences, with initial trees obtained by stepwise addition, followed by branch swapping using the tree bisection-reconstruction (TBR) method implemented in PAUP*.

Phylogenetic Confidence.— Confidence in the phylogenetic signal for this molecular data set was assessed in two ways. First, both maximum parsimony and maximum likelihood were used to estimate a phylogenetic hypothesis (Kim, 1993). Second, both

maximum parsimony and maximum likelihood analyses were bootstrapped to assess confidence for each node (Felsenstein, 1985; Hillis and Bull, 1993; Swofford and Olson, 1990).

Results

Three hundred and fifty seven unambiguously aligned sites for twenty eight taxa were used in the phylogenetic analysis. Of these, 176 sites were variable and 106 sites were parsimony-informative. Two insertions or deletions (indels) were observed. *Lampropholis* and *Carlia* share a three base-pair (one codon) indel and *E. parkeri*, *E. tongana*, *Eugongylus*, *Lipinia*, *Lampropholis* and *Carlia* all share a three base-pair (one codon) indel. Despite indels, an open reading frame for both genes was observed by alignments based on codon positions by translating DNA sequence into protein sequences using MacClade (version 4). Using maximum likelihood, the ti/tv ratio was estimated at 2.6. This ti/tv ratios was used as a weighting scheme in the parsimony and likelihood phylogenetic analyses. The genetic distance matrix for uncorrected corrected distances is presented in Appendix 1. *C-mos* is a protein encoding gene and, as expected, there was more variation at third position sites ($96/119 = 80\%$) compared with first and second position sites ($81/238 = 34\%$).

Maximum parsimony (MP) recovered four equally parsimonious trees. The strict consensus of these trees is

presented in Figure 1. The ML analyses using empirical nucleotide frequencies ($A=0.29$, $C=0.20$, $G=0.22$, $T=0.29$) produced a single best tree and is presented in Figure 2. The overall topologies between the two analyses are congruent. The tree length was 482.6 for the parsimony analyses, $CI=0.64$, $HI=0.36$, $RC=0.54$. The log likelihood value was -2124.457 . Bootstrap proportions are for 500 and 100 pseudoreplicates, for MP and ML, respectively.

Five generally well supported clades are evident from both the MP and ML analyses. Four of these clades represent the previously recognized lygosomine *Eugongylus*-, *Mabuya*-, *Egernia*-, or *Sphenomorphus*-groups and the fifth well supported clade represents members of the genus *Lankascincus*. The nodes determining the relationships among these five major clades, however, are not well supported (bootstrap proportions less than 50). The inclusion of south Asian (e.g., Indian/other Sri Lankan) taxa would have been useful for comparison.

Discussion

Phylogenetic results demonstrate that *Lankascincus* represents an independent lineage separate from the *Eugongylus*-, *Mabuya*-, *Egernia*-, or *Sphenomorphus* - groups (Figs 1 and 2). The phylogenetic affinities of the *Lankascincus*-group with the other lygosomine groups, however, remain uncertain. The internodes connecting the major lineages are very short (Fig.

2) possibly as a result of a rapid radiation of lygosomines early in their evolutionary history. More data are clearly needed to help fully resolve the relationships among lineages, and it is likely that a large amount of additional data will be necessary to fully resolve the short internodes connecting these lineages.

The lygosomine skinks represent a large squamate radiation, and the present study presents molecular data for a broad but small subset. Greater sampling effort may uncover other distinct lineages. In particular, sampling of lygosomines from the Indian subcontinent and Africa will likely provide additional phylogenetic information. In addition, greater generic-level sampling will also likely further refine our understanding of phylogenetic affinities. For example, this study demonstrates that within the *Mabuya*-group, two well-supported clades exist, including one clade with representatives of the genus *Mabuya* and another clade with the genera *Apterygodon* and *Dasia*. The genus *Mabuya* includes over 100 species, and the phylogenetic affinities of this large group are not well understood in relation to the large Lygosominae radiation. Honda et al. (1999) showed that the *Mabuya* group is paraphyletic (see also Mausfeld and Vrcibradic, 2002). In support of long separated evolutionary lineages, representing distinct monophyletic radiations of the South American, Asian, Afro-Madagasy

and Cape Verdian groups, Mausfeld et al. (2002) partitioned *Mabuya* Fitzinger, 1826, into four genera. The Asian species were allocated to *Eutropis* Fitzinger, 1843 (type species: *Gongylus sebae* Duméril and Bibron, 1839, type locality: Batavia [= Jakarta], at present synonymous with *Mabuya multifasciata* [Kuhl, 1820]). Our study only includes one of the two Asian *Mabuya* groups and greater sampling combined with additional data will help to resolve relationships. Three other Sri Lankan skinks are currently assigned to the genus *Sphenomorphus*. Greer considered *S. dorsicatenatus* to be incertae sedis within *Lankascincus* and this is likely to be correct (CCA personal observation). Two other *Sphenomorphus* species, *S. dussumieri* and *S. megalops*, appear to be uncommon and have not been observed by either the senior or junior author and we therefore are unsure of their phylogenetic affinities. *Sphenomorphus dussumieri* is a south Indian endemic, and the record from India, a single specimen is in error. Specimens and tissue samples of *S. dussumieri* and *S. megalops* will undoubtedly be critical to further our understanding of the extent of biodiversity and phylogenetic affinities of the Sri Lankan scincid fauna. Further, Greer (1991) suggested that *Lankascincus* is related to the Western Ghats endemic *Ristella* and this relationship needs to be explored.

The major result from this study is that the endemic *Lankascincus* represents a distinct lineage of the lygosomine

scincid radiation. This result compliments ongoing work in the vertebrate assemblages of Sri Lanka that reinforce the diversity and uniqueness of the Sri Lankan fauna. Additionally, it illustrates the grave need for additional taxonomic and phylogenetic work on Sri Lankan lizards.

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Appendix 1.
Genetic distances (uncorrected) for 28 taxa
(see Table 1 for locality and accession information).

	1	2	3	4	5	6	7
1 <i>Emoia parkeri</i>	-	0.02260	-	-	-	-	-
2 <i>Euglyptus</i>	0.00565	0.02825	-	-	-	-	-
3 <i>Emoia tongana</i>	0.07647	0.07367	-	-	-	-	-
4 <i>Corucia</i>	0.08789	0.09632	0.09069	0.06443	-	-	-
5 <i>S. scutatus</i>	0.12179	0.11328	0.08123	0.04482	-	-	-
6 <i>S. jajori</i>	0.09911	0.11037	0.09911	0.07563	0.03361	0.05602	-
7 <i>Scincella</i>	0.11334	0.10488	0.08683	0.04202	0.05322	0.05322	-
8 <i>S. sinus</i>	0.10169	0.11299	0.10452	0.08197	0.04245	0.06502	0.04524
9 <i>Lipinia noctua</i>	0.09674	0.10797	0.09954	0.07598	0.02812	0.05340	0.03092
10 <i>Prasinohamea</i>	0.08789	0.09632	0.09069	0.06443	0.00000	0.04482	0.03361
11 <i>S. solomonis</i>	0.08209	0.07649	0.04202	0.07003	0.08964	0.08123	-
12 <i>M. multicastrata</i>	0.07648	0.08779	0.08208	0.05882	0.07563	0.10084	0.08403
13 <i>A. vittatum</i>	0.08797	0.09923	0.09078	0.06723	0.01681	0.03922	0.02801
14 <i>Saiphos</i>	0.07664	0.08507	0.08227	0.05042	0.07003	0.10364	0.08964
15 <i>L. gansi</i>	0.06795	0.07926	0.07360	0.01681	0.06723	0.08683	0.07563
16 <i>Tiliqua</i>	0.07369	0.08490	0.07929	0.05042	0.07283	0.09804	0.08123
17 <i>M. multifasciata</i>	0.07350	0.08762	0.07910	0.05602	0.07843	0.10364	0.08403
18 <i>Dasia</i>	0.07075	0.07641	0.07641	0.01681	0.06723	0.08964	0.07843
19 <i>Egernia</i>	0.02568	0.03707	0.03137	0.07997	0.09719	0.12301	0.11436
20 <i>Lampropholis</i>	0.07087	0.07930	0.07650	0.04482	0.07003	0.09804	0.08403
21 <i>L. fallax</i>	0.09914	0.11326	0.10475	0.07003	0.08403	0.10084	0.09804
22 <i>Brachymyces</i>	0.06528	0.07648	0.07088	0.04202	0.06443	0.08964	0.07563
23 <i>Mabuya</i> sp.	0.05429	0.04852	0.10010	0.10029	0.13176	0.11744	-
24 <i>Carlia</i>	0.06808	0.07651	0.07370	0.04202	0.06723	0.09524	0.08123
25 <i>L. tapro</i>	0.17879	0.18169	0.18439	0.16527	0.15406	0.18487	0.17927
26 <i>Xantusia</i>	0.17827	0.18670	0.18110	0.15966	0.16807	0.17647	0.16246
27 <i>Cordylus</i>	0.26278	0.26849	0.26281	0.25536	0.24686	0.26090	0.26377
28 <i>Sphenodon</i>							

	8	9	10	11	12	13	14
8 <i>S. simus</i>	0.06236	-	-	-	-	-	-
9 <i>Lipinta</i>	0.05067	0.01989	-	-	-	-	-
10 <i>Prasinohaema</i>	0.04202	0.04245	0.02812	-	-	-	-
11 <i>S. solomonis</i>	0.08403	0.08490	0.07872	0.07003	0.04762	-	-
12 <i>M. multicaerinata</i>	0.09804	0.08779	0.08155	0.07563	0.06723	0.07283	-
13 <i>Apterygodon</i>	0.03641	0.03972	0.02535	0.01681	0.06723	0.06443	0.07843
14 <i>Saiphos</i>	0.10364	0.09062	0.08719	0.07003	0.05322	0.06443	0.07843
15 <i>Igansi</i>	0.08190	0.07592	0.06723	0.04762	0.05882	0.06723	-
16 <i>Tiliqua</i>	0.09804	0.08770	0.08152	0.07283	0.01961	0.04482	0.07003
17 <i>M. multifasciata</i>	0.10364	0.09322	0.08713	0.07843	0.04202	0.03641	0.07843
18 <i>Dasia</i>	0.09524	0.08471	0.07872	0.06723	0.05042	0.06162	0.07003
19 <i>Egernia</i>	0.10875	0.11141	0.10618	0.09719	0.08012	0.09428	0.10019
20 <i>Lampropholis</i>	0.09804	0.08485	0.08156	0.07003	0.04762	0.05882	0.07283
21 <i>L. fallax</i>	0.11204	0.10195	0.09560	0.08403	0.07003	0.07563	0.08683
22 <i>Brachymyces</i>	0.08964	0.07928	0.07311	0.06443	0.01120	0.04202	0.06162
23 <i>Mabuya sp.</i>	0.12032	0.12291	0.11786	0.10029	0.10310	0.10881	0.10607
24 <i>Carlia</i>	0.09524	0.08205	0.07875	0.06723	0.04482	0.05602	0.07003
25 <i>L. tapro</i>	0.18487	0.18149	0.17147	0.15406	0.15686	0.16246	0.15966
26 <i>Xantusia</i>	0.17087	0.16383	0.16298	0.16807	0.15966	0.16246	0.16246
27 <i>Cordylus</i>	0.26660	0.25995	0.26457	0.24686	0.26656	0.25248	0.24978
28 <i>Sphenodon</i>							

	15	16	17	18	19	20	21
15 <i>L. garai</i>	-						
16 <i>Tiliqua</i>	0.05602	-					
17 <i>M. multifasciata</i>	0.05602	0.04482	-				
18 <i>Dasia</i>	0.06162	0.05602	0.04482	-			
19 <i>Egernia</i>	0.05602	0.00840	0.05322	0.05882	-		
20 <i>Lampropholis</i>	0.09163	0.07996	0.08297	0.08859	0.08274	-	
21 <i>L. fallax</i>	0.01681	0.05042	0.05042	0.05602	0.05042	0.08580	-
22 <i>Brachymyces</i>	0.08123	0.07003	0.06443	0.07283	0.07563	0.11726	0.07563
23 <i>Mabuya</i> sp.	0.04762	0.04202	0.01401	0.03641	0.04482	0.07442	0.04202
24 <i>Carlia</i>	0.10036	0.10301	0.10312	0.11161	0.10293	0.05999	0.09456
25 <i>L. tapro</i>	0.00840	0.04762	0.04762	0.05322	0.04762	0.08300	0.00840
26 <i>Xantusia</i>	0.14006	0.17087	0.16527	0.16246	0.16527	0.19468	0.14566
27 <i>Cordylus</i>	0.15966	0.16246	0.16527	0.17367	0.16527	0.18829	0.15406
28 <i>Sphenodon</i>	0.26664	0.26374	0.26656	0.26931	0.26374	0.26505	0.26661
22 <i>Brachymyces</i>	22	23	24	25	26	27	28
23 <i>Mabuya</i> sp.	0.06443	-					
24 <i>Carlia</i>	0.12306	0.09740	-				
25 <i>L. tapro</i>	0.07283	0.03922	0.09174	-			
26 <i>Xantusia</i>	0.15966	0.15686	0.19505	0.13725	-		
27 <i>Cordylus</i>	0.16246	0.15966	0.18332	0.15126	0.17367	-	
28 <i>Sphenodon</i>	0.25307	0.25535	0.26604	0.26381	0.25830	0.24707	-

Figure 1

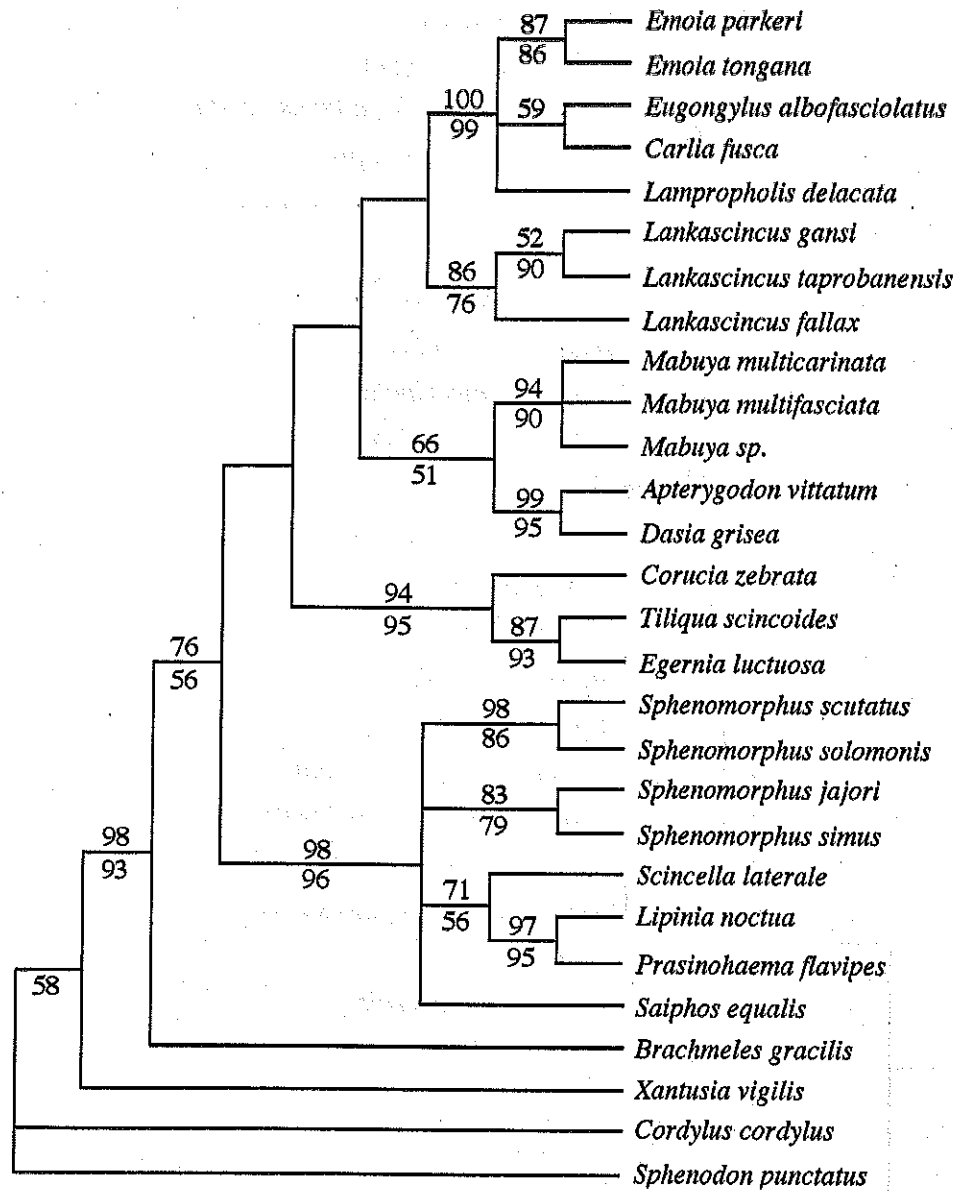


Figure 2

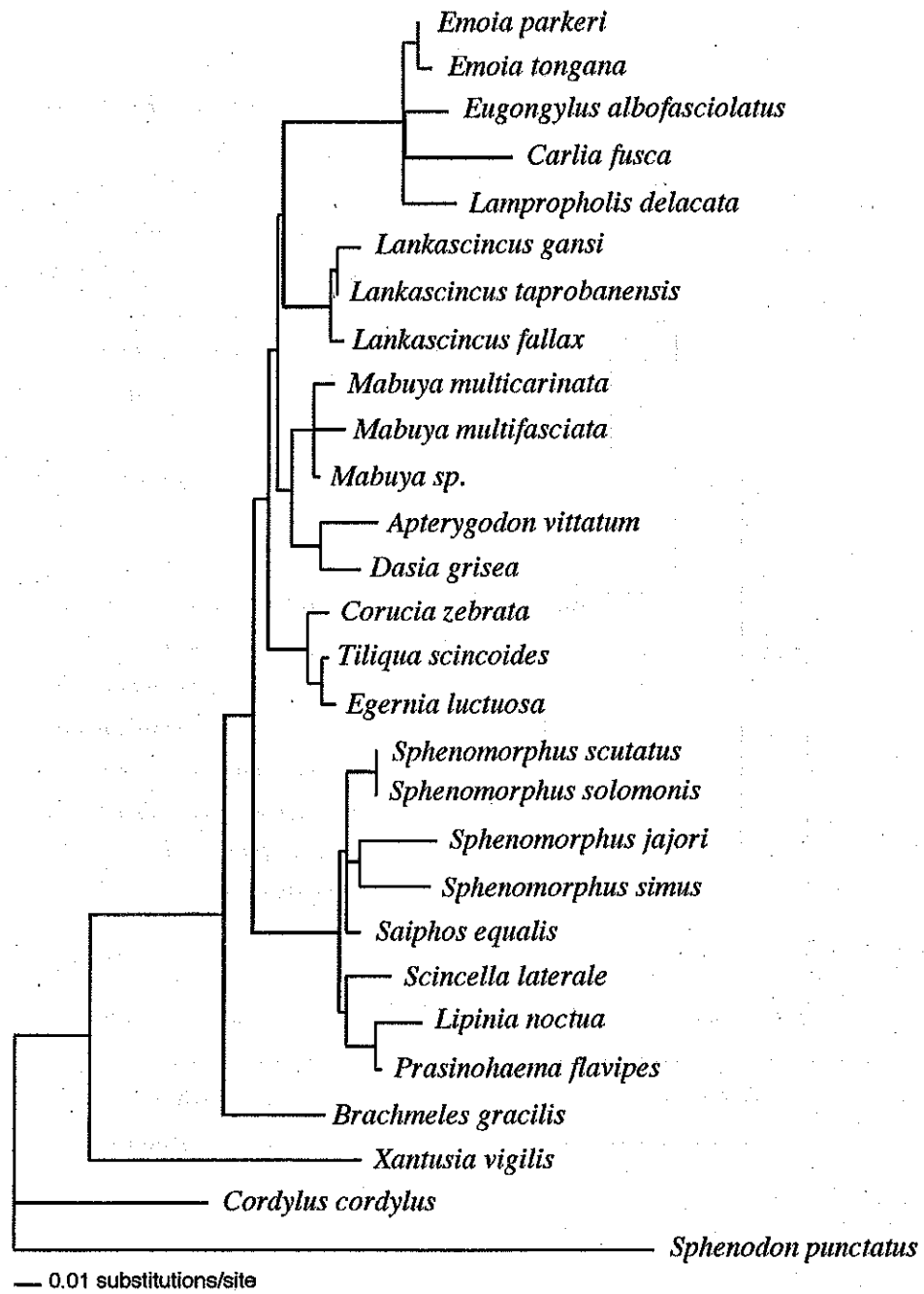


Plate 1



Fig.1. *Lankascincus fallax* (Photo: Austin)



Fig.2. *Lankascincus taprobanensis* (Photo: Austin)



Fig. 3. *Mabuya* sp. (Photo: Austin)



Fig. 4. *Mabuya* sp. (Photo: I. Das)



Fig. 5. *Lankascincus fallax* (Photo: A. Drion)



Fig. 6. *Acrochordus granulatus* (Photo: Anslem de Silva)



Fig. 7. *Nannophrys ceylonensis*
(Photo: Wickramasinghe)



Fig. 8. *Nannophrys ceylonensis* tadpole
(Photo: Wickramasinghe)