Phylogeny and biogeography of water skinks of the genus *Tropidophorus* (Reptilia: Scincidae): a molecular approach

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Phylogenetic relationships of the Oriental semiaquatic lygosomine skinks of the genus *Tropidophorus* were inferred from 1219 base positions of mitochondrial 12S and 16S rRNA genes. Results of the phylogenetic analyses incorporating data for representatives of other lygosomine genera indicated that the basal phylogenetic split within *Tropidophorus* separated a clade of continental Indochinese species exclusive of *T. cocincinensis* and *T. microlepis* from one comprising *T. cocincinensis*, *T. microlepis* and species from Borneo, Sulawesi and the Philippines. Of the latter group, the two continental species form the sister taxon to a clade comprising the island species. Diversification among species in Indochina and among Borneo, the Philippines and Sulawesi was likely concentrated in the Miocene, with no apparent dispersal among these regions during the Pleistocene. The body depression recognized in several Indochinese species is likely to have occurred twice in parallel as an adaptation to saxicolous habitats.

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Introduction

The Oriental lygosomine genus *Tropidophorus* Duméril & Bibron, 1839 (type species: *T. cocincinensis*) contains 24 species of semiaquatic skinks (Table 1). The genus exhibits considerable local endemism (e.g. Greer & Biswas 2004). Morphologically, it is diagnosed by several characteristics, such as exposure of the tympanum and presence of a single scale at the corner of the eyelid (e.g. Greer 1970; Hikida *et al*. 2002; Greer & Biswas 2004).

The species of *Tropidophorus* occur in two regions: (1) Indochina and adjacent parts of continental Eurasia exclusive of the Malay Peninsula, and (2) the South-east Asian islands of Borneo, Sulawesi, and the Philippines (Boulenger 1887; de Rooij 1915; Smith 1923, 1935; Taylor 1963; Brown & Alcala 1980; Welch *et al*. 1990; Wen 1992; Zhao & Adler 1993; Ngo *et al*. 2000; Hikida *et al*. 2002, 2003; Greer & Biswas 2004) (Fig. 1). These skinks are not known from Sumatra, Java, or the Lesser Sunda Archipelago.

The distributional pattern of *Tropidophorus* is distinct from those of other nonvolant terrestrial vertebrate genera occurring in both Borneo and Indochina because most of these other genera also occur on the Malay Peninsula, Sumatra, and Java (e.g. Heaney 1984; Inger & Stuebing 1997; Stuebing & Inger 1999; Lim & Das 1999). The occurrence of *Tropidophorus* on Sulawesi and the Philippine Islands is a biogeographic puzzle, because these islands have supposedly been isolated from Borneo and Indochina since at least the middle Tertiary (e.g. Inger & Voris 2001). In contrast, the Malay Peninsula, Sumatra and Java are considered to have been connected to Indochina when sea levels were lower during late Pleistocene glacial events (e.g. Dunn & Dunn 1977; Heaney 1991; Voris 2000). Therefore, the current distribution of *Tropidophorus* does not simply reflect the geological history of South-east Asia. To date, no studies have addressed this enigmatic distribution using phylogenetic relationships of the species.

Herein, we examine the phylogenetic relationships of representative species of *Tropidophorus* by analysing mitochondrial DNA sequence data. We assess the monophyly and timing of divergence for species assemblages in Indochina, Borneo, Sulawesi, and the Philippines. Our purpose is to

Table 1 List of species of the genus *Tropidophorus*, with the numbers of preanal scales and distributions taken from the literature (Boulenger 1887; de Rooij 1915; Smith 1923, 1935; Mittleman 1952; Taylor 1963; Brown & Alcala 1980; Welch *et al*. 1990; Wen 1992; Zhao & Adler 1993; Ngo *et al*. 2000; Hikida *et al*. 2002, 2003; Greer & Biswas 2004). Those species whose representatives were analysed in the present study are shown in bold. *sample examined in our previous study (Honda *et al*. 2000). See Appendix for further details.

Species	Preanals	Mittleman (1952)	Distribution
Indochinese peninsula			
T. assamensis	2	*Tropidophorus*	Bangladesh
T. baviensis	2	*Tropidophorus*	Vietnam
T. berdmorei*	2	*Tropidophorus*	China (Yunnan), Burma, Thailand, Vietnam, Laos
T. cocincinensis	2	*Tropidophorus*	Thailand, Vietnam
T. guangxiensis	2	*Tropidophorus*	China (Guangxi)
T. hainanus	2	*Tropidophorus*	China (Hainan, Guangxi, Jiangxi), Vietnam
T. laotus	2	*Tropidophorus*	Thailand, Laos
T. latiscutatus	2	*Tropidophorus*	Thailand
T. matsuii	2	*Tropidophorus*	Thailand
T. microlepis	2	*Tropidophorus*	Thailand, Vietnam
T. murphyi	2	*Tropidophorus*	Vietnam
T. robinsoni	2	*Tropidophorus*	Thailand
T. sinicus	2	*Tropidophorus*	China (Guangxi, Guangdong, Hong Kong), Vietnam
T. thai	2	*Tropidophorus*	Thailand
Borneo			
T. beccarii	1	*Norbea*	Borneo
T. brookei	1	*Norbea*	Borneo
T. iniqua	1	*Norbea*	Borneo
T. micropus	1	*Norbea*	Borneo
T. perplexus	1	*Norbea*	Borneo
Sulawesi			
T. baconi	3	*Tropidophorus*	Sulawesi
Philippines			
T. davaoensis	1 (rarely 2)	*Norbea*	Mindanao, Dinagat
T. grayi	3	*Tropidophorus*	Luzon, Polillo, Masbate, Negros, Cebu, Leyte
T. misaminius	1	*Norbea*	Mindanao, Basilan, Camiguin
T. partelloi	1 (rarely 2)	*Norbea*	Mindanao, Dinagat

establish reliable hypotheses for the phylogeny of *Tropidophorus* and the formation of its current geographical distribution.

Materials and methods

Tissues were obtained for 10 of the 14 species from the continent, two of the five species from Borneo, the single species from Sulawesi, and three of the four species from the Philippines (Table 1; see Appendix 1 for details). We also incorporated published sequence data for *T. berdmorei* and several other skinks representing the five major lineages of the subfamily Lygosominae: *Sphenomorphus*, *Lygosoma*, *Egernia*, *Eugongylus* and *Mabuya* groups (Honda *et al*. 1999b,c, 2000, 2003). *Eumeces schneiderii* and *Scincus scincus* were used as outgroups because the subfamily Scincinae, to which these two species belong, is phylogenetically outside of the Lygosominae (Greer 1970).

Extraction, amplification and sequencing procedures of DNA were described elsewhere (Honda *et al*. 1999a,b). Parts of mitochondrial 12S and 16S rRNA genes, approximately 1200 base pairs (bp), were amplified using the polymerase chain reaction with the following primers: L1091 and H1478 (Kocher *et al*. 1989) for 12S rRNA, and L2206, L2606, H3056 (Hedges *et al*. 1993) and H2741 (Honda *et al*. 2000) for 16S rRNA.

Alignments for DNA sequences were determined based on the maximum nucleotide similarity using CLUSTAL W 1.4 (Thompson *et al*. 1994) with default gap penalties (gap opening penalty = 10). The output was then adjusted by eye using manual aligner SeqApp 1.9 (Gilbert 1993) by considering the possible presence of secondary structures in the rRNA genes (Kumazawa & Nishida 1993). However, secondary structures uncovered as a result of this treatment were rather unstable because of the lack of comparable information for closely related taxa.

Next, we identified ambiguously aligned regions by comparing various gap cost sequence alignments (gap opening penalties = 6, 9, or 12) and excluded them from the phylogenetic analysis following Reeder (2003). Topologies of resultant trees based on the latter two procedures of alignments were

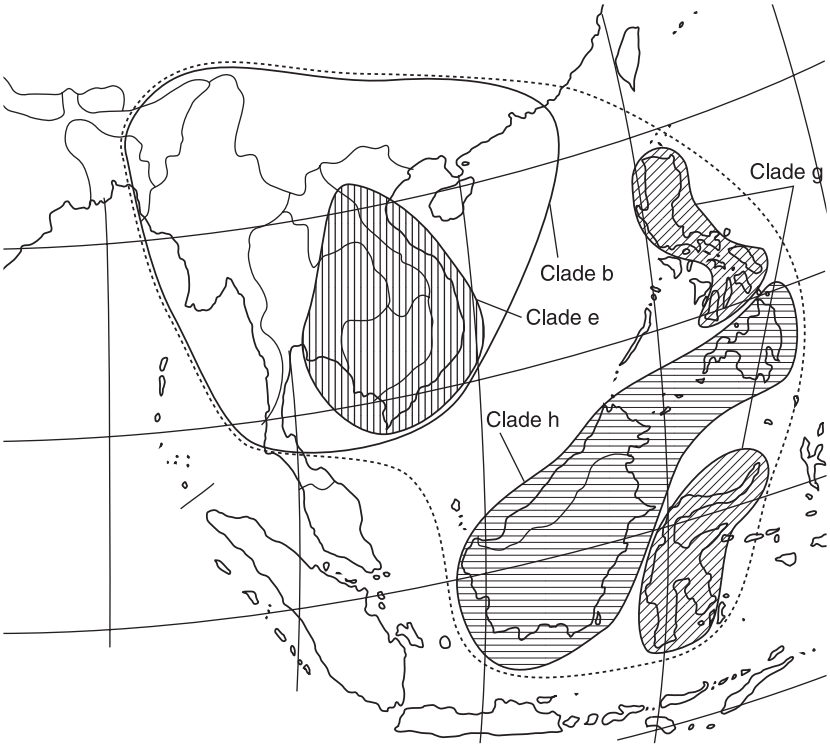

Fig. 1 A map of South-east Asia showing distribution of *Tropidophorus*. Dotted line encloses the range of the genus. Geographical ranges of clades elucidated in the present study are enclosed by solid lines. Clade names correspond to the nodes in Figs 2 and 3. Node b: *T. berdmorei*, *T. latiscutatus*, *T. matsuii*, *T. sinicus*, *T. robinsoni*, *T. thai*, *T. murphyi*, *T. baviensis*, and *T. hainanus*; node e (vertically hatched area): *T. cocincinensis* and *T. microlepis*; node g (obliquely hatched area): *T. baconi* and *T. grayi*; and node h (horizontally hatched area): *T. brookei*, *T. beccarii*, *T. partelloi*, *T. misaminius* and *T. partelloi*.

virtually identical with that based simply on the maximum similarity criterion. Thus, we henceforth refer only to phylogenetic analyses using the maximum similarity criterion excluding insertions and deletions. The aligned sequences used in the present study are available from TreeBase (study accession number: SN2418-9164).

Neighbour-joining (NJ) (Saitou & Nei 1987) was applied to infer relationships among taxa on the basis of a pairwise matrix of distances from Kimura's (1980) two-parameter model. Maximum likelihood (ML) analysis was performed under GTR + I + gamma, which was selected in a series of hierarchical likelihood ratio tests using Modeltest 3.0 (Posada & Crandall 1998). Maximum parsimony (MP) analysis was conducted using the heuristic search option with TBR branch swapping, 500 random taxon addition replicates per analysis, and no bias between transitions and transversions. All analyses were performed using PAUP* 4.0b (Swofford 1998).

Confidence of branches for NJ and MP analyses was assessed by 2000 bootstrap resamplings (Felsenstein 1985a). For MP, decay indices (Bremer 1994) were also calculated for all internal branches using TreeRot v.2.c (Sorenson 1999). With respect to the ML analysis, because of computational limitations it was almost impossible to perform extensive bootstrapping for the analysis on a data set containing as many taxa as in this study (Sanderson & Kim 2000). Larget & Simon (1999) demonstrated that with an assessment using the Bayesian (BI) method, complex nucleotide substitution models and the likelihood function can be implemented quickly and efficiently for large data sets (see Leaché & Reeder 2002 for empirical examples). Thus, BI analysis was used not only to infer phylogenetic relationships of problematic taxa, but also to assess the validity of nodes shared by BI and ML trees by posterior probabilities.

BI analysis was conducted using MrBayes 3.04 (Huelsenbeck & Ronquist 2001). With this method, all analyses were initiated from random starting trees, and run for 2 million generations, sampling every 100 generations. Stationarity was evaluated by plotting likelihood against generation time. Likelihood values were stabilized by 100 000 generations, but the first 200 000 were discarded as burn-in. To ensure that the BI analyses were not trapped within local optima, we performed analyses twice for each data set, and apparent stationarity levels were compared for convergence (Huelsenbeck & Bollback 2001).

Comparisons of the shortest tree relative to alternative hypotheses which constrain monophyly of both the whole genus and the three depressed-bodied species (see Appendix 2) were made using the SH test (Shimodaira & Hasegawa (1999) with 10 000 resamplings and estimated log-likelihood (RELL) approximations under the GTR + I + gamma model of sequence evolution. The SH test is considered to have advantages both over the more commonly used Kishino–Hasegawa (Kishino & Hasegawa 1989) and Templeton (1983) tests (= two-tailed Wilcoxon signed ranks test: Felsenstein 1985b) (Goldman *et al.* 2000; Buckley *et al.* 2001).

The extent of mitochondrial DNA substitutions between taxa was used to date evolutionary divergences. A rate of 2% nucleotide substitution per million years (Myr) (Brown *et al.* 1982) was broadly applied (e.g. Wilson *et al.* 1985; Avise 1994). However, ND1, ND2, and COI genes evolved at a rate of approximately 0.65% change per Myr in iguanid, agamid, varanid and gekkonid lizards, bufonid toads, salamandrid salamanders, and in some fishes (Bermingham *et al.* 1997; Macey *et al.* 1997, 1998a,b; Schulte *et al.* 2000, 2003; Weisrock *et al.* 2001). Moreover, 12S and 16S rRNA genes sometimes evolved even more slowly (e.g. Keogh 1998; Lee 2000). Recent studies suggested that the rate of change in frogs was 0.22% per Myr (Graybeal 1997; Emerson *et al.* 2000). Therefore, we adopted a maximum rate of 0.65% per Myr and a minimum of 0.22% per Myr for our data because of the lack of comparable information of the 12S and 16S rRNA genes for *Tropidophorus* or other scincid lizards.

Divergence times were also estimated using the nonparametric rate-smoothing algorithm (NPRS) (Sanderson 1997) in TreeEdit 1.0a10 (Rambaut & Charleston 2001), following Schulte *et al.* (2003). This method is considered to be appropriate when evolutionary rates vary between lineages. Outgroups were removed prior to NPRS to prevent overestimation of the mean evolutionary rate across the phylogeny. Branch lengths were calculated using ML distances to obtain the probability of change along each branch of the phylogenetic tree, and were scaled 0.65% per Myr and 0.22% per Myr as the maximum and minimum rates, respectively (see above).

To determine whether evolutionary rates were variable among lineages, the likelihood values were calculated with and without a molecular clock enforced in PAUP* and subsequently used to perform a likelihood ratio test (LRT). The test statistic is distributed according to a chi-squared distribution with n-2 degrees of freedom where n is the number of taxa (Muse & Weir 1992).

Results

The 12S rRNA fragment consisted of 399 aligned sites, of which 236 varied among taxa. For 16S rRNA, we resolved 820 total aligned sites, of which 443 were variable. Within *Tropidophorus*, interspecific nucleotide replacements varied from 45 bp (4.0% replacement = uncorrected 'p' distances: *T. misaminius* vs. *T. partelloi*) to 205 bp (18.1%: *T. beccarii* vs. *T. sinicus*). In comparison, divergence varied between 82 and 199 bp (6.6–17.6%) and 128 and 190 bp (11.2–16.7%) among the members of *Mabuya sensu lato* and *Sphenomorphus*, respectively.

The result of ML (Fig. 2) is consistent with the BI dendrogram (not shown) in terms of presence of the *Sphenomorphus*, *Lygosoma*, *Egernia*, *Eugongylus* and *Mabuya* groups (Honda *et al.* 1999b,c, 2000, 2003), and branching topology within the *Sphenomorphus* group. The monophyly of each of the five groups was supported with Bayesian posterior probabilities (BPP) of 1.0 (= 100%). A portion of the *Sphenomorphus* group, to which all members of the genus *Tropidophorus* belonged, was divided into four well supported nodes: node a (BPP = 1.0) consisted of *T. brookei*, *T. beccarii*, *T. partelloi*, *T. misaminius*, *T. baconi*, *T. grayi*, *T. cocincinensis*, and *T. microlepis*; node b (BPP = 1.0) of *T. berdmorei*, *T. latiscutatus*, *T. matsuii*, *T. sinicus*, *T. robinsoni*, *T. thai*, *T. murphyi*, *T. baviensis*, and *T. hainanus*; node c (BPP = 1.0) of *Isopachys anguinoides*, *Lipinia vittigera*, *Scincella rupicola*, *Sc. lateralis*, *Sph. cherriei*, *Sph. indicus*, and *Sph. maculatus*; and node d of *Sph. praesignis*. Nodes a and b, though both were composed solely of the *Tropidophorus* species, were sister groups of nodes c and d, respectively, not with each other. However, BPP was rather weak for these relationships.

There was a further split into two clusters, of which one (node e, BPP = 1.0) consisted of continental species (*T. cocincinensis* and *T. microlepis*), and the other (node f, BPP = 0.89) accommodated all insular species examined. Within the latter, the first node separated a clade consisting of *T. baconi* and *T. grayi* (node g, BPP = 1.0) from a clade comprising two Bornean species (*T. beccarii* and *T. brookei*; node h) and two Philippine species (*T. misaminius* and *T. partelloi*; node i, BPP = 1.0). Within node b, the two Thai species with depressed bodies, *T. latiscutatus* and *T. matsuii*, comprised a well-supported monophyletic group (node j, BPP = 1.0). They were the sister group to *T. berdmorei* (BPP = 0.96), and not to the Vietnamese species that also had a depressed body, *T. murphyi* (Hikida *et al.* 2002). *Tropidophorus murphyi* clustered consistently with *T. baviensis* and *T. hainanus* (BPP = 1.0).

The NJ analysis (not shown) showed no inconsistency with the ML and BI dendrograms at the level of significant bootstrap proportion (*sensu* Shaffer *et al.* 1997: ≥ 70%). Also, the MP cladogram (Fig. 3) did not conflict with the ML and BI analyses with respect to the nodes mentioned above except for the position of *T. beccarii*. This species was resolved as the sister lineage to the cluster consisting of *T. partelloi* and *T. misaminius* in the ML, BI and NJ analyses, but to *T. brookei* in the MP cladogram. The position of *T. beccarii* in the MP analysis had bootstrap support of only < 50% and a decay index < 10. In comparison, the BI analysis provided a high BPP value (0.98) to the nonmonophyly of *T. beccarii* and *T. brookei*.

Our trees did not show monophyly for the whole of *Tropidophorus* or the three depressed bodied species. We thus tested monophyly of these two assemblages by applying the SH test to the ML dendrogram (see Appendix 2 for constrained trees). The topology was not significantly different from that in the alternative hypothesis, in which *Tropidophorus* was constrained to be monophyletic (difference of –ln L = 1.74, P = 0.405). In contrast, the topology was significantly different from that in the alternative hypothesis in which the three depressed-bodied species were constrained to be monophyletic (difference of –ln L = 42.7, P = 0.000).

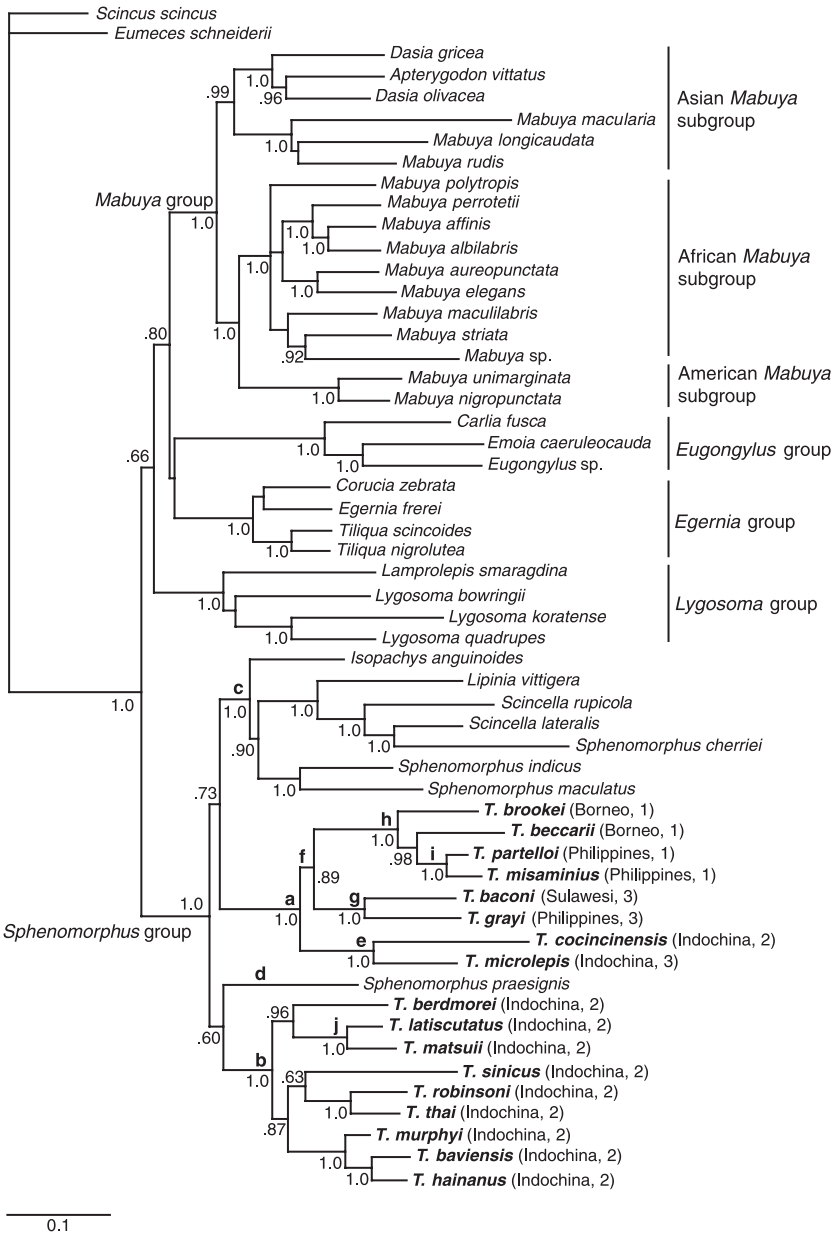

Fig. 2 Maximum likelihood (ML) phylogeny among lygosomine lizards derived from 12S and 16S rRNA sequence data (–Ln likelihood = 20330.9). Numbers beneath branches correspond to Bayesian posterior probabilities of at least 50% in 2 million generations. Distribution and the number of preanal scales for each species of *Tropidophorus* are given in parentheses following the scientific name. Scale bar equals 0.1 nucleotide substitution per site. Bold letters above branches are identical with those in Fig. 3.

LRT test rejected the length homogeneity among ML tree branches (2 ln L = 171.1, d.f. = 53; $P < 0.0001$), and therefore, the divergence dates were estimated using NPRS. The estimated divergence date of the two major nodes of *Tropidophorus* (nodes a and b) was 21.4–63.2 Mya. Within node a, between the continental species (node e) and the insular members (node f) it was estimated to be 14.5–42.9 Mya. Between nodes g (*T. baconi–T. grayi*) and h (the Bornean and Philippine species exclusive of *T. grayi*) time of isolation was estimated to be 13.4–39.6 Mya; between *T. baconi* (Sulawesi) and *T. grayi* (Philippines) it was estimated to be 8.9–26.4 Mya. Finally, the time of isolation of the Bornean and Philippine species exclusive of *T. grayi* (node i) was estimated to be 5.5–16.3 Mya.

Discussion

Phylogenetic relationships of the genus Tropidophorus

Phylogenetic relationships inferred from the mtDNA sequence indicated the presence of two distinct lineages within *Tropidophorus* (Fig. 2). This divergence appeared to have

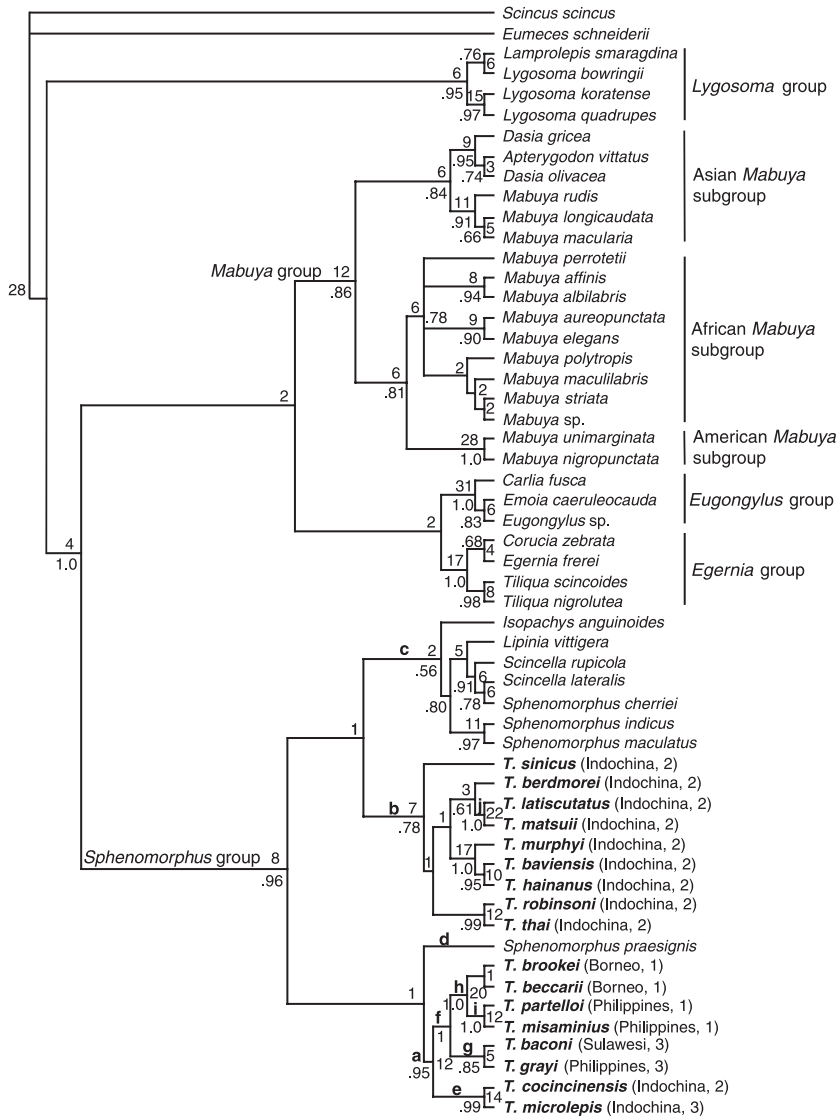

Fig. 3 Maximum parsimony (MP) cladogram from 12S and 16S rRNA sequence data for lygosomine lizards. The tree is a strict consensus of three equally parsimonious trees (541 bp potentially informative sites, 4589 steps, CI = 0.264, RI = 0.455). Bootstrap values of at least 50% in 2000 replications are presented beneath branches, and decay indices are shown above branches. Bold letters above branches are identical with those in Fig. 2.

occurred in the Tertiary (see below). Although SH test failed to reject the null hypothesis for the monophyly of *Tropidophorus*, branching patterns in the phylogenetic trees from our analyses still suggest a possible nonmonophyly of the genus (nodes a and b) and symplesiomorphic or convergent nature of some apparently derived character states common to both branches, such as the exposed tympanum. More comprehensive studies are required to test the monophyly of the genus.

Variation in the number of preanal scales within *Tropidophorus* (Taylor 1963; Brown & Alcala 1980; Hikida *et al*. 2003) largely corresponded to geographical distribution. The Indochinese members exclusive of *T. microlepis* have two preanal scales. In contrast, *T. microlepis*, *T. baconi* (Sulawesi), and *T. grayi* (Philippines) have three. Furthermore, Bornean and Philippine species exclusive of *T. grayi* usually possess a single large preanal scale (de Rooij 1915; Brown & Alcala 1980), a unique state within the subfamily Lygosominae (Greer 1970).

Mittleman (1952) regarded the presence of a single enlarged preanal scale in the Bornean and most Philippine species as diagnostic at the generic level. He resurrected the genus *Norbea* Gray, 1945 (type species: *N. brookei*) for these species (Table 1). However, this nomenclature has been almost completely ignored by subsequent authors. Our results supported monophyly of the species having a single preanal scale (node h) and thus potentially the validity of *Norbea*. For recognition of the genus *Norbea*, however, nodes e and g would also need to be recognized as separate genera to avoid paraphyly.

Our estimates of genealogical relationships also supported the hypothesis of monophyly for the insular species that have three preanal scales (node g), and of all insular species (node

f). In contrast, the trees conflicted with the hypothesis of monophyly of the continental species and strongly suggested a sister-group relationship of two Indochinese species (node e) to the insular clade (node f).

The substantial interspecific genetic differentiation within *Tropidophorus* (4.0–18.1%) was comparable to those in *Mabuya sensu lato* (6.6–17.6%) and *Sphenomorphus* (11.2–16.7%). Both *Mabuya* and *Sphenomorphus* were reported to be non-monophyletic (e.g. Greer 1977; Brown & Alcala 1980; Honda *et al*. 1999c, 2000, 2003; Mausfeld *et al*. 2002), and the same appeared true for *Tropidophorus*. However, more comprehensive studies are required to revise the classification of *Tropidophorus*.

Hikida *et al*. (2002) described three new species, *T. latiscutatus*, *T. matsuii*, and *T. murphyi*, which exclusively shared distinctly depressed bodies, as well as saxicolous habitats. Hikida *et al*. (2002) assumed that the characteristic body shape reflected an adaptation to using narrow rock crevices as shelters, as observed in a few other lizard families (Vitt 1981; Daughty & Shine 1995; Ballinger *et al*. 2000). Our analyses suggested that it has independently evolved in *T. murphyi* and in the common ancestor of *T. latiscutatus* and *T. matsuii*.

Biogeography of Tropidophorus

Within clade a of *Tropidophorus*, the basal node separated two continental species (*T. cocincinensis*, *T. microlepis*; node e) from the insular species (node f). Within the insular clade, *T. baconi* (Sulawesi) and *T. grayi* (Philippines) formed the sister group (node g) to a clade comprising two Bornean species (*T. beccarii*, *T. brookei*) and two Philippine species (*T. misaminius*, *T. partelloi*) (node h). Within clade h, the latter formed a clade by themselves, although exact relationships among this Philippine clade and the two Bornean species varied among analyses (Figs 2 and 3). These relationships collectively suggest a history of vicariance and subsequent dispersal of *Tropidophorus* lizards among Borneo, Indochina, Sulawesi, and the Philippines.

There were great opportunities for terrestrial faunal exchanges among Indochina, Malay Peninsula and Borneo from the Eocene (*c*. 50 Mya) to the middle Miocene (*c*. 10 Mya), and also several opportunities during the Pleistocene glaciations (1.7–0.01 Mya) (Inger & Voris 2001; Hall 1998). In addition, faunal exchanges between Borneo and Sulawesi likely occurred mainly during the early to middle Eocene by overland migrations, and during the Pleistocene by dispersals across the Makassar Strait, which has separated these two regions consistently since the middle Eocene (*c*. 42 Mya) (Moss & Wilson 1998). Our estimations of divergence times suggested that isolation of nodes a and b within the *Sphenomorphus* group occurred during the early Miocene (23.1 Mya) or earlier. This event, perhaps vicariance, isolated species from the insular region (Borneo, Sulawesi and the Philippines) and Indochina. Subsequently, a representative of the insular lineage (node a) may have returned to the continent, splitting from the common ancestor of node f in the insular region by 14.5 Mya, and become the common ancestor of node e (*T. cocincinensis* and *T. microlepis*). Further isolation formed the common ancestor of *T. baconi* from Sulawesi and *T. grayi* from the Philippines (node g) and that of the Bornean and other Philippine species (node h) by 13.4 Mya. Alternatively, the initial divergence of nodes a and b may have occurred within Indochina and the common ancestor of node f may have invaded the insular region from the continent .

The major faunal exchanges between Sulawesi and the Philippines likely occurred twice: during the late Miocene (*c*. 10–20 Mya), when the south-eastern Philippines were relatively close to north-eastern Sulawesi, and during the Pliocene (*c*. 5 Mya), when a chain of volcanoes extended northward from Sulawesi (Inger & Voris 2001). These events were more recent than the establishment of the Makassar Strait (*c*. 42 Mya). Thus, the more recent events were responsible for the higher faunal similarity of Sulawesi and the Philippines relative to the other parts of South-east Asia (e.g. Inger & Voris 2001), even though the Philippine fauna maintained a relatively high percentage of endemic species (e.g. Alcala 1986). Recent molecular studies discovered relatively close affinities between representatives of Sulawesi and the Philippines (e.g. *Limnonectes*: Emerson *et al*. 2000). The sister-species relationship between *T. baconi* (Sulawesi) and *T. grayi* (Philippines) favours this scenario. This divergence likely occurred 8.9 Mya or earlier in the late Miocene (see above).

Bornean species of *Tropidophorus* were not resolved as a monophyletic group in the ML and BI analyses because a Philippine lineage was shown to be the sister species to *T. beccarii*. These results suggest that the Bornean lineage represented by *T. beccarii* invaded the Philippines about 5.5 Mya or earlier, where it subsequently diverged into several species. *Tropidophorus grayi* is broadly distributed in the Philippines (Luzon, Polillo, Masbate, Negros, Cebu and Leyte islands), but not Mindanao. In contrast, the other Philippine species are confined either to Mindanao or to Mindanao and a few adjacent islands (Brown & Alcala 1980). This distributional pattern may have been a consequence of competition between these two Philippine lineages. Although the MP analysis found that the Bornean species form a monophyletic group (Fig. 3), speciation was likely to have been an older event, given the relatively long branch lengths (Fig. 2).

During the Pleistocene, Bornean terrestrial animals had many opportunities to invade the continent and vice versa, because additional land areas were formed on the Sunda Shelf several times during glaciations (Dunn & Dunn 1977; Heaney 1984, 1991; Inger & Voris 2001). However, our results consistently indicate that all dispersals of *Tropidophorus*, including those between these two regions, were Tertiary events. The preference for semiaquatic, humid habitats may have prevented

species of *Tropidophorus* from dispersing via temporary Pleistocene land bridges.

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Appendix 1. Localities, catalogue numbers and, DDBJ database accession numbers of voucher specimens

Specimens used in this study have been deposited in the reptile collections of Kyoto University Museum (KUZR), Royal Ontario Museum (ROM), and Muséum national d'Histoire naturelle (MNHN). In the list below, localities and catalogue numbers of materials already cited in Honda *et al*. (1999b,c, 2000, 2003) are omitted. Asterisk denotes materials obtained through pet dealers; detailed information regarding their localities is thus not available.

Tropidophorus baconi: Sulawesi*, KUZR 38805, AB222937, AB222953. *Tropidophorus baviensis*: Ha Tay, Vietnam, ROM 25552–3, AB222942, AB222958. *Tropidophorus beccarii*: Sarawak, Borneo, KUZR 35005, AB222935, AB222951. *Tropidophorus berdmorei*: AB028811, AB028823. *Tropidophorus brookei*: Sarawak, Borneo, KUZR 19008, AB222933, AB222949. *Tropidophorus cocincinensis*: Gia Lai, Vietnam, ROM 32129, AB222943, AB222959. *Tropidophorus grayi*: Philippines*, KUZR 51147, AB222941, AB222957, AB222944, AB222960. *Tropidophorus hainanus*: Tuyen Quang, Vietnam, ROM 30497. *Tropidophorus latiscutatus*: Phu Wua, Thailand, KUZR 40256, AB222934, AB222950. *Tropidophorus matsuii*: Phu Pa Namtip, Thailand, KUZR 40540, AB222936, AB222952. *Tropidophorus misaminius*: Mindanao, Philippines*, KUZR 59084, AB222948, AB222964. *Tropidophorus microlepis*: Indochina*, unnumbered specimen in KUZR, AB222947, AB222963. *Tropidophorus murphyi*: Cao Bang, Vietnam, ROM 41223-4, AB222945, AB222961. *Tropidophorus robinsoni*: Phang-Nga, Thailand & MNHN 1999–7694, AB222939, AB222955. *Tropidophorus sinicus*: Hong Kong, China, KUZR 37673, AB222938, AB222954. *Tropidophorus thai*: Doi Suthep, Thailand, KUZR 27510, AB222940, AB222956. *Tropidophorus partelloi*: Mindanao, Philippines*, KUZR 60096, AB222946, AB222962.

Apterygodon vittatus: AB028771, AB028782, AB028825. *Carlia fusca*: AB028792, AB028796, AB028826. *Corucia zebrata*: AB028793, AB028797, AB028827. *Dasia gricea*: AB028773, AB028784, AB028828. *Dasia olivacea*: AB028772, AB028783, AB028829. *Egernia frerei*: AB028794, AB028798,

AB028830. *Emoia caeruleocauda*: AB028801, AB028813. *Eugongylus* sp. AB028802, AB028814. *Eumeces schneiderii*: AB028770, AB028781, AB028824. *Isopachys anguinoides*: AB028803, AB028815. *Lamprolepis smaragdina*: AB028774, AB028785, AB028831. *Lipinia vittigera*: AB028804, AB028816. *Lygosoma bowringii*: AB028775, AB028786, AB028832. *Lygosoma koratense*: AB028805, AB028817. *Lygosoma quadrupes*: AB028806, AB028818. *Mabuya affinis*: AB028807, AB028819. *Mabuya albilabris*: AB057381, AB057396. *Mabuya aureopunctata*: AB057389, AB057404. *Mabuya elegans*: AB057380, AB057395. *Mabuya longicaudata*: AB028776, AB028787, AB028833. *Mabuya macularia*: AB057379, AB057394. *Mabuya maculilabris*: AB057382, AB057397. *Mabuya nigropunctata* AB057384, AB057399. *Mabuya perrotetii*: AB057386, AB057401. *Mabuya polytropis*: AB057385, AB057400. *Mabuya rudis*: AB028779, AB028790, AB028835. *Mabuya striata*: AB028780, AB028791, AB028836. *Mabuya unimarginata*: AB057378, AB057393. *Mabuya* sp. AB057383, AB057398. *Scincella lateralis*: AB057387, AB057402. *Scincella rupicola*: AB057388, AB057403. *Scincus scincus*: AB028800, AB028812. *Sphenomorphus cherriei*: AB057377, AB057392. *Sphenomorphus indicus*: AB028808, AB028820. *Sphenomorphus maculatus*: AB028809, AB028821. *Sphenomorphus praesignis*: AB028810, AB028822. *Tiliqua nigrolutea*: AB057376, AB057391. *Tiliqua scincoides*: AB028795, AB028799, AB028837.

Appendix 2. Constrained trees which hypothesized the whole of *Tropidophorus* and the three depressed bodied species as monophyletic groups

Monophyly of the genus *Tropidophorus*: (*Scincus scincus*, *Eumeces schneiderii*, (((((((*Apterygodon vittatus*, *Dasia gricea*), *Dasia olivacea*), ((*Mabuya longicaudata*, *Mabuya macularia*), *Mabuya rudis*)), (((((*Mabuya affinis*, *Mabuya albilabris*), *Mabuya perrotetii*), (*Mabuya aureopunctata*, *Mabuya elegans*)), ((*Mabuya striata*, *Mabuya* sp.), *Mabuya maculilabris*), *Mabuya polytropis*), (*Mabuya unimarginata*, *Mabuya nigropunctata*))), ((*Carlia fusca*, (*Emoia caeruleocauda*, *Eugongylus* sp.)), ((*Corucia zebrata*, *Egernia frerei*), (*Tiliqua scincoides*, *Tiliqua nigrolutea*)))), ((*Lamprolepis smaragdina*, *Lygosoma bowringii*), (*Lygosoma koratense*, *Lygosoma quadrupes*))), (((*Isopachys anguinoides*, ((*Lipinia vittigera*, ((*Scincella lateralis*, *Sphenomorphus cherriei*), *Scincella rupicola*)), (*Sphenomorphus indicus*, *Sphenomorphus maculatus*))), (((*Tropidophorus berdmorei*, (*Tropidophorus latiscutatus*, *Tropidophorus matsuii*)), ((*Tropidophorus sinicus*, (*Tropidophorus robinsoni*, *Tropidophorus thai*)), ((*Tropidophorus baviensis*, *Tropidophorus hainanus*), *Tropidophorus murphyi*))), (((*Tropidophorus brookei*, (*Tropidophorus beccarii*, (*Tropidophorus partelloi*, *Tropidophorus misaminius*))), (*Tropidophorus baconi*, *Tropidophorus grayi*)), (*Tropidophorus cocincinensis*, *Tropidophorus microlepis*))))), *Sphenomorphus praesignis*))).

Monophyly of the three depressed-bodied species: (*Scincus scincus*, *Eumeces schneiderii*, (((((((*Apterygodon vittatus*, *Dasia gricea*), *Dasia olivacea*), ((*Mabuya longicaudata*, *Mabuya rudis*), *Mabuya macularia*)), (((((*Mabuya affinis*, *Mabuya albilabris*), *Mabuya perrotetii*), (*Mabuya aureopunctata*, *Mabuya elegans*)), ((*Mabuya striata*, *Mabuya* sp.), *Mabuya maculilabris*), *Mabuya polytropis*), (*Mabuya unimarginata*, *Mabuya nigropunctata*))), ((*Carlia fusca*, (*Emoia caeruleocauda*, *Eugongylus* sp.)), ((*Corucia zebrata*, *Egernia frerei*), (*Tiliqua scincoides*, *Tiliqua nigrolutea*)))), (*Lamprolepis smaragdina*, (*Lygosoma bowringii*, (*Lygosoma koratense*, *Lygosoma quadrupes*)))), (((*Isopachys anguinoides*, ((*Lipinia vittigera*, ((*Scincella lateralis*, *Sphenomorphus cherriei*), *Scincella rupicola*)), (*Sphenomorphus indicus*, *Sphenomorphus maculatus*))), (((*Tropidophorus brookei*, (*Tropidophorus beccarii*, (*Tropidophorus partelloi*, *Tropidophorus misaminius*))), (*Tropidophorus baconi*, *Tropidophorus grayi*)), (*Tropidophorus cocincinensis*, *Tropidophorus microlepis*))), (*Sphenomorphus praesignis*, (*Tropidophorus berdmorei*, ((((*Tropidophorus latiscutatus*, *Tropidophorus matsuii*), *Tropidophorus murphyi*), (*Tropidophorus baviensis*, *Tropidophorus hainanus*)), (*Tropidophorus sinicus*, (*Tropidophorus robinsoni*, *Tropidophorus thai*))))))).