

Phylogenetics of Fanged Frogs: Testing Biogeographical Hypotheses at the Interface of the Asian and Australian Faunal Zones

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Abstract.—The interface of the Asian and Australian faunal zones is defined by a network of deep ocean trenches that separate intervening islands of the Philippines and Wallacea (Sulawesi, the Lesser Sundas, and the Moluccas). Studies of this region by Wallace marked the genesis of the field of biogeography, yet few workers have used molecular methods to investigate the biogeography of taxa whose distribution spans this interface. Some taxa, such as the fanged frogs of the ranid genus *Limnonectes*, have distributions on either side of the zoogeographical lines of Wallace and Huxley, offering an opportunity to ask how frequently these purported barriers were crossed and by what paths. To examine diversification of *Limnonectes* in Southeast Asia, the Philippines, and Wallacea, we estimated a phylogeny from mitochondrial DNA sequences obtained from a robust geographic sample. Our analyses suggest that these frogs dispersed from Borneo to the Philippines at least twice, from Borneo to Sulawesi once or twice, from Sulawesi to the Philippines once, and from the Philippines to Sulawesi once. Dispersal to the Moluccas occurred from Sulawesi and to the Lesser Sundas from Java/Bali. Species distributions are generally concordant with Pleistocene aggregate island complexes of the Philippines and with areas of endemism on Sulawesi. We conclude that the recognition of zoogeographic lines, though insightful, may oversimplify the biogeography of widespread taxa in this region. [Dispersal; Philippines; Sulawesi; vicariance; Wallace's Line.]

The sharp transition between the Asian and Australian biotas that occurs in central Indonesia is of long-standing interest to biologists (Huxley, 1868; Lydekker, 1896; Wallace, 1860, 1863; Weber, 1904). Perhaps the most obvious faunal transition is seen in large mammals in this region. For example, tigers, bears, orangutans, elephants, and rhinos occur in western Indonesia but not in central and eastern Indonesia. Similarly, many marsupial species are found in Australia and New Guinea, a few occur in central Indonesia, and none are endemic to western Indonesia (Musser, 1987). Anuran diversity is less conspicuous but similarly partitioned; the families Megophryidae and Bombinatoridae, for example, occur in western Indonesia and/or the Philippines but not in central or eastern Indonesia, whereas frogs of the family Microhylidae and the subfamily Platymantinae have high diversity on New Guinea and the Philippines and comparatively depauperate or no representation in western Indonesia. These faunal differences are echoed in many other groups such as butterflies (Holloway, 1987) and plants (van Balgooy, 1987). Wallace (1863) proposed a biogeographical division between Bali and Lombok, Borneo and Sulawesi, and the Philippines and Sulawesi (Fig. 1) but later moved it to divide Sulawesi from the Moluccas (Wallace, 1910). Huxley's Line is similar to Wallace's but runs between Palawan and the oceanic islands of the Philippines (Huxley, 1868). Lydekker's Line lies on the eastern extent of Wallacea (Sulawesi, the Lesser Sunda Islands, and the Moluccas) between the Moluccas and New Guinea and follows the

edge of the Sahul Shelf (Lydekker, 1896). These attempts to characterize a multitaxon break between the Asian and Australian regions underscore a remarkable faunal transition.

Despite this abrupt transition, some taxa are widespread in this region (Heaney, 1986; Boer and Duffels, 1996; How and Kitchener, 1997), offering an opportunity to assess the potentially powerful impact of abiotic factors on biodiversity. Only recently, however, have researchers used a phylogenetic approach to examine biogeography in this region (Holloway, 1998; Evans et al., 1999; McGuire and Kiew, 2001; Brown and Guttman, 2002).

Frogs are considered poor dispersers across ocean barriers (Meyers, 1953; Savage, 1973), and their species richness on islands is generally lower than that in comparably sized areas on continents (Duellman, 1999). Species of the ranid genus *Limnonectes*, however, have a diverse representation in South Asia and in Southeast Asia, the Philippines, and Wallacea (Fig. 2; Inger, 1999). The unexpected distribution of *Limnonectes* raises questions about the frequency and paths of dispersal across ancient ocean barriers and about the evolutionary consequences of fragmentation.

Systematics of Limnonectes

Previously, most fanged frogs were placed in the subgenus *Limnonectes* and further partitioned among

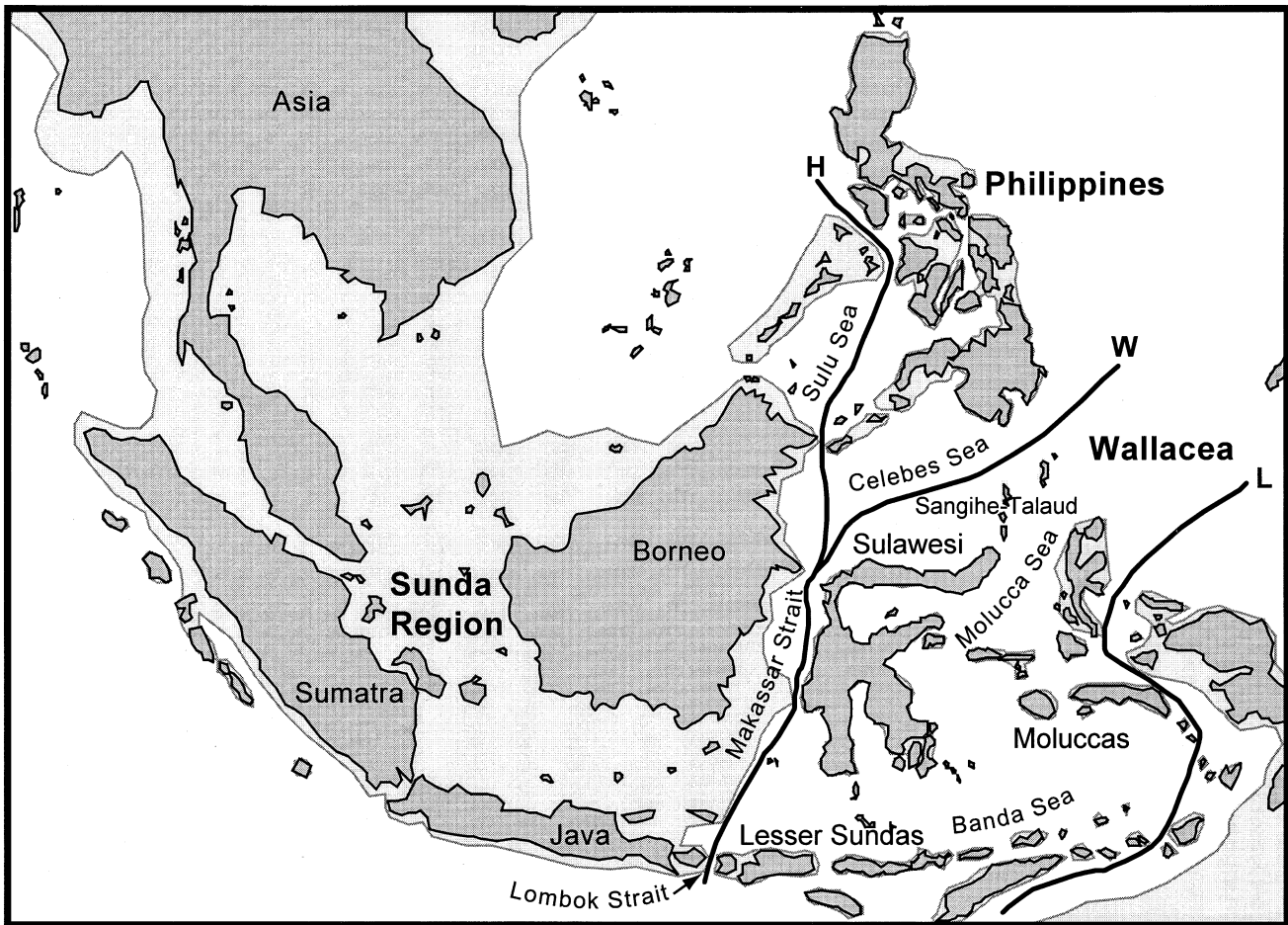


FIGURE 1. Distribution of land and sea during late Pleistocene during sea level reduction of 120 m (modified from Voris, 2000). Wallace's 1963 (W), Huxley's (H), and Lydekker's (L) lines are labeled. Also labeled are long-standing bodies of water within the distribution of *Limnonectes* and islands mentioned in the text.

three species groups, the *grunniens* group, the *kuhlii* group, and the *microdiscus* group (Dubois, 1987, 1992), although this classification was not based on systematic analysis of characters (Inger, 1996). Morphological and molecular data support monophyly of *Limnonectes* and its recognition as a genus (Emerson and Berrigan, 1993; Emerson et al., 2000), but do not support other groupings in Dubois's (1992) classifications. A molecular analysis (Emerson et al., 2000) identified five monophyletic species groups within *Limnonectes* (Table 1).

The Sunda region includes at least 27 species of *Limnonectes*, of which 21 are endemic (Inger and Voris, 2001). On Sulawesi, 4 endemic species (*L. arathooni*, *L. heinrichi*, *L. microtympnum*, *L. modestus*) have been described and at least 12 others are known (Cranbrook, 1981; Iskandar and Tjan, 1996; Inger, 1999; Inger and Voris, 2001). On the oceanic islands of the Philippines (not including Palawan), 8 endemic species have been described (Inger, 1954, 1966; Alcalá and Brown, 1998; Brown and Diesmos, 2002). The present study includes approx-

imately 45 species; we increased sampling of individuals from Sulawesi and the Philippines relative to members of species group 3 (Table 1; Emerson et al., 2000) and as well as the Lesser Sunda Islands, the Sunda region, and outgroups.

Biogeography and Geology

For significant periods during the past 50 million years, parts of Southeast Asia (Peninsular Malaysia, Borneo, Sumatra, and Java) were united into a land-positive peninsula, known as the Sunda Shelf (Fig. 1; Hall, 1996, 1998). However, most islands in the Philippines and Wallacea have been separated from the Sunda Peninsula and from each other by deep oceanic trenches ever since they became land positive. Southwestern Sulawesi was accreted underwater to Borneo during the Early Eocene (55 million years ago), and this region and other parts of Sulawesi were still completely submerged by the end of the Oligocene (25 million years

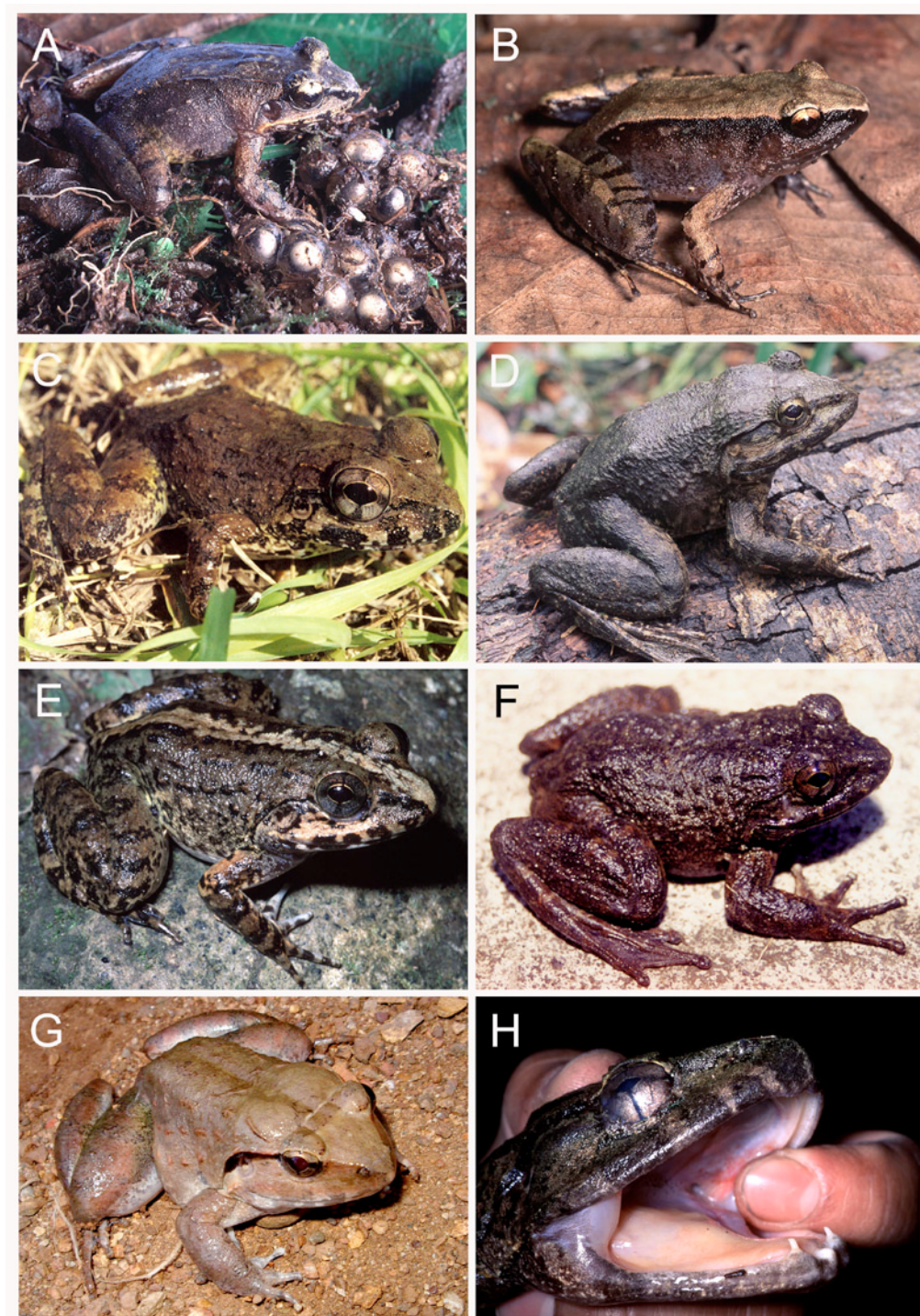


FIGURE 2. Morphological variation in *Limnonectes*. (A) Male *L. arathooni* brooding eggs; TNHC 59087; Indonesia, Sulawesi Island, Sulawesi Selatan Province, Desa Parang Bintolo (photo: R. M. Brown). (B) Male *L. parvus*; PNM 7447; Philippines, Mindanao Island, Davao City Province, Municipality of Calinan, Barangay Malagos, Philippine Eagle Foundation Center (photo: R. M. Brown). (C) *L. sp. 2*; AMNH 167171; Indonesia, Sulawesi Island, Sulawesi Tenggara Province, Desa Tolala (photo: B. J. Evans). (D) Male *L. sp. 1*; TNHC 59017; Indonesia, Sulawesi Island, Sulawesi Tengah Province, Kabupaten Banggai, Kecamatan Bagimana, Desa Siuna (photo: R. M. Brown). (E) *L. sp. T*; RMB 2499 (deposited in MZB); Indonesia, Sulawesi Island, Sulawesi Selatan Province, Kabupaten Tana Toraja, Kecamatan Rindingallo, Desa Awan (photo: R. M. Brown). (F) Female *L. cf. microtympanum 2*; AMNH 167145; Indonesia, Sulawesi Island, Sulawesi Selatan Province, Desa Barru (photo: B. J. Evans). (G) Male *L. kardashani*; TNHC 62607; Indonesia, Nusa Tenggara Province, Flores Island, Desa Tondong Belang (photo: B. J. Evans). (H) Male *L. macrocephalus* fangs; FMNH 259573 (deposited in PNM); Philippines, Luzon Island, Kalinga Province, Municipality of Balbalan, Barangay Balbalasang (photo: R. M. Brown).

TABLE 1. Comparison of phylogenetic estimations (MP = maximum parsimony, ML = maximum likelihood) in Emerson et al. (2000; E2000) and the present study.

Clade name, MP analysis of E2000	Clade in ML analysis, E2000	Species in clade, E2000	Species included in present study	Clade present in MP analysis of present study	Clade present in ML and Bayesian analyses of present study	Additional members of clade in present study	
Group 1a	no	<i>L. laticeps</i>	yes	yes	yes		
		<i>L. gyldenstolpei</i> (formerly <i>L. pileata</i>)	yes				
		<i>L. limborgii</i>	no				
Group 1b	yes	<i>L. kuhlii</i> (Sahah)	yes	yes	yes		
		<i>L. kuhlii</i> (Brunei)	yes				
		<i>L. asperatus</i>	yes				
Group 2	yes	<i>L. leporinus</i> (Sabah)	yes	yes	yes		
		<i>L. leporinus</i> (Brunei)	yes				
		<i>L. leporinus</i> (Kalimantan)	yes				
Group 3	yes	<i>L. leytsensis</i> (Philippines)	yes	yes	yes	<i>L. cf. magnus</i> <i>L. visayanus</i> <i>L. woodworthi</i>	
		<i>L. acanthii</i> (Philippines)	yes				
		<i>L. sp. nov. = L. sp. D</i> (Sulawesi)	yes				
		<i>L. modestus</i> (Sulawesi)	yes			<i>L. heinrichi</i> complex <i>L. sp. T</i> <i>L. sp. 1</i>	
		<i>L. magnus</i> (Philippines)	yes				
		<i>L. microtypanum</i> (Sulawesi)	yes				
		<i>L. macrocephalus</i> (Philippines)	yes				
							<i>L. sp. G2</i>
Group 4	yes	<i>L. blythii</i> (Endau)	yes	yes	yes	<i>L. sp. 2</i> <i>L. arathooni</i> <i>L. sp. V complex 1</i> <i>L. sp. V complex 2</i> <i>L. blythi</i> (Sumatra)	
		<i>L. blythii</i> (Thailand)	yes				
		<i>L. blythii</i> (Kuala Lumpur)	yes				
		<i>L. ingeri</i>	yes				
		<i>L. malesianus</i> (Sarawak)	yes				
		<i>L. malesianus</i> (Kalimantan)	no				
		<i>L. shompenorum</i>	no				
		<i>L. macrodon</i>	yes				

ago; Hall, 2001). Palawan was periodically connected to Borneo during and before the Pleistocene but was never connected to the oceanic islands of the Philippines (Hall, 1998, 2001). Thus, the distribution of *Limnectes* spans several of these long-standing water barriers, including the Sulu Sea between the Philippines and Borneo, the Celebes Sea between Sulawesi and the Philippines, the Makassar Strait between Borneo and Sulawesi, the Lombok Strait between Bali and Lombok, the Molucca Sea between Sulawesi and the Moluccas, and the Banda Sea between Sulawesi and the Lesser Sundas (Fig. 1). These bodies of water can be considered permanent with respect to *Limnectes* evolution because they have existed ever since these islands became land positive (Hall, 1996, 1998, 2001).

In the Pleistocene, the Philippine islands were less fragmented than they are now; groups of islands formed composite Pleistocene aggregate island complexes (PAICs; Brown and Diesmos, 2002) that were isolated from one another by deep-water channels (Fig. 3; Heaney, 1985, 1986). In contrast, Sulawesi was probably more fragmented in the Pleistocene than it is today. Sulawesi is a mosaic assembled from the accretion of

many islands (Hall, 2001), but the boundaries of congruent areas of endemism (AOEs) shared by unrelated taxa do not correspond in location with the suture sites of most of Sulawesi's island precursors (Fig. 4; Evans et al., 2003b).

Goals

Here, we test the general hypothesis that phylogenetic relationships of *Limnectes* are strongly influenced by long-standing aquatic barriers. We predict (1) dispersal to be rare across "permanent" water barriers (the Makassar Strait, Celebes Sea, etc.) between the Sunda Shelf, Sulawesi, the Philippines, and other parts of the range of *Limnectes*. Specifically, we test the hypothesis of monophyly of Philippine sequences, monophyly of Sulawesi sequences, and corollaries of these hypotheses (Fig. 5). We also predict that (2) species distributions on the Philippines should correspond with PAICs (Heaney, 1985, 1986; Brown and Diesmos, 2002) and (3) distributions on Sulawesi should correspond with AOEs defined by other taxa (Evans et al., 2003b). We predict monophyly of sequences within Philippine PAICs and within

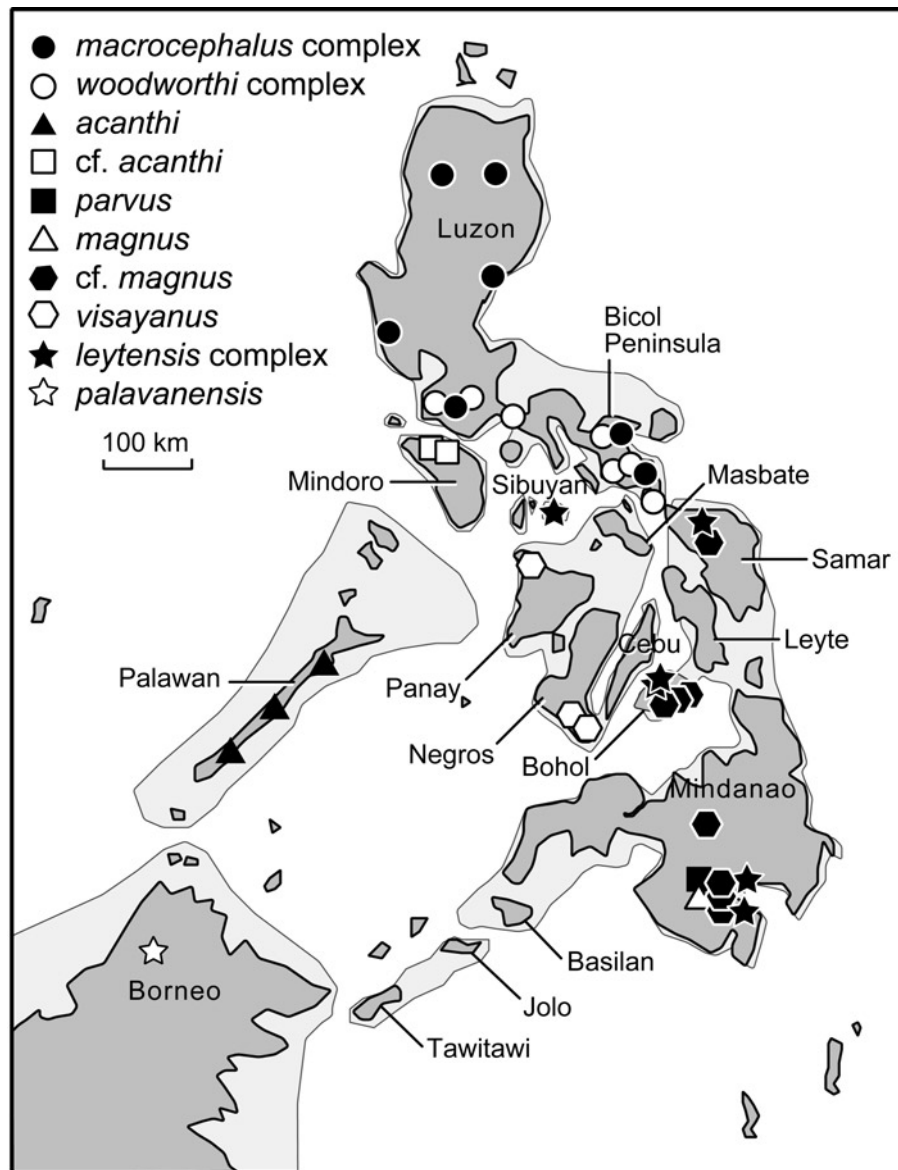


FIGURE 3. Distributions of Philippine *Limnonectes* samples examined and names of islands mentioned in the text. Borders of seven PAICs (corresponding to 120 m underwater bathymetric contour) are shaded.

Sulawesi AOE. To these ends, we estimated a phylogeny from mitochondrial DNA (mtDNA) sequences from a broad geographic sampling of *Limnonectes*.

MATERIALS AND METHODS

Molecular Data

New mitochondrial sequences were obtained from 146 individuals, including some outgroups, some species from the Sunda region, one species from the Lesser Sunda Islands, and many sequences from Sulawesi and the Philippines (Appendix). The gene order of the region sequenced (5'-3') is tRNA^{phe}, 12S ribosomal DNA (rDNA), tRNA^{val}, 16S rDNA. Most

of our sequences have 21 base pairs (bp) of the 3' section of the tRNA^{phe}, the entire 12S and tRNA^{val} gene, and most of the 16S rDNA gene (positions 2,690–5,119 in the *Rana nigromaculata* complete mtDNA sequence, accession no. AB043889) for a total of about 2,430 bp. These sequences are approximately 179 bases short of the 3' end of the 16S gene. We used an ABI Prism 3100 capillary automated sequencer and primers MVZ 59, tRNA^{val}-H, H3296, and 16Sa-H (Goebel et al., 1999) and 12Sm-L (5'-GGCAAGTCGTAACATGGTAAG-3'), 16Sc-L (5'-GTRGGCCTAAAAGCAGCCAC-3'), and 16Sd-H (5'-CTCCGGTCTGAACTCAGATGACGTAG-3') to amplify and sequence this region.

Additional partial sequences for the 12S and 16S mtDNA for 31 individuals, mostly species from Asia and

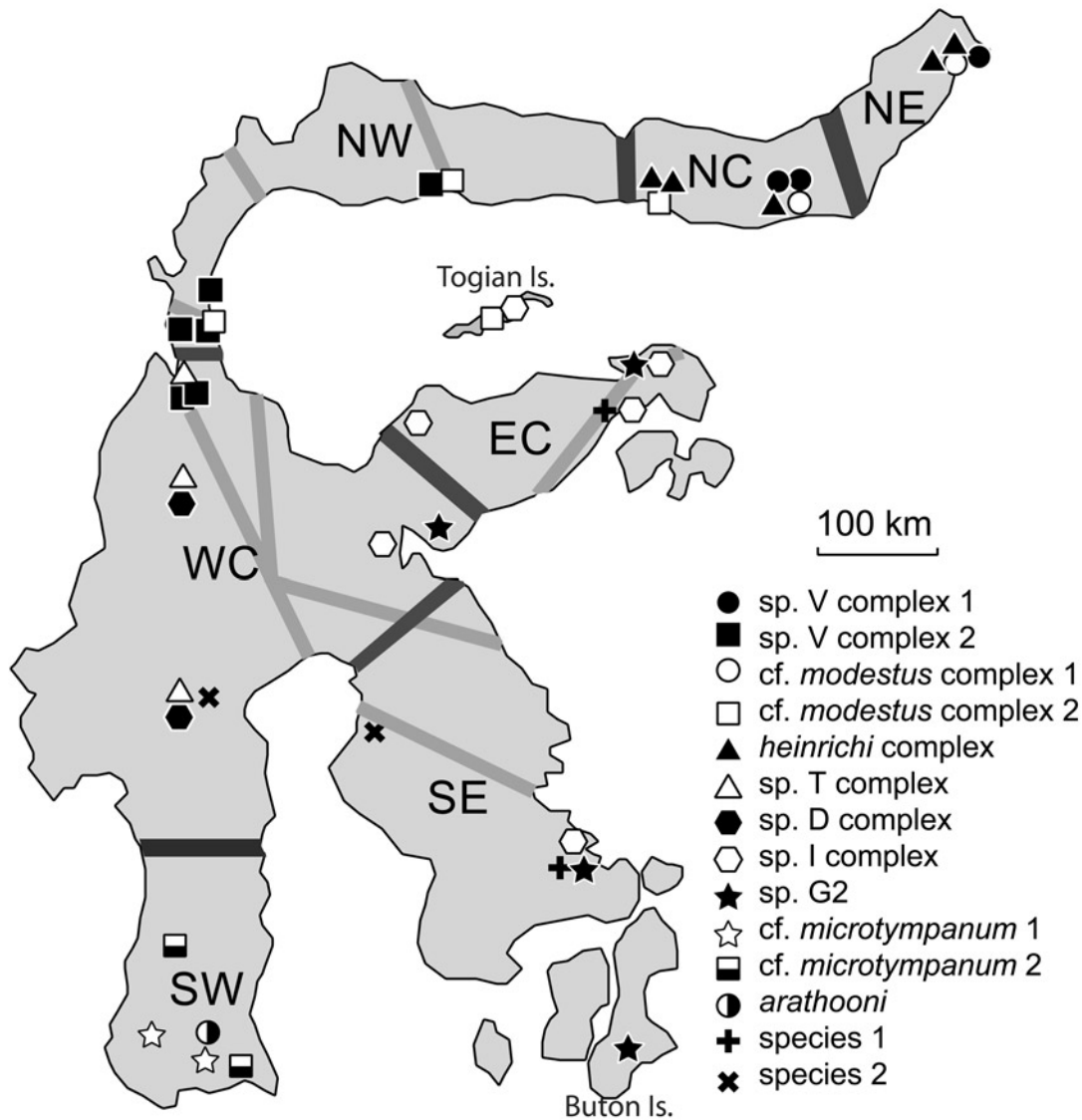


FIGURE 4. Distribution of Sulawesi *Limnonectes* samples examined in this study. Dark lines indicate the margins of AOEs on Sulawesi (Evans et al., 2003b) labeled northwest (NW), north central (NC), northeast (NE), west central (WC), east central (EC), southwest (SW), and southeast (SE). Gray lines indicate suture sites of Sulawesi’s island precursors (from Hall, 2001).

the Sunda Shelf, were obtained from GenBank (see the Appendix; Emerson et al., 2000). Most of those sequences include a ~330-base fragment of 12S rDNA and a ~813-base fragment of 16S rDNA. Our sequences overlap both of these regions. Portions of the GenBank sequences with unavailable information were coded as missing for phylogenetic analysis.

To facilitate analysis, 61 sequences were not used because they differed from others by <0.005 (<12 bp), leaving a total of 115 terminals (GenBank accession nos. in the Appendix). We used five taxa as outgroups: *Occidozyga laevis* (two individuals), *Fejervarya limnocharis* (two individuals), *F. vittigera*, *Hoplobatrachus occipitalis*, and *H. rugulosus*. The choice of these taxa as appropriate outgroups is based on work in progress by R.M.B., F. Bossuyt, and D.C.C. Sequences

were aligned with Sequence Navigator 1.01 (Applied Biosystems, 1994) using the Clustal V alignment algorithm (Higgins et al., 1991) and then fine-tuned by eye with MacClade 4.0 (Maddison and Maddison, 2000). When possible, regions of ambiguous homology were resolved so that informative sites were minimized.

We deleted the last 132 bases of *Limnonectes asperatus* (GenBank AF183128) because this region does not align well even though this region is conserved in other homologous sequences. Additionally, 34 bases from positions 2,283–2,316 were excluded from outgroups and Asian and Sunda Shelf *Limnonectes* because homology in this region was difficult to assess for these individuals but was possible for individuals from the Philippines and Sulawesi.

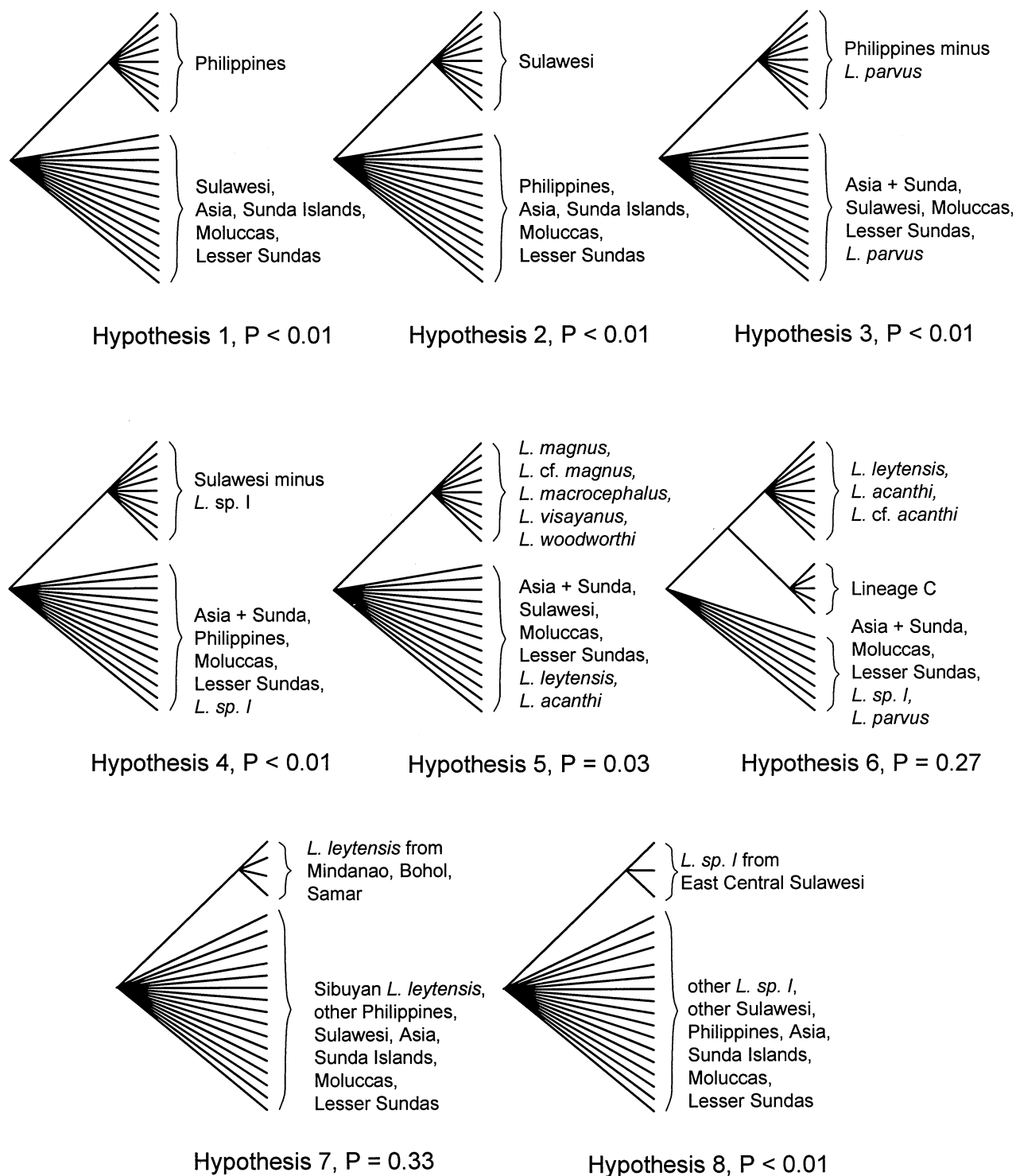


FIGURE 5. Eight phylogeographic null hypotheses tested with parametric bootstrap tests. P values are indicated. After Bonferroni correction, hypotheses 5, 6, and 7 were not rejected.

We suspect an error in sequence assembly in a 100-base portion of *Limnnectes malesianus* from Borneo (GenBank U66129), based on comparison of this sequence to another individual of the same species. In sequence U66129,

bases from positions 42–142 have two segments that are rearranged. Bases 42–99 are homologous to sequences that should begin in position 84 of this sequence and bases 100–142 are homologous to sequences that should

begin in position 42. We excluded this individual and sequenced another (GenBank AY313692).

To compare error rates of published sequences, we resequenced an individual used by Emerson et al. (2000) (USNM 222570, accession nos. U66118 and U66119). Divergence between them was only 0.002 (2 differences out of ~1,100 bases). Only our sequence (GenBank AY313704) was used in this analysis.

Phylogenetic Analysis

Phylogenetic analysis used maximum parsimony, maximum likelihood, and Bayesian methods. For maximum parsimony analysis, we performed a heuristic search for the most-parsimonious tree with 100 replicates of random taxon addition with tree bisection-reconnection branch swapping on a starting tree obtained by stepwise addition, using PAUP* 4.0 (Swofford, 2002). All characters were weighted equally, and gaps were treated as missing data. Nonparametric bootstrap values were obtained with 2,000 replicates, each with a single replicate of random taxon addition, and other settings identical to the heuristic maximum parsimony search. Decay index values were calculated for each node with Autodecay 4.0.2 (Eriksson, 1999).

For model-based analyses, we used Modeltest 3.06 (Posada and Crandall, 1998) to evaluate different models of evolution. We used a likelihood ratio test (Goldman, 1993) to determine whether the likelihood of a tree with a molecular clock enforced was significantly less likely than one without a molecular clock under the general time reversible model of evolution with some invariable sites and variable sites assumed to follow a gamma distribution (GTR+I+ Γ), in which degrees of freedom are equal to the number of terminals minus two (Huelsenbeck and Rannala, 1997). Maximum likelihood analysis was performed with PAUP* with two rounds of successive approximation, each with one replication of random addition of taxa. Initial parameters were set to those estimated from a neighbor-joining tree and then reestimated from the resulting topology and set to these new values for the second iteration. Swapping was terminated after 50,000 rearrangements in the first round and after 30,000 rearrangements in the second round. Further rounds of successive approximation were not performed because the resulting topologies were so similar and because the difference in likelihood score ($-\ln$) of each was only 0.24.

Bayesian analysis was performed with MrBayes 2.01 (Huelsenbeck and Ronquist, 2001) under the model selected by Modeltest (GTR+I+ Γ , see below). We ran four Markov chain Monte Carlo analyses starting with random trees for each of four simultaneous chains for 1,000,000 total generations, with a burn-in of 200,000 generations, flat prior distributions for model parameters, and the differential heating parameter set to 0.2. The parameter values from each run were similar, suggesting that the chains were run for a sufficient number of gen-

erations to adequately sample the posterior probability landscape. Additionally, pairwise distances among sequences were estimated with the uncorrected "p" distance with PAUP*.

Taxonomy

We examined mtDNA sequences from a small number of individuals per species over a wide geographic range. Many of the species are undescribed, and further taxonomic work is needed for allocation of individuals to available names. As a crude way of sorting species and delimiting species boundaries, we applied some informal names to monophyletic groups of individual sequences. Thus, we allocated individual sequences to groups based on phylogeny rather than characters per se. Because our goal was to examine phylogeography and not to name new species, we did not name every clade, we referred to some sets of clades as species complexes, and we viewed these species assignments as working hypotheses.

Hypothesis Testing

In general, we expect a group of species on an island to form a clade because of diversification *in situ*. If this null hypothesis is rejected because portions of the clade are present on another island, this can be explained by (1) dispersal over a preexisting water barrier or (2) vicariance, *i.e.*, fragmentation of a once continuous distribution. In the present case, most of the islands were never in contact (see details above); thus, if the null hypothesis is rejected, explanation 2 (vicariance) is not feasible and explanation 1 (dispersal) is the better alternative.

To test whether the data are inconsistent with various biogeographical hypotheses that differ from the estimated phylogeny, we used parametric bootstrapping (SOWH test; Hillis et al., 1996; Huelsenbeck et al., 1996; Goldman et al., 2000). A heuristic search for the most-parsimonious tree consistent with each biogeographical (null) hypothesis was performed using 100 replications of random taxon addition. The set of most-parsimonious trees was ranked under the Kimura two-parameter plus gamma distribution (K2P+ Γ) model of evolution (Kimura, 1980), and the most likely tree was selected for data simulation. For each parametric bootstrap test, we used this tree and the data to select a model of evolution with a hierarchical likelihood ratio test (GTR+I+ Γ was selected in each case). We simulated 100 datasets with this model under the null hypothesis with Seq-Gen 1.2.5 (Rambaut and Grassly, 1997). For each simulated data set, we calculated the difference in tree length (parsimony score) among searches unconstrained and constrained for the null hypothesis. The Logreader program (unpublished program written by D. Zwickl) was used to parse the output files. Given the null hypothesis, the probability (P) of obtaining the

observed tree length difference is the fraction of simulations in which the tree length difference is as extreme as or more extreme than the observed tree length difference. We applied the sequential Bonferroni procedure to adjust the alpha value for hypothesis rejection in multiple tests (Rice, 1989). We tested two major biogeographical hypotheses: that the species of *Limnonectes* on the Philippines are monophyletic (hypothesis 1) and that the species on Sulawesi are monophyletic (hypothesis 2). Hypotheses 3–8 were derived from the results of our phylogenetic analyses. Hypotheses are summarized in Figure 5 and described in detail in the results section since their formulation is based on inferred phylogenies.

Area Cladograms

We made area cladograms from the maximum likelihood topology and from topologies not rejected by parametric bootstrap tests by changing the name of each species to the name of one of the five regions (Asia-Sunda region, the Philippines, Sulawesi, the Moluccas, or the Lesser Sunda Islands) from which they originated. We inferred the minimum number of dispersal events from these topologies by (1) constructing a single character data matrix in which the character state of each taxon was a number referring to one of the five major locations and then (2) using delayed transformation for character optimization on the topology using PAUP*. The location of outgroups was defined as Asia-Sunda region. To evaluate uncertainty in our phylogenetic estimate (Huelsenbeck et al., 2000), we used constraint trees (described below) to compute the proportion of trees saved from the post-burn-in Bayesian analysis that is consistent with all seven of the inferred dispersal events and also with specific dispersal events.

RESULTS

Phylogeny

Parsimony searches recovered four equally parsimonious trees of 7,950 steps (consistency index = 0.294, retention index = 0.665; Figs. 6, 7). The four trees differ only in intraspecific relationships within a clade of three *L. acanthi* sequences from Palawan and within a clade of three *L. sp. V* complex 2 sequences from Sulawesi.

For model-based phylogeny estimation, the GTR+I+ Γ model was selected by the hierarchical likelihood ratio test. The hypothesis that these sequences conformed to a molecular clock was rejected ($P < 0.001$). Parameters estimated from Modeltest were base frequencies (A, C, G) = (0.3662, 0.2294, 0.1563), rate matrix (A-C, A-G, A-T, C-G, C-T, G-T) = (4.9663, 16.6902, 6.9353, 1.3348, 43.5866, 1), shape parameter = 0.5895, and proportion of invariant sites = 0.2913. Bayesian analysis using this model recovered a consensus topology (Figs. 8, 9) that is

identical to the likelihood tree after the second round of searching ($-\ln = 38014.16$). These model-based topologies are similar to the parsimony tree, with a few exceptions discussed below. Branches unique to the Bayesian and likelihood trees have high posterior probabilities (mostly > 80), whereas branches unique to the parsimony tree have low bootstrap values or are not in the bootstrap consensus at all.

All five of the species groups identified by Emerson et al. (2000) are also supported by our analyses, although expanded taxon sampling and more data altered some relationships within and among these species groups (Table 1). Also supported by Emerson et al. (2000) and our analyses is the monophyly of groups 2, 3, and 4 plus *L. paramacrodon*, *L. grunniens*, *L. ibanorum*, *L. cf. blythi* 3, *L. finchi*, *L. palavanensis*, and *L. parvus* (this last taxon is in our study only), with respect to a paraphyletic assemblage containing groups 1a and 1b.

In our analyses, most Asian and Sunda Shelf species form multiple paraphyletic assemblages with respect to Philippine and Sulawesi sequences (Figs. 6, 8), but the topology of our analyses differ from those of Emerson et al. (2000). In both of our analyses, for example, group 2 is sister to a clade containing group 3, group 4, and *L. finchi*, *L. palavanensis*, *L. parvus*, *L. paramacrodon*, *L. ibanorum*, *L. grunniens*, *L. sp. I* complex, and *L. cf. blythi* 3, whereas in the parsimony analyses of Emerson et al. (2000) group 2 is sister to group 3 only. In their likelihood analysis, group 2 is sister to a clade containing group 3, group 4, and *L. paramacrodon*, *L. grunniens*, *L. ibanorum*, and *L. blythi* 3 (*L. sp. I* was not in their analysis), and all of these taxa form a clade that is sister to *L. finchi* and *L. palavanensis* (*L. parvus* was not in their analysis).

Most of our sequences from the Philippines and Sulawesi are members of clade A (Figs. 7, 9). The Philippines species consist of four primary clades: (1) *L. parvus*, which is a close relative of Bornean *L. palavanensis* and *L. finchi*, (2) the *L. leytensis* complex, (3) the *L. acanthi* complex, and (4) other Philippine species, which are derived from a paraphyletic assemblage of Sulawesi species. Sulawesi species are also not monophyletic and consist of a clade with a single undescribed giant species (*L. sp. I*) and a group of at least 15 mostly undescribed species that is paraphyletic to a mostly Philippine clade (lineage D, Fig. 7) or an entirely Philippine clade (lineage E, Fig. 9). *Limnonectes sp. I* is one of three undescribed giant species on Sulawesi and is related to *L. grunniens* on the Moluccas. A large paraphyletic assemblage of sequences on Sulawesi share a more recent common ancestor with *L. acanthi* and *L. cf. acanthi* than with *L. leytensis*. These topologies also differ from those of Emerson et al. (2000) in that *L. leytensis* and *L. acanthi* are basal to most other species from Sulawesi and the Philippines in our study, whereas in the parsimony and likelihood analysis of Emerson et al. (2000) *L. microtympanum* is the most basal member of group 3.

Results from our parsimony and model-based analyses differ in some respects. Parsimony analysis, for

example, places northern Sulawesi sequences (species groups *L. cf. modestus* 1 and *L. cf. modestus* 2) sister to *L. woodworthi* (within lineage D, Fig. 7). Bayesian and likelihood analyses infer a clade containing most Philippine species (*L. magnus* 1, *L. cf. magnus*, *L. woodworthi*, *L. macrocephalus*, *L. visayanus*) as sister taxon (lineage E, Fig. 9) to *L. cf. modestus* 1 and *L. cf. modestus* 2. Other conflicting relationships in the model-based and parsimony trees mostly concern Bornean taxa. In the parsimony analysis, for example, a clade containing *L. finchi*, *L. palawanensis*, and *L. parvus* is sister to a clade containing *L. ibanorum*, *L. grunniens*, and *L. sp. I* (Fig. 6). In the Bayesian and likelihood analyses, however, this former clade is sister to a clade including *L. ibanorum*, *L. grunniens*, *L. sp. I*, *L. cf. blythi* 1, 2, and 3, *L. macrodon*, *L. ingeri*, *L. malesianus*, *L. paramacrodon*, and also clade A.

Biogeographic Hypotheses

Hypothesis 1 postulates monophyly of all Philippine species (Fig. 5) and is consistent with a single origin of *Limnonectes* on the Philippines. The most-parsimonious tree under this hypothesis has a length of 8,023 compared with a length of 7,950 under no constraint. Hypothesis 1 is rejected at $P < 0.01$. Given that the Philippine species are not monophyletic, we tested hypothesis 3, which postulates monophyly of Philippine sequences excluding *L. parvus*, which was found to be outside of lineage A (Figs. 6, 8). This hypothesis is consistent with a single origin of *Limnonectes* (excluding *L. parvus*) on the Philippines; in other words, monophyly of Philippines *Limnonectes* within lineage A (Figs. 5, 7, 9). The shortest tree under this hypothesis is 7,980 steps long; hypothesis 3 also is rejected at $P < 0.01$.

Hypothesis 2 postulates monophyly of all Sulawesi species (Fig. 5). The best parsimony tree under this hypothesis is 8,029 steps, and this hypothesis is rejected at $P < 0.01$. Hypothesis 4 postulates monophyly of Sulawesi sequences not including *L. sp. I*, which was found to be outside of lineage A (Figs. 6, 8). In other words, it tests the monophyly of the Sulawesi species within lineage A (Figs. 5, 7, 9). Under this hypothesis the best tree is 7,968 steps, compared with the unconstrained length of 7,950. Hypothesis 4 is rejected at $P < 0.01$. Thus, our data indicate that the Sulawesi species are paraphyletic with respect to Philippine species in lineage A (Figs. 7, 9).

Hypothesis 5 posits monophyly of the following Philippine species: *L. magnus*, *L. cf. magnus*, *L. macrocephalus*, *L. visayanus*, and *L. woodworthi* (Fig. 5). This hypothesis conflicts with the parsimony analysis that postulates dispersal of part of lineage D (Fig. 7) from the Philippines to Sulawesi but is consistent with the topology of the Bayesian and likelihood analyses, where these Philippine species are monophyletic (lineage E, Fig. 9). The shortest tree under this hypothesis is 7,951, only 1 step longer than the unconstrained length of 7,950. This hypothesis is not rejected by parametric bootstrapping after Bonferroni correction ($P = 0.03$). Thus, we cannot reject monophyly of the Philippine species in this cluster.

Hypothesis 6 postulates a clade containing two Philippine species groups, *L. leytensis* and *L. acanthi* and that this clade is the sister of lineage C (Figs. 5, 7, 9). Monophyly of a lineage that includes *L. leytensis* and *L. acanthi* to the exclusion of lineage C (Figs. 7, 9) is potentially consistent with a direct dispersal of an ancestor of lineage C from Borneo to Sulawesi rather than dispersal of this ancestor from the Philippines to Sulawesi. In contrast to this scenario, unconstrained parsimony and model-based analyses suggest that lineage C was derived from Philippine species (Figs. 7, 9). The shortest tree under hypothesis 6 is 7,954 steps or 7,950 steps under no constraint, and hypothesis 6 is not rejected ($P = 0.27$). The shortest trees under hypothesis 6 are also consistent with hypothesis 5.

Hypotheses 7 and 8 test the significance of two phylogeographic patterns that are inconsistent with Philippine PAICs and Sulawesi AOE. Hypothesis 7 postulates monophyly of *L. leytensis* sequences from the Greater Mindanao PAIC (Mindanao, Bohol, Samar) and is consistent with the geological history of this region that suggests these islands were connected to one another but not to Sibuyan Island. The shortest tree under hypothesis 7 is 7,953 steps or 7,950 steps under no constraint, and this hypothesis is not rejected ($P = 0.33$). Hypothesis 8 postulates a clade containing Sulawesi *L. sp. I* sequences from the east central AOE (Fig. 5) and is consistent with patterns of differentiation seen in other taxa such as monkeys and toads (Evans et al., 2003b). The shortest tree under hypothesis 8 is 7,964 steps or 7,950 steps under no constraint, and this hypothesis is rejected ($P < 0.01$).

Area Cladograms

Seven dispersal events are suggested by the likelihood topology (Fig. 10a). Topologies consistent with hypotheses not rejected by parametric bootstrapping have alternative interpretations for the origin and destination of dispersal events (Figs. 10b–d). The joint posterior probability of all of these dispersal events as quantified by the proportion of the trees saved by the Bayesian analysis that are consistent with the constraint tree in Figure 11 is 0.929. Posterior probabilities of each independent dispersal event are generally even higher because a more relaxed constraint tree can be used to filter the set of all trees. For example, a tree retaining only constraints 3, 4, 5, 6, and 7 (Fig. 11) is consistent with dispersal from the Philippines to Sulawesi and from Sulawesi back to the Philippines. Topologies consistent with these constraints have a joint posterior probability of 0.985. A tree with constraints 1, 2, 3, 8, 9, 10, 11, 12, and 13 (Fig. 11) is consistent with dispersal from Asia to the Lesser Sundas, from Asia to the Philippines (*L. parvus*), and from Asia to (Sulawesi + Moluccas). Topologies consistent with these constraints have a joint posterior probability of 0.943. The posterior probability of dispersal from Asia to the Philippines (*L. leytensis* and *L. acanthi*) requires the addition of constraints 4, 5, 14, and 15 to the latter set of constraints. This dispersal has the same joint posterior probability as the full constraint topology depicted in Figure 11 (0.929).

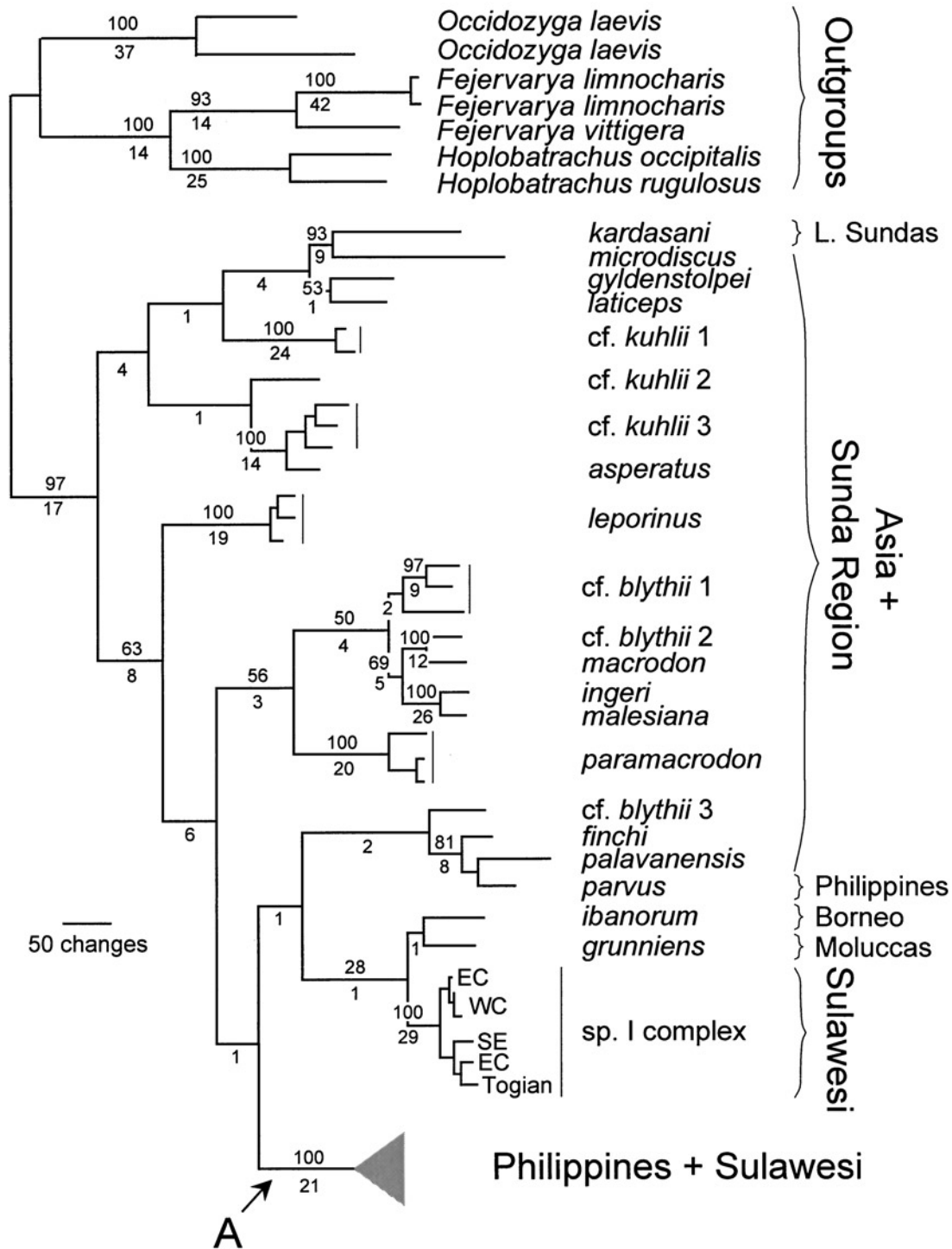


FIGURE 6. Basal relationships of one of four similar most-parsimonious topologies. Branch lengths are proportional to number of steps on each branch. Bootstrap values >50 are above branches; decay values are below. For clarity, bootstrap and decay values of some terminal clades are not shown. Locations of Sulawesi samples are indicated by EC, WC, and SE in reference to AOE (Fig. 4) and samples from the Togian Islands are also indicated. Lineage A is depicted in Figure 7.

DISCUSSION

Vicariance and Dispersal

Hypotheses of vicariance versus dispersal differ in the assumed age of the barrier relative to the age of ge-

netic differentiation (Wiley, 1988). Under a vicariance hypothesis, a continuously distributed taxon is fragmented, whereas under a dispersal hypothesis a barrier to dispersal exists prior to diversification. There is considerable debate over the use of dispersal and vicariance

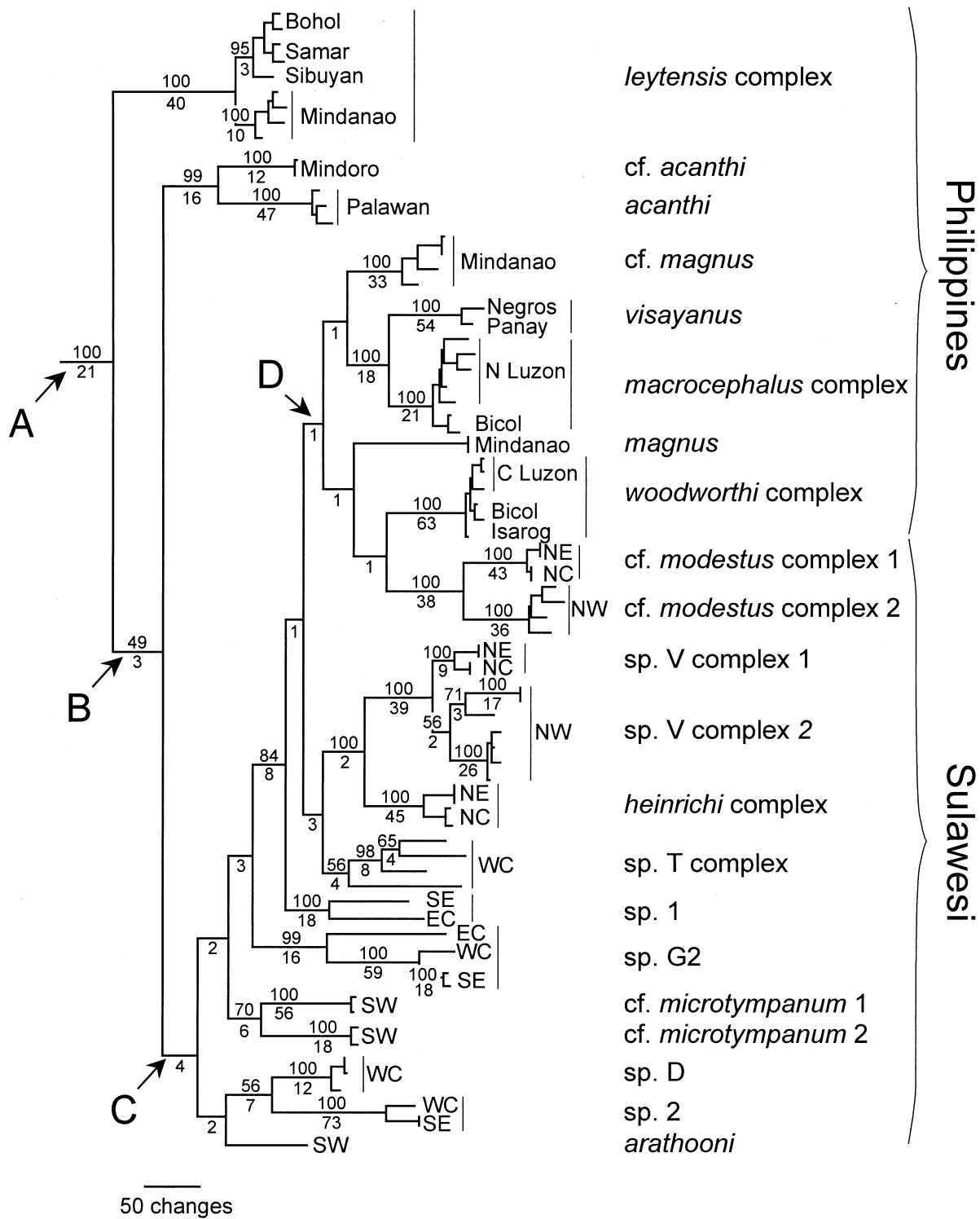


FIGURE 7. Relationships among Philippine and Sulawesi members of lineage A (Fig. 6) in one of four similar most-parsimonious trees. Sulawesi AOE's are indicated by NE, NC, NW, WC, SE, EC, SW (Fig. 4). Additional lineages of interest indicated with letters B, C, and D.

hypotheses to explain phylogeographic patterns (Stace, 1989). In the present case, geological reconstructions suggest that most islands divided by Wallace's and Huxley's lines were never in contact (Hall, 2001), and for this rea-

son a dispersal hypothesis is justified to explain phylogenetic relationships that span some of these ocean barriers. When it is necessary to posit dispersal, we assume that agents such as floating mats of vegetation

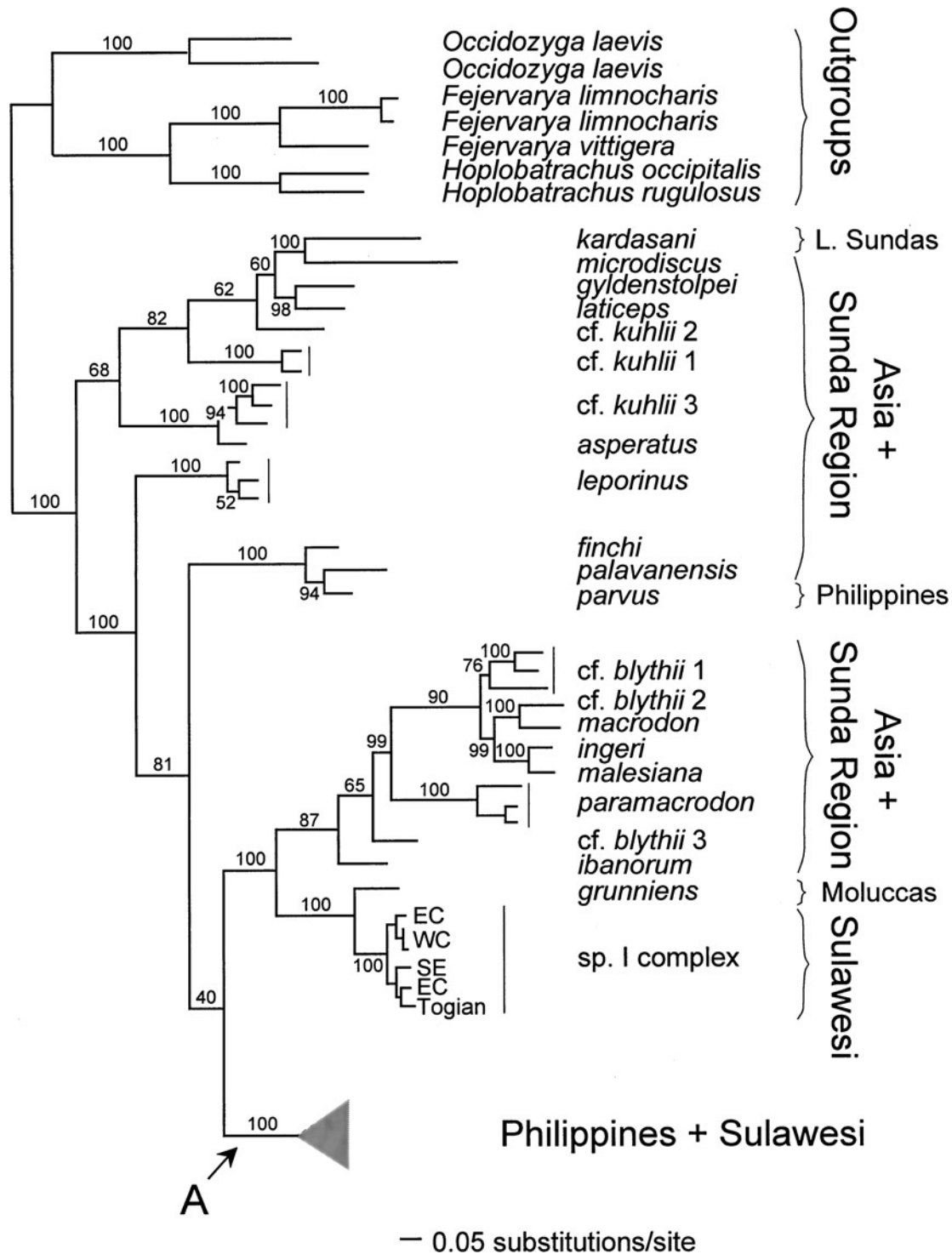


FIGURE 8. Basal relationships in Bayesian consensus topology. Bayesian support values are above branches. Location and lineage labels are as in Figure 6. Lineage A is depicted in Figure 9.

facilitated travel of *Limnonectes* adults and larvae over water.

Within the Philippines a combination of dispersal and vicariance hypotheses can be employed because some islands were united during the Pleistocene (PAICs)

whereas some groups of islands remained isolated by deep oceanic trenches. Within PAICs, sea level vicariance divided islands into their current geography (Heaney, 1986; Voris, 2000). Distributions such as that of the *L. leytenis* complex that span multiple PAICs, however,

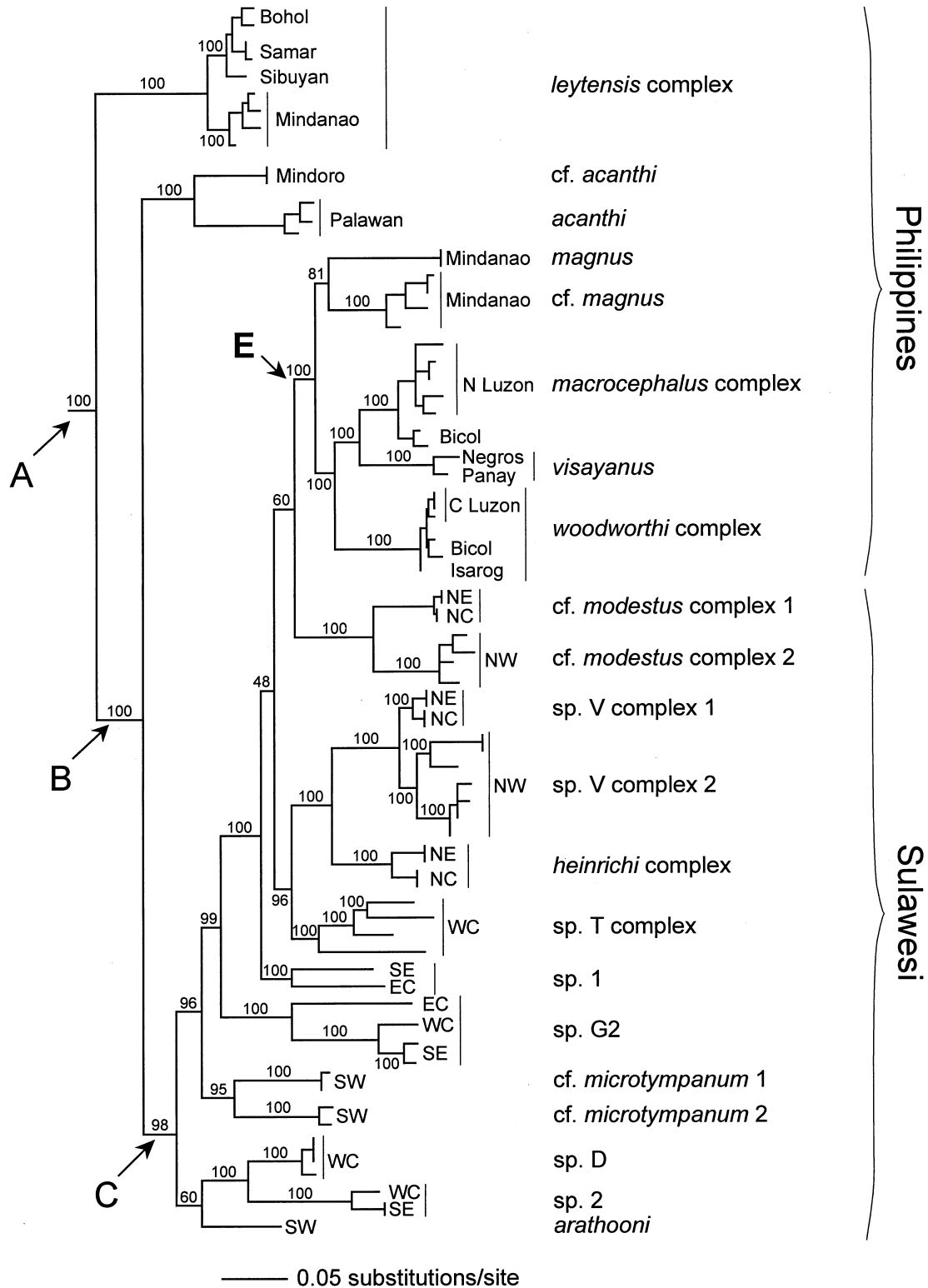


FIGURE 9. Relationships among Philippine and Sulawesi members of lineage A (Fig. 8) as inferred from Bayesian analysis. Labeling as in Figure 7, except that a new lineage E is depicted instead of D.

arose from dispersal over permanent water barriers between PAICs. On Sulawesi, we defer to a hypothesis of vicariance to account for patterns of diversification and assume this island was once a continuously con-

nected landmass that was fragmented by ocean and then reunited into its current state. It is also possible, however, that Sulawesi was an archipelago with ocean between AOEs, the constituents of which were only

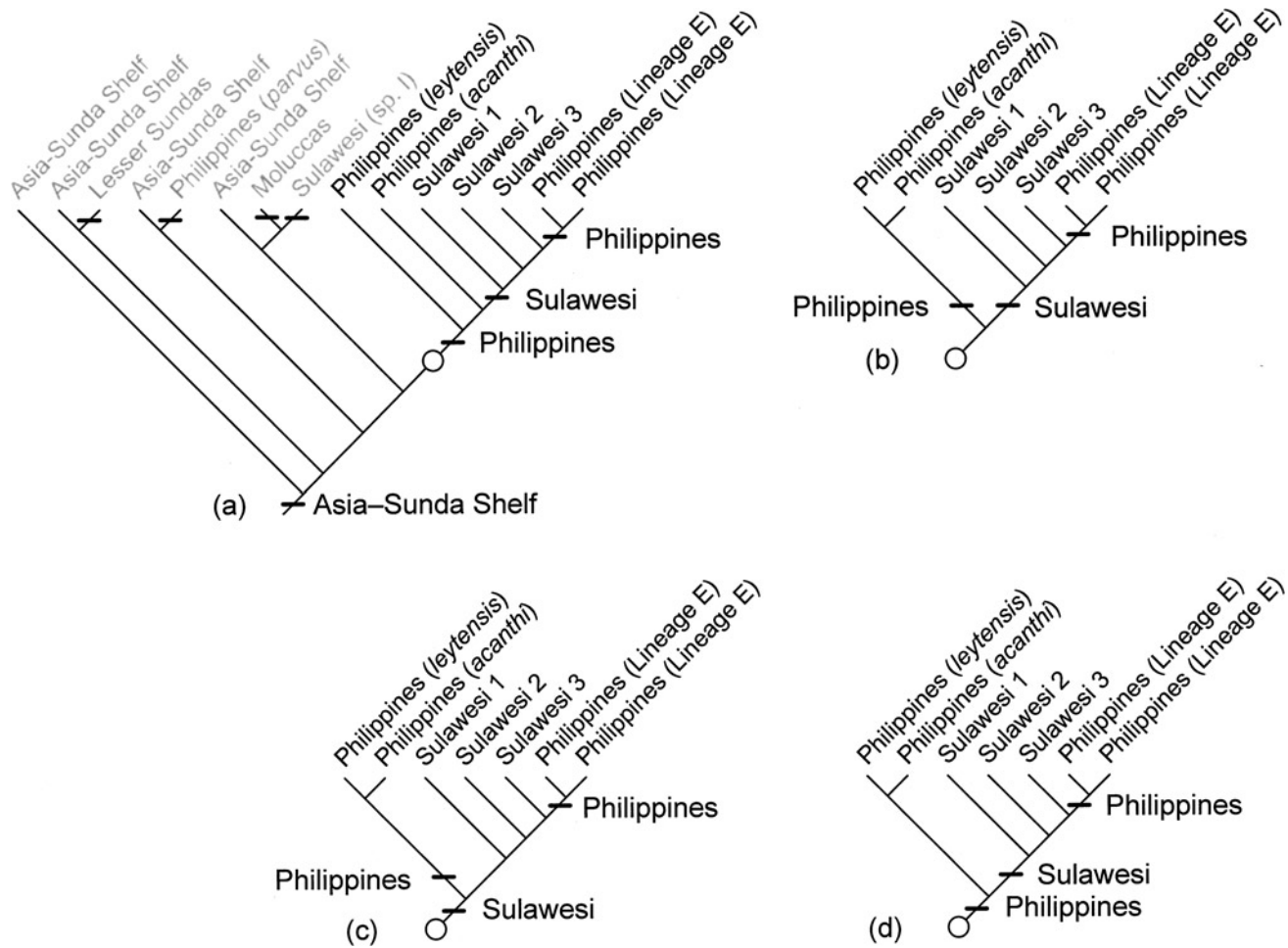


FIGURE 10. Simplified area cladograms with major dispersal events of *Limnonectes* as inferred from the observed likelihood topology (a) and the most-parsimonious tree consistent with hypotheses 5 and 6 (b, c, d). The topology in the portion of the tree depicted in b, c, and d differs from those in a in the relationship between *L. leytensis* and *L. acanthi*. Inferred ancestral locations are mapped on tree branches.

recently united into a single island (Evans et al., 2003a, 2003b).

Diversification in Asia and the Sunda Shelf

Although rDNA genes generally evolve slowly relative to other mtDNA genes, levels of divergence are high (0.185 among some comparisons) on the Sunda Shelf. Using a molecular clock, Emerson et al. (2000) estimated that *Limnonectes* may have occupied the Sunda region since before the Miocene. For much of this period, the Sunda Shelf was a peninsula fringed by volcanic arcs that eventually became Sumatra and Java (Hall, 1998). The land bridge that connected Sumatra, Java, and Borneo was narrow at this time and may have hindered dispersal among these landmasses and promoted diversification on them. Basal lineages in our trees (Figs. 6, 8) are Asian and Sundaic, suggesting that the ancestor of *Limnonectes* originated here rather than on the Philippines or Sulawesi.

Morphological differentiation of some *Limnonectes* species is low compared with levels of molecular differentiation. Indeed, molecular relationships among some species with widespread distributions in Asia and the Sunda Shelf, such as *L. kuhlii* and *L. blythii*, suggest that these “species” are comprised of morphologically homogeneous yet genetically differentiated independent lineages (Figs. 6, 8; Emerson et al., 2000). Other species that also have widespread distributions on Asia and the Sunda Shelf, such as *L. malesiana* and *L. paramacrodon* (which have limited geographic sampling in this study), may (1) likewise exhibit considerable intraspecific differentiation or be species complexes or (2) exhibit low levels of diversification consistent with rapid range expansion during Pleistocene exposure of the entire Sunda Shelf (Fig. 1).

Dispersal Across Wallace’s and Huxley’s Lines

Our phylogenetic analysis and hypothesis testing support a simple scenario for *Limnonectes* colonization of the

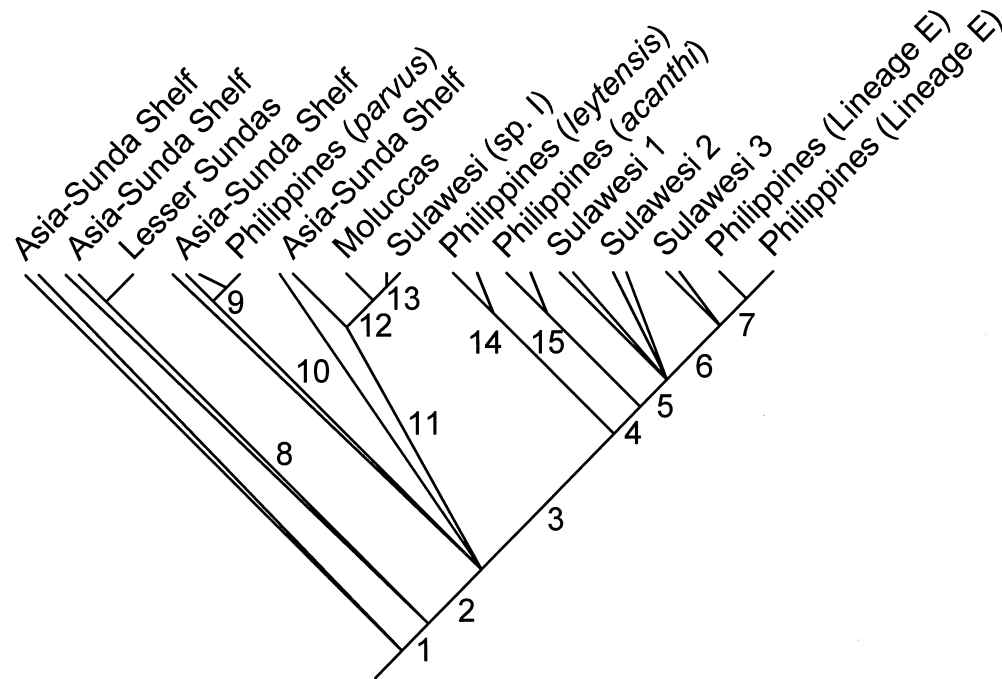


FIGURE 11. Area cladogram with 15 constraints that support the origin and destination of seven dispersal events depicted in Figure 10a. The following constraints are imposed: (1) ingroup monophyly; (2) monophyly of *L. asperatus*, *L. leonina*, *L. finchi*, *L. palavanensis*, *L. cf. blythi* 1–3, *L. macrodon*, *L. ingeri*, *L. malesianus*, *L. paramacrodon*, *L. ibanorum*, *L. grunniens*, *L. sp. I*, and clade A; (3, 4, 5, 7) clades A, B, C, and E from Figure 9 are each constrained; (6) *L. sp. I*, *L. sp. T*, *L. heinrichi* complex, *L. sp. V2*, *L. sp. V1*, and clade E are a clade; (8) *L. kardasani* is sister to *L. microtympnum*; (9) *L. parvus* is sister to *L. palavanensis*; (10) these taxa are sister to *L. finchi*; (11) *L. sp. I*, *L. grunniens*, *L. ibanorum*, *L. cf. blythi* 3, *L. paramacrodon*, *L. malesianus*, *L. ingeri*, *L. macrodon* are a clade; (12) *L. grunniens* is sister to *L. sp. I*; (13) *L. sp. I* is a clade; (14) *L. leytensis* and (15) *L. acanthi* are a clade. The joint posterior probability of trees consistent with this topology is 0.929.

Philippines and Wallacea, with relatively few dispersal events over permanent water barriers (Figs. 10, 12). A strict interpretation of relationships (Figs. 6–9) suggests an ancestor of lineage C dispersed to Sulawesi from the Philippines, where its sister taxon, the *L. acanthi* complex, occurs (Fig. 10a). This relationship is surprising in light of contemporary geography; *L. acanthi* and *L. cf. acanthi* occupy the northwestern Philippines and basal representatives of lineage C occupy southwest and central Sulawesi, a considerable geographic distance from the Philippines. However, the geography of this region differed considerably at the time of *Limnectes* dispersal. The northern peninsula of Sulawesi, for example, was underwater until 10 million years ago (Hall, 1996, 1998, 2001).

The hypothesis of monophyly of the *L. leytensis* and *L. acanthi* complexes is not rejected (hypothesis 6, Fig. 5). Under the most-parsimonious tree consistent with this hypothesis, ancestors of lineage A (Figs. 7, 9) could have dispersed from the Sunda Shelf to the Philippines (except Luzon) and from the Sunda Shelf to Sulawesi (Fig. 10b). Some descendants of lineage A evolved into *L. leytensis* and *L. acanthi* and other descendants evolved into a paraphyletic assemblage on Sulawesi and a clade on the Philippines (lineages C and E, Fig. 9). One alternative dispersal scenario under this topology (Fig. 10c) posits dispersal first to Sulawesi from Borneo and then two separate dispersal events to the Philippines from Sulawesi.

Another alternative (Fig. 10d) is similar in terms of dispersal events to the reconstruction based on the observed topology (Fig. 10a). The hypothesis of separate dispersal events from the Sunda Shelf to the Philippines and to Sulawesi (Fig. 10b) is not consistent with our phylogenetic analyses (Figs. 6–9) but is consistent with less parsimonious and less probable hypotheses that were not rejected by the data (hypotheses 3 and 6; Fig. 5).

The relationships in lineage E based on the Bayesian analysis (Fig. 9) are not significantly different from relationships in lineage D based on parsimony (Fig. 7) according to a parametric bootstrap test (hypothesis 5, Fig. 5), suggesting that dispersal from Sulawesi to the Philippines may have occurred only once (Figs. 10–12). Island hopping routes for dispersal between Sulawesi and the Philippines probably occurred via the Sangihe-Talaud Islands (Moss and Wilson, 1998), and descendants of lineage E (Fig. 9) never reached Palawan or Mindoro.

A separate dispersal from Borneo introduced the *L. sp. I* complex to Sulawesi; this lineage then dispersed to the Moluccas to become *L. grunniens* (Fig. 12). Dispersal of an ancestor of *L. microdiscus* from Java across Wallace's and Huxley's lines to the Lesser Sundas gave rise to a sister species, *L. kardasani*, on Lombok. One other species not included in this study, *L. dammermani*, also has been described from the Lesser Sunda Islands, but its phylogenetic position remains unknown.

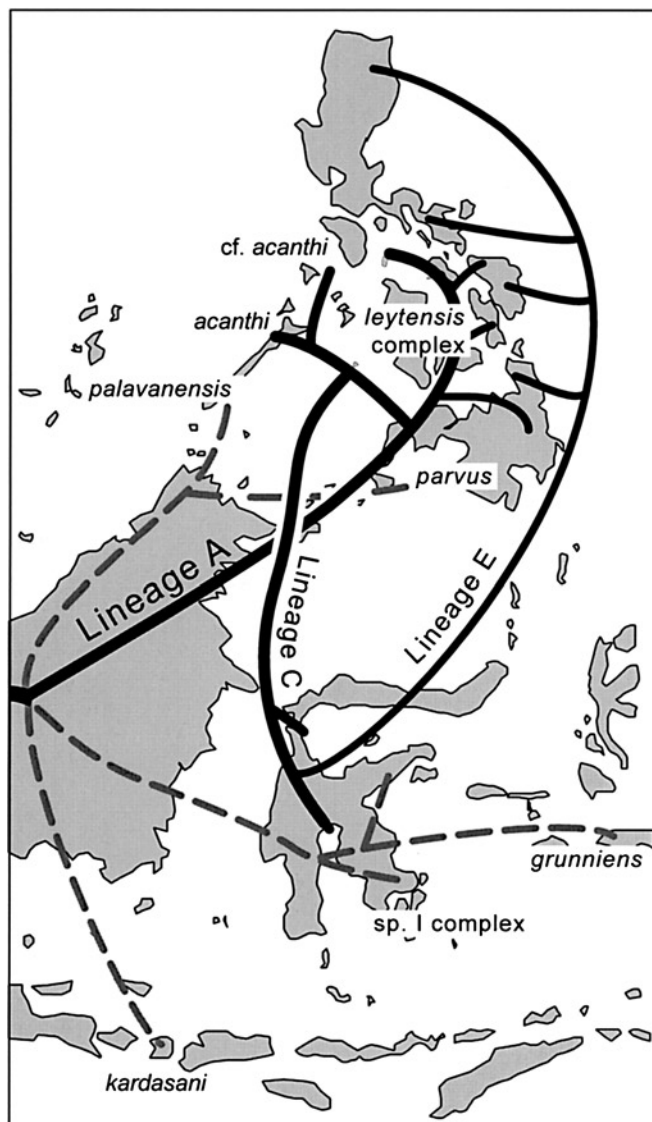


FIGURE 12. Simplified mtDNA phylogeography as inferred from Bayesian and likelihood topology overlaid on a map. Lineage A (Figs. 7, 9) is plotted with solid lines and other lineages are dashed.

Distributions Within the Philippines

During a middle Pleistocene sea level regression of 160 m, Palawan Island may have been connected to Borneo, but it has been autonomous for at least 160,000 years (Heaney, 1986; McGuire and Alcala, 2000; McGuire and Kiew, 2001). Mindoro was isolated throughout the Pleistocene, although this island has faunal affinities to nearby Palawan and Luzon (Heaney, 1986; Brown and Diesmos, 2002). The Sulu Archipelago was probably a series of islands that were fewer and more expansive, as were Sibuyan, Romblon, and Tablas (Fig. 3). During sea level regressions, Luzon and some smaller islands were single landmasses, Panay, Negros, Cebu, and Masbate were joined, and Mindanao, Leyte, Samar, and Bohol were also a single island (Figs. 1, 3). Each of these PAICs is characterized by endemic fauna (Steere, 1890; Semper,

1892; Vane-Wright and Smiles, 1975; Heaney, 1986; McGuire and Alcala, 2000; Brown and Diesmos, 2002).

Philippine Lineages from Borneo

Two scenarios of dispersal could explain relationships and distributions of *L. leytensis* and *L. acanthi* complexes. One is that an ancestor of both complexes dispersed once from Borneo and radiated throughout both of their ranges (all the Philippines except Luzon). Probable avenues of dispersal from Borneo include the Sulu Archipelago or Palawan. This hypothesis is most parsimonious in terms of dispersal events from Borneo to the Philippines. A second scenario is that this ancestor differentiated into the *L. leytensis* and *L. acanthi* lineages on Borneo and that each lineage separately dispersed to the Philippines via Palawan (*L. acanthi*) and via the Sulu Archipelago (*L. leytensis*). This hypothesis matches biogeographical scenarios recently invoked to explain distributions of frogs of the *Rana signata* complex in Borneo and the Philippines (Brown and Guttman, 2002) but is less parsimonious in terms of the number of dispersal events (Figs. 6–9). It is possible that further taxon sampling in Borneo might clarify this issue.

The *L. leytensis* complex has a wide distribution and high divergence (0.038) and spans at least three PAICs, Mindanao + Leyte + Samar + Bohol, Panay + Negros + Cebu + Masbate, and Sibuyan, and possibly a fourth PAIC, the Sulu Archipelago, including the Tawitawi and Jolo Island groups (Taylor, 1921; Inger, 1954). Within its range, sequences from Mindanao are monophyletic and sister to lineages from Bohol, Samar, and Sibuyan. Sequences on Bohol and those on Samar are each monophyletic and together are sister to a lineage on Sibuyan (Figs. 7, 9). This finding was unexpected because Bohol, Samar, and Leyte were part of the same PAIC as Mindanao, whereas Sibuyan was part of a separate PAIC (Fig. 2). The *L. leytensis* complex is the only clade with paraphyletic mtDNA within a PAIC, but a parametric bootstrap test does not reject the null hypothesis of monophyly of *L. leytensis* sequences in the Greater Mindanao PAIC (Mindanao + Leyte + Samar + Bohol; Hypothesis 7, Fig. 5). A paraphyletic assemblage may have arisen because an oceanic barrier to dispersal between Mindanao and other islands arose before a monophyletic lineage became fixed on the entire PAIC. Mitochondrial DNA of flying lizards (*Draco*) is also partitioned into two clades on this PAIC, with one clade on Mindanao and another on Leyte, Samar, and Bohol (McGuire and Kiew, 2001).

All other Philippine sequences are monophyletic within a PAIC (Figs. 7, 9). The *L. acanthi* complex includes *L. acanthi* (Taylor, 1923) and an undescribed sister species on Mindoro, *L. cf. acanthi*. Sequences from Mindoro are monophyletic, sister to monophyletic sequences from Palawan, and more divergent between these two PAICs (0.065) than is the *L. leytensis* complex across its range. Under an assumption of similar rates of evolution (although not necessarily clocklike), the former two lineages were split among more than one PAIC before the *L. leytensis* complex.

Limnectes parvus was derived from a different dispersal event from Borneo than were *L. leytensis* and *L. acanthi*. The sequence of *L. palavanensis* is from Borneo but the range of this species is thought to include Palawan as well. If these two populations are in fact conspecific, another dispersal event would be needed to explain its distribution. *Limnectes palavanensis* from Borneo probably diverged from *L. parvus* as a consequence of dispersal of an ancestor of *L. parvus* to Mindanao via the Sulu Archipelago. At some point after the dispersal of the ancestor of *L. parvus*, *L. palavanensis* may have expanded its range from Borneo to also include Palawan (Fig. 12). Divergence among these species (0.105) is greater than that among other members of the Philippine lineages derived from Sulawesi (pairwise divergences in lineage E in Fig. 9 are 0.055–0.083) but is similar to that among *L. leytensis* and *L. acanthi* (0.075–0.111). If sequences of these animals evolved at similar rates, ancestors of *L. parvus*, *L. leytensis*, and *L. acanthi* may have dispersed to the Philippines at similar times and potentially by similar routes.

Interestingly, Philippine lineages from Borneo occupy central and southern Philippines but not Luzon and associated islands. Why Luzon was not colonized by the oldest *Limnectes* ancestors in the Philippines is not clear. One possibility is that Luzon was underwater at this time or far away from the other Philippine islands, although geological reconstructions suggest otherwise (Hall, 1998).

Philippine Lineages from Sulawesi

The *L. macrocephalus* and *L. woodworthi* complexes have similar phylogeography on Luzon and fringe islands (Taylor, 1923; Inger, 1954), but the former has twice the intraspecific divergence (0.020 and 0.009, respectively) and thus may be older or have a larger effective population size. A clade that contains *L. macrocephalus* complex sequences from south Luzon (Mt. Isarog, Mt. Malinao) is sister to a clade containing sequences from the rest of Luzon. Similarly, most *L. woodworthi* complex sequences from south Luzon (Mt. Malinao, Mt. Bulusan, Tabaco) are sister to conspecific sequences from the rest of Luzon except one sequence from Mt. Isarog at the base of the Bicol peninsula of Luzon; this sequence is sister to all other *L. woodworthi* complex sequences (Figs. 7, 9). The *L. macrocephalus* complex shares recent ancestry with *L. visayanus* (Inger, 1954), which occupies the neighboring PAIC that includes Panay, Negros, Cebu, and Masbate (Fig. 3).

Limnectes cf. *magnus*, another undescribed species, occupies the Mindanao + Samar + Leyte + Bohol PAIC. In this species, sequences from Mindanao are sister to sequences from Samar; these sequences together are sister to *L. cf. magnus* sequences from Bohol. Our samples from *L. magnus* were collected near the type locality at high elevation habitats on Mt. Apo (Stejneger, 1910), whereas specimens of the widespread species *L. cf. magnus* were collected in lower elevation parts of Mindanao (including low elevations on Mt. Apo). *Limnectes* cf. *magnus* may also occur on Basilan Island (Inger, 1954).

Two additional species have been described from the Philippines that were not included in this study, and both have ranges restricted to single islands. *Limnectes micrixalus* occurs only on Basilan Island (Fig. 3; Taylor, 1923), and this species may be synonymous with *L. parvus* (Inger, 1966). *Limnectes diuatus* occurs on north-east Mindanao (Brown and Alcalá, 1977). Other undescribed species with restricted ranges are also present on Mindanao (R.M.B., unpubl. data).

Distributions Within Sulawesi

Sulawesi was formed by accretion of multiple islands that were near one another and partially land positive 20 million years ago, although the northern peninsula may have been submerged again 15 million years ago (Hall, 2001). Sulawesi's island precursors do not correspond with AOE's (Fig. 4; Evans et al., 2003b), possibly in part because of underwater accretion of some of these island precursors. Sulawesi is fringed by precipitous continental shelves; low sea level during the Pleistocene did not significantly alter the connectivity of Sulawesi to other landmasses, although it did narrow the width of the Makassar Strait to <40 km at one point (Voris, 2000). Portions of Sulawesi were at a lower position relative to sea level at various times, and ocean barriers may have been permanent or intermittent until recently across the base of the southwestern peninsula, across the middle of the northern peninsula, and possibly across other parts of this island (Whitten et al., 2002). Other barriers such as ultrabasic soil types or large rivers may further subdivide biota of Sulawesi (Whitten et al., 2002; Evans et al., 2003b). Genetic introgression among AOE's appears low even among hybridizing species of highly mobile Sulawesi macaque monkeys, which suggests that barriers to dispersal have been present until recently (Evans et al., 2001, 2003a).

Phylogeography of *Limnectes* on Sulawesi is highly structured and is generally concordant with patterns of diversity observed in other endemic taxa, such as toads and monkeys, that define seven areas of endemism (Evans et al., 2003b). On Sulawesi, southern and central *Limnectes* are basal to northern peninsula species (Figs. 7, 9). Basal species may have reached Sulawesi before the northern peninsula became land positive. Distributions of *Limnectes* on Sulawesi can be broadly divided into species whose distributions are (1) congruent with AOE's, (2) partially congruent with AOE's in that a species is widely distributed in one AOE with limited extensions into others, or (3) incongruent with AOE's in that a species is widely distributed in more than one AOE.

Congruence with Sulawesi AOE's

At least five species groups occur on the northern peninsula, and diversity of three of these groups is partitioned according to AOE's (Figs. 4, 7, 9). Three of these complexes are endemic to the north central and northeast AOE's, and each of these has reciprocally monophyletic mtDNA clades that occur on either side of the boundary between the north central and northeast AOE's (NC/NE

boundary). This boundary roughly corresponds with the city of Kotamobagu and the Dumoga River (Evans et al., 2003b). Average divergence of clades on either side of the NC/NE boundary of the *L. cf. heinrichi* complex is 0.021, that of the *L. sp. V* complex 1 is 0.015, and that of the *L. cf. modestus* 1 complex is only 0.006.

Other species with distributions that are congruent with Sulawesi AOE include *L. arathooni*, *L. cf. microtympanum* 1, and *L. cf. microtympanum* 2 in the southwest AOE, and *L. sp. D* and *L. sp. T* in the west central AOE.

Partial Congruence with Sulawesi AOE

We designate a distribution as partially congruent with Sulawesi AOE if the range is primarily in one AOE and only partially in adjacent portions of other AOE. The *L. cf. modestus* complex 2 and the *L. sp. V* complex 2 for example occur throughout the northwest AOE (Fig. 4) but extend slightly into adjacent parts of the west central or north central AOE. These species probably were once restricted to the northwest AOE but have recently dispersed beyond the now absent barriers to dispersal between these AOE.

Incongruence with Sulawesi AOE

Limnionectes sp. I complex crosses two AOE boundaries, is widely distributed in two areas of endemism, and has at least a marginal distribution in a third (Fig. 4). This species occurs on the eastern side of Sulawesi and has a maximum intralineage divergence of 0.022. This species is derived from a dispersal event separate than that of other Sulawesi *Limnionectes* in this study. Interestingly, one clade in this complex includes sequences sampled on the Togian Islands and the eastern extremes of southeast and east central AOE, whereas a second clade includes sequences on either side of the border between the west central and east central AOE. A parametric bootstrap test rejects the hypothesis of monophyly of *L. sp. I* sequences from east central Sulawesi (hypothesis 8, Fig. 5). One explanation for this distribution is that an ancestor of this species reached Sulawesi after the retreat of ocean that compartmentalized diversity in other fauna (Evans et al., 2003b). The wide distribution and incongruent phylogeography of *L. sp. I* may simply be a reflection of the high dispersability of this lineage that facilitated colonization of Sulawesi and the Moluccas.

Limnionectes sp. G2 is widespread in the southeast AOE, and divergent lineages in this clade were also sampled in the west central and east central AOE (Fig. 4). *Limnionectes* sp. 1 and sp. 2 each also include two divergent lineages from two separate AOE. Because these three taxa may each comprise a pair of diverged sister species, taxon sampling in this study is inadequate to determine whether they are congruent with Sulawesi AOE (Fig. 4).

CONCLUSIONS

Limnionectes species are often found in sympatry with one or more congeners, but dispersal across ocean barriers is rare and diversity is highly compartmental-

ized in the Philippines and Sulawesi. On Asia and the Sunda Shelf, morphologically cryptic but molecularly distinct species are present in different areas (Emerson et al., 2000; this study). Despite the narrow width of the Makassar Strait during the Pleistocene, dispersal from Borneo to Sulawesi probably occurred only once and we found no evidence of westward dispersal from the Philippines or Sulawesi to Borneo. Other parts of Wallace's (1863) and Huxley's lines were crossed multiple times by *Limnionectes*, and dispersal across the northern part of Wallace's line led to a diverse assemblage on the Philippines. Reports of faunal exchange among the Philippines and Sulawesi are rare, and *Limnionectes* may be unusual from this perspective. Even species of the rodent genus *Crunomys*, which is shared by Sulawesi and the Philippines, may be of independent origin in each region (Musser, 1987). Dispersal among the Lesser Sundas and Sulawesi has been postulated to explain the distribution of extinct stegodonts in this region (Cranbrook, 1981), but we found no indication that dispersal of *Limnionectes* has occurred between these areas or between the Philippines and the Moluccas.

Dispersal across narrow channels between Philippine paleoislands was also infrequent and, with the exception of *L. leytensis*, left no evidence of paraphyly among lineages that span multiple PAICs. Early lineages of *Limnionectes* did not reach Luzon, and a lineage from Sulawesi (clade E, Fig. 9) did not reach Palawan or Mindoro. Separate areas of endemism exist on Luzon in the Bicol Peninsula and in North/Central Luzon. Although they were once part of the same PAIC, separate areas of endemism also exist on Mindanao and on Bohol + Samar.

On Sulawesi, barriers to dispersal isolated lineages and bounded diversification into separate AOE (Evans et al., 2003b). Now these barriers are gone, but ranges of most *Limnionectes* species are congruent with AOE of other fauna (Evans et al., 2003b), although some ranges have expanded across these boundaries. Lack of exact congruence in some species could stem from (1) migration across areas where biogeographic barriers once existed but have now retreated, (2) mtDNA introgression associated with hybridization, (3) lumping of multiple divergent monophyletic lineages into a single species group when only one individual is sampled from a lineage, and (4) an unusual ability to disperse across biogeographical barriers, as may be the case of *L. sp. I*.

On the Sunda Shelf, the Philippines, and Sulawesi (and probably the Moluccas and the Lesser Sunda Islands), vicariance due to oceanic barriers influenced dispersal and compartmentalized diversity on a fine scale. A single line to demarcate the interface of the Asian and Australian faunal regions, although insightful, is an oversimplification of biogeography in Southeast Asia.

ACKNOWLEDGMENTS

We thank the Indonesian Institute of Sciences and the Indonesian Department of Forestry for permission to conduct research in Indonesia, the University of Indonesia for their hospitality and sponsorship, the Muzeum Zoologicum Bogoriense for assistance with permits,

R. Fernandez, G. Probowo, and M. I. Setiadi for assistance with fieldwork, A. Alcalá, W. Brown, R. Crombie, R. DeSalle, J. Ferner, L. Heaney, J. C. Morales, and L. Ruedas for helpful discussions on fanged frog taxonomy, biodiversity, species concepts, and biogeography, and D. Zwickl for assistance with analysis. We thank D. A. J. W. K. Min, O. Bracken, S. Bin Ahmad, R. Cutter, N. Schiff, and the Subterranean Explorers for providing genetic samples and the Sarawak Department of Forestry for assistance with permits. We thank B. Inger, E. Jockusch, L. Grismer, T. Macrini, and K. Zamudio for valuable comments on earlier versions of this manuscript. We thank the Protected Areas and Wildlife Bureau of the Philippines Department of the Environment and Natural Resources for facilitating collecting and export permits between 1994 and 2001. For loans of specimens and assistance while visiting museum collections, we thank the following individuals and their respective institutions (museum acronyms follow Leviton et al., 1985): J. Vindum, A. Leviton, and R. Drewes (CAS); R. Crombie, K. de Queiroz, and G. Zug (USNM); A. Resetar, C. Redhead, H. Voris, and R. Inger (FMNH); L. Ford (AMNH); J. Rosales (TNHC); J. Ferner and R. Kennedy (CMNH); R. Sison (PNM); and M. Leonida (De La Salle University). Financial support for fieldwork of B.J.E. was provided by the National Science Foundation, Conservation International, the Center for Environmental Research and Conservation, and the Wenner-Gren Foundation. Financial support for visits by A.C.D. and R.M.B. to CAS was provided by the Charles Stearns Fellowship. Financial support for Philippine fieldwork of R.M.B. and A.C.D. was provided by the Society of Systematic Biologists, the U.S. National Science Foundation, the Society for the Study of Amphibians and Reptiles, the American Society of Ichthyologists and Herpetologists, The Explorers Club, the Texas Memorial Museum, and the Section of Integrative Biology of the University of Texas at Austin. We also acknowledge the National Science Foundation for funding from NSF grant DEB-9981631 to D.C.C.

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First submitted 4 December 2002; reviews returned 30 March 2003;
final acceptance 29 June 2003
Associate Editor: Jack Sites

APPENDIX. Specimens, locations, and Genbank accession numbers of genetic samples used in this study.

Species	General locality	Specific locality	GPS coordinates	Museum catalog number	Accession number(s)
Outgroups					
<i>Fejervarya limnocharis</i>	China, Sichuan	Hongya Xian, Bing Ling		HKV 37049 deposited in FMNH	AF261244, AF261262
<i>Fejervarya limnocharis</i>	Malaysia, Borneo Isl., Sabah Prov.	Kota Kinabalu		SBE 098' deposited in Sabah Museum of Natural History	U55265, U55272
<i>Hoplobatrachus occipitalis</i>	Ivory Coast	Comoe N. P.		FMNH 257224	AF261245, AF261263
<i>Hoplobatrachus rugulosus</i>	Phil., Luzon Isl., Laguna Prov.	Mun. Los Baños, Barangay Batong Malake, Mt. Makiling Selangor Dist.	N 14 09.300 E 121 14.080	PNM 7827	AY313685
<i>Occidozyga laevis</i>	Malaysia			SBE 072' deposited in University of Malaysia	U66138, U66139
<i>Occidozyga laevis</i>	Phil., Luzon Isl., Quezon Prov.	Mun. Tayabas, Barangay Lao	N 14 03.020 E 121 32.460	PNM 7446	AY313684
<i>Rana vittigera</i>	Phil., Luzon Isl., Quezon Prov.	Mun. Tayabas, Barangay Lao	N 14 03.020 E 121 32.460	PNM 7826	AY313683
Limnionectes					
<i>L. acanthii</i>	Phil., Palawan Isl., Palawan Prov.	Mun. of Puerto Princesa, Barangay Irawan	N 09 48.330 E 118 41.160	PNM 7604	AY313722
<i>L. acanthii</i>	Phil., Palawan Isl., Palawan Prov.	Mun. Naga, Barangay Estrella, Estrella Falls	N 09 21.450 E 118 23.870	PNM 7606	AY313723
<i>L. acanthii</i>	Phil., Palawan Isl., Palawan Prov.	Mun. of Brooke's Point, Barangay Mainit, Mainit Falls	N 08 47.760 E 117 47.460	PNM 7605	AY313724
<i>L. arathooni</i>	Indo., Sulawesi Isl., Sulawesi Selatan Prov.	Desa Cikoro, Mt. Lompobatang		TNHC 59087	AY313744
<i>L. asperatus</i>	Indo., Borneo Isl., Kalimantan Selatan Prov.	Palangkaraya		FMNH 252416	AF183127, AF183128
<i>L. cf. acanthii</i>	Phil., Mindoro Isl., Oriental Mindoro Prov.	Mun. Puerto Gallera	N 13 30 E 120 56	RMB 507#	AY313721
<i>L. cf. acanthii</i>	Phil., Mindoro Isl., Oriental Mindoro Prov.	Mun. San Teodoro, Tamaraw Falls	N 13 26.3 E 121 4	USNM 556096	U66120.66121
<i>L. cf. acanthii</i>	Phil., Mindoro Isl., Oriental Mindoro Prov.	Mun. San Teodoro, Tamaraw Falls	N 13 26.3 E 121 4	TNHC 54922	U66126, U66127
<i>L. cf. blythii 1</i>	Thailand	Uthai Thani		FMNH 950701	U55263, U55270
<i>L. cf. blythii 1</i>	Malaysia (Peninsular)	Endau Rompin N. P.		SBE 062'	U66134, U66135
<i>L. cf. blythii 1</i>	Malaysia (Peninsular)	Kuala Lumpur, Gombak Field Study Centre		SBE 066' no voucher	
<i>L. cf. blythii 2</i>	Indonesia, Sumatra Isl.	Malibou Anai, Anai Valley			U66130, U66131
<i>L. cf. blythii 3</i>	Vietnam, Gia Lai Prov.	Ankhe Dist, Buoenloy		ROM25130	U66136, U66137
<i>L. heinrichii</i> complex	Indo., Sulawesi Isl., Sulawesi Utara Prov.	near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167136	
<i>L. heinrichii</i> complex	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Klabat Mt.	N 01 29.386 E 124 50.520	AMNH 167137	AY313747
<i>L. heinrichii</i> complex	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Klabat Mt.	N 01 29.386 E 124 50.520	AMNH 167138	
<i>L. heinrichii</i> complex	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Gorontalo		TNHC 59710	AY313749
<i>L. heinrichii</i> complex	Indo., Sulawesi Isl., Sulawesi Utara Prov.	near Bogani Nani Wartabone N. P.	N 00 34.004 E 123 53.272	AMNH 167139	AY313748
<i>L. heinrichii</i> complex	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Tolabulu	N 00 30.801 E 123 14.571	AMNH 167140	
<i>L. cf. kuhlii 1</i>	Indo., Java Isl.	Sukabumi		MZB Amph.6501	AY313687
<i>L. cf. kuhlii 1</i>	Indo., Java Isl.	Cibodas, Mt. Gede		Deposited in MZB	AF183137, AF183138
<i>L. cf. kuhlii 2</i>	Taiwan	Wulai		FMNH 257133	AF183131, AF183132
<i>L. cf. kuhlii 3</i>	Indo., Borneo Isl., Kalimantan Timur Prov.	Near Kutai N. P.	N 00 22.293 E 11728.638	AMNH 167141	AY313686
<i>L. cf. kuhlii 3</i>	Indo., Borneo Isl., Kalimantan Timur Prov.	Near Kutai N. P.	N 00 31.913 E 117 27.892	AMNH 167142	
<i>L. cf. kuhlii 3</i>	Indo., Borneo Isl., Kalimantan Timur Prov.	Near Kutai N. P.	N 00 22.293 E 11728.638	AMNH 167143	
<i>L. cf. kuhlii 3</i>	Malaysia, Borneo Isl., Sabah Prov.	Lahad Dist.		FMNH 230302	AF183135, AF183136
<i>L. cf. kuhlii 3</i>	Brunei, Borneo Isl.	Belait Dist.		FMNH 248357	AF183133, AF183134
<i>L. cf. magnus</i>	Phil., Samar Isl., Samar Prov.	Mun. Bagakay, Bagakay Mines	N 11 26.2 E 124 22.7	USNM 534311	U66118, U66119
<i>L. cf. magnus</i>	Phil., Samar Isl., Samar Prov.	Mun. Bagakay, Bagakay Mines	N 11 26.2 E 124 22.7	USNM 534311	AY313704
<i>L. cf. magnus</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Calinan, Barangay Malagos	N 07 11.14, E 125 24.97	PNM 7449	AY313705
<i>L. cf. magnus</i>	Phil., Mindanao Isl., Bukidnon Prov.	Mun. Malaybalay, Mt. Kitanglad	N 08 9.2, E 125 4.9	PNM 7444	

(Continued on next page)

APPENDIX. Continued

<i>L. cf. magnus</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Toril, Barangay Baracatan, Mt. Apo	N 06 59, E 125 16	PNM 5667	
<i>L. cf. magnus</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Monkayo, PICOP Forest	N 07 51.700, E 125 11.600	JWF 94092*	AY313706
<i>L. cf. magnus</i>	Phil., Bohol Isl., Bohol Prov.	Mun. Carmen, Chocolate Hills	N 09 49.5, E 124 44.9	TNHC 56398	AY313743
<i>L. cf. magnus</i>	Phil., Bohol Isl., Bohol Prov.	Mun. Antequera, Barangay Villa Aurora	N 09 46.8, E 123 53.7	PNM 7607	AY313745
<i>L. cf. magnus</i>	Phil., Bohol Isl., Bohol Prov.	Mun. Bilar	S 05 15.561 E 119 55.594	PNM 7829	AY313746
<i>L. cf. microtymppanum 1</i>	Indo., Sulawesi Isl., Sulawesi Selatan Prov.	Malino		AMNH 167144	U66110, U66111
<i>L. cf. microtymppanum 1</i>	Indo., Sulawesi Isl., Sulawesi Selatan Prov.	Desa Cikoro, Mt. Lompobatang		TNHC 59062	AY313735
<i>L. cf. microtymppanum 2</i>	Indo., Sulawesi Isl., Sulawesi Selatan Prov.	Barru	S 04 29.643 E 119 45.998	AMNH 167145	
<i>L. cf. microtymppanum 2</i>	Indo., Sulawesi Isl., Sulawesi Selatan Prov.	Barru	S 04 29.643 E 119 45.998	AMNH 167146	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Selatan Prov.	Loka		Deposited in MZB	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Bogani Nani Wartabone N. P.	N 00 33.748 E 123 54.230	AMNH 167147	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Bogani Nani Wartabone N. P.	N 00 33.748 E 123 54.230	AMNH 167148	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Bogani Nani Wartabone N. P.	N 00 33.748 E 123 54.230	AMNH 167149	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Toraut near Bogani Nani N. P.	S 00 33.72 E 123 54.23	MZB Amph.8080	AY313736
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167150	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167151	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167152	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167153	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167154	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167155	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167156	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167157	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167158	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167159	
<i>L. cf. modestus complex</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167160	AY313763
<i>L. cf. modestus complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Moutong	N 00 27.847 E 121 13.867	AMNH 167161	
<i>L. cf. modestus complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Moutong	N 00 27.847 E 121 13.867	AMNH 167162	AY313765
<i>L. cf. modestus complex 2</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Tolabulu	N 00 30.801 E 123 14.571	AMNH 167163	AY313766
<i>L. cf. modestus complex 2</i>	Indonesia, Sulawesi Island, Sulawesi Tengah Prov.	Marantali	S 00 37.674 E 120 30.495	AMNH 167164	
<i>L. cf. modestus complex 2</i>	Indo., near-Sulawesi Isl., Sulawesi Tengah Prov.	Togian Islands, Pulau Batudaka	S 00 26.241 E 121 51.540	JAM38571	AY313764
<i>L. finchi</i>	Malaysia, Borneo Isl., Sabah Prov.	Sipitang Dist.		FMNH 242870	U55264, U55271
<i>L. grunniens</i>	Indo., Haruku Isl.	Saparua		Deposited in MZB	U66124, U66125
<i>L. guldenslotpei</i>	Thailand, Loei	Phuluang Wildlife Research Center		PWRC 002	AFI83123, AFI83124
<i>L. ibanorum</i>	Indo., Borneo Isl., Kalimantan Barat Prov.	Bentuang N. P.		FMNH 251721	U66122, U66123
<i>L. ingeri</i>	Malaysia, Borneo Isl., Sarawak Prov.	Belaga Dist.		FMNH 251722	U55268, U55275
<i>L. karadasani</i>	Indo., Lombok Isl.			LSUMZ 81722	AY313693
<i>L. laticeps</i>	Malaysia	Selangor Dist, Gombak Field Study Center		SBE 071 deposited at the University of Malaysia	AFI83125, AFI83126
<i>L. leporinus</i>	Indo., Borneo Isl., Kalimantan Timur Prov.	Near Kutai N. P.	N 00 31.913 E 117 27.891	AMNH 167165	AY313691
<i>L. leporinus</i>	Malaysia, Borneo Isl., Sabah Prov.	Lahad Datu Dist., Danum Valley Research Centre		FMNH 230212	U55262, U55269
<i>L. leporinus</i>	Indo., Borneo Isl., Kalimantan Selatan Prov.	Barito Ulu, Mentaya Hulu		DJI S 18 deposited in MZB	U66114, U66115
<i>L. leytensis</i>	Phil., Bohol Isl., Bohol Prov.	Mun. Carmen, Chocolate Hills	N 09 49.5 E 124 44.9	TNHC 56369	AY313695
<i>L. leytensis</i>	Phil., Bohol Isl., Bohol Prov.	Mun. Antequera, Barangay Villa Aurora	N 09 46.8 E 123 53.7	PNM 7828	AY313696
<i>L. leytensis</i>	Phil., Sibuyan Isl., Romblon Prov.	Mun. Magdiwang, Barangay Tampayan	N 12 28.96 E 122 32.99	PNM 7601	AY313698
<i>L. leytensis</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Caliman, Barangay Malagos	N 07 11.14 E 125 24.97	PNM 7830/TNHC 61940	AY313700

<i>L. leytensis</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Calinan, Barangay Malagos	N 07 11.14 E 125 24.98	PNM 7831/TNHC 61941	AY313702
<i>L. leytensis</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Calinan, Barangay Malagos	N 07 11.14 E 125 24.99	TNHC 59865	AY313699
<i>L. leytensis</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Toril, Barangay Baracatan, Mt. Apo	N 06 59 E 125 16	TNHC 59867	AY313701
<i>L. leytensis</i>	Phil., Samar Isl., Samar Prov.	Mun. Bagakay, Bagakay Mines	N 11 26.2 E 124 22.7	USNM 556107	AY313697
<i>L. leytensis</i>	Phil., Samar Isl., Samar Prov.	Mun. Bagakay, Bagakay Mines	N 11 26.2 E 124 22.8	USNM 222546	AF183129, AF183130
<i>L. macrocephalus</i>	Phil., Luzon Isl., Cagayan Prov.	Cagayan River Valley	N 17 30 E 121 45	F50 54563	U66116,66117
<i>L. macrocephalus</i>	Phil., Luzon Isl., Zambales Prov.	Mun. Masinloc, Barangay Coto	N 15 32.4 E 119 57	CMNH 4056	AY313713
<i>L. macrocephalus</i>	Phil., Luzon Isl., Laguna Prov.	Mun. Los Baños, Barangay Batong Malake, Mt. Makiling	N 14 9.30 E 121 14.08	PNM 7603	AY313714
<i>L. macrocephalus</i>	Phil., Luzon Isl., Camarines Sur Prov.	Mun. Naga City, Barangay Panicason, Mt. Isarog	N 13 39.3 E 123 23	TNHC 61913	AY313716
<i>L. macrocephalus</i>	Phil., Luzon Isl., Albay Prov.	Mun. Tiwi, Barangay Banhao, Mt. Malinao	N 13 27.5 E 123 10.6	TNHC 61914	AY313717
<i>L. macrocephalus</i>	Phil., Luzon Isl., Albay Prov.	Mun. Malinao, Barangay Tagoytoy, Mt. Malinao	N 13 24.8 E 123 35.8	TNHC 61917	
<i>L. macrocephalus</i>	Phil., Luzon Isl., Aurora Prov.	Mun. Maria Aurora, Barangay Villa Aurora, Kamatis River		CMNH 5556	AY313715
<i>L. macrocephalus</i>	Phil., Luzon Isl., Kalinga Prov.	Mun. Balbalan, Barangay Balbalasang Tarogong, Garut	N 17 29.08 E 121 3.56	FMNH 259268	AY313718
<i>L. macrodon</i>	Indo., Java Isl., Java Barat Prov.	Mun. Toril, Barangay Baracatan, Mt. Apo	N 6 59 E 125 16	FMNH 257159	U66132, U66133
<i>L. magrus</i>	Phil., Mindanao Isl., North Cotobato Prov.	Mt. Apo		CMNH 5520	
<i>L. magrus</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Kidapawan, Barangay Ilomavis, Mt. Apo	N 7 1.3 E 125 3	Deposited in CMNH	
<i>L. magrus</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Kidapawan, Barangay Ilomavis, Mt. Apo	N 7 1.3 E 125 3	CMNH 5513	AY313703
<i>L. malesiatus</i>	Malaysia, Borneo Isl., Sarawak Prov.	Gunung Buda, near Multu N. P.	N 04 13.076 E 114 55.730	Specimen sent to Sarawak State Museum in Kuching	AY313692
<i>L. microdiscus</i>	Indo., Java Isl.	Sukabumi		LSUMZ 81739	AY313688
<i>L. palawanensis</i>	Malaysia, Borneo Isl., Sabah Prov.	Lahad Dist.		FMNH 230800	U55266, U55273
<i>L. paramacrodon</i>	Brunei	Tutong Dist.		FMNH 248283	U55267, U55274
<i>L. paramacrodon</i>	Indo., Borneo Isl., Kalimantan Timor Prov.	Near Kutai N. P.	N 0022.293 E 117 28.638	AMNH 167166	AY313689
<i>L. paramacrodon</i>	Indo., Borneo Isl., Kalimantan Timor Prov.	Near Kutai N. P.	N 00 31.913 E 117 27.891	AMNH 167167	AY313690
<i>L. parous</i>	Phil., Mindanao Isl., Davao del Norte Prov.	Mun. Calinan, Barangay Malagos	N 07 11.14, E 125 24.97	PNM 7447	AY313694
<i>L. sp. 1</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kendari	S 03 54.434 E 122 30.281	AMNH 167168	AY313761
<i>L. sp. 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Luwuk	S 00 57.054 E 122 47.493	AMNH 167169	AY313762
<i>L. sp. 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Gunung Karua	S 02 54.130 E 119 41.840	AMNH 167170	AY313741
<i>L. sp. 2</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Tolala	S 02 55.936 E 121 10.701	AMNH 167171	AY313742
<i>L. sp. 2</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Tolala	S 02 55.936 E 121 10.701	AMNH 167172	
<i>L. sp. 2</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Tolala	S 02 55.936 E 121 10.701	AMNH 167173	
<i>L. sp. D</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Kamarora, Lore Lindu N. P.		Deposited in MZB	U66112, U66113
<i>L. sp. D</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Near Lore Lindu N. P.	S 01 27.016 E 119 59.394	AMNH 167174	
<i>L. sp. D</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Near Lore Lindu N. P.	S 01 27.016 E 119 59.394	AMNH 167175	
<i>L. sp. D</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Near Lore Lindu N. P.	S 01 27.016 E 119 59.394	AMNH 167176	AY313739
<i>L. sp. D</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Gunung Karua	S 02 54.130 E 119 41.839	AMNH 167177	AY313740
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kendari	S 03 58.963 E 122 22.269	AMNH 167178	AY313733

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APPENDIX. Continued

Species	General locality	Specific locality	GPS coordinates	Museum catalog number	Accession number(s)
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kendari	S 03 58.963 E 122 22.269	AMNH 167179	
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kendari	S 03 58.169 E 122 30.887	AMNH 167180	
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kendari	S 03 58.169 E 122 30.887	AMNH 167181	
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Buton Isl.	S 05 27.014 E 122 38.516	AMNH 167182	
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Buton Isl.	S 05 27.014 E 122 38.516	AMNH 167183	AY313734
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	near Morowali N. P.	S 01 50.659 E 121 29.398	AMNH 167184	AY313732
<i>L. sp. G</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Banggai Regency; 5 km E of Situna		TNHC 59107	AY313731
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kolonodale	S 01 59.196 E 121 20.369	AMNH 167185	AY313727
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kolonodale	S 01 59.196 E 121 20.368	AMNH 167186	AY313726
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kendari	S 03 54.434 E 122 30.281	AMNH 167187	AY313728
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Kendari	S 03 58.169 E 122 30.887	AMNH 167188	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Luwuk	S 00 57.054 E 122 47.493	AMNH 167189	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Luwuk	S 00 57.054 E 122 47.493	AMNH 167190	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Luwuk	S 00 57.054 E 122 47.493	AMNH 167191	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Luwuk	S 00 57.054 E 122 47.493	AMNH 167192	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Luwuk	S 00 57.054 E 122 47.493	AMNH 167193	AY313729
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Luwuk	S 00 57.44 E 122 46.33	LSUMZ 84194	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Salodik, near Luwuk	S 00 49.832 E 122 52.178	LSUMZ 84211	AY313730
<i>L. sp. I</i>	Indo., near Sulawesi Isl., Sulawesi Tenggara Prov.	Togian Islands, Pulau Batudaka	S 00 26.241 E 121 51.540	MZB Amph.8151	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Poso Regency; Kecamatan Ulubongka; Desa Marowo		TNHC 59254	AY313725
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Banggai Regency; 5 km E of Situna		TNHC 59263	
<i>L. sp. I</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Banggai Regency; 5 km E of Situna		TNHC 59256	
<i>L. sp. T</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Near Lore Lindu N. P.	S 01 27.016 E 119 59.394	AMNH 167194	AY313757
<i>L. sp. T</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Awan		RMB 2482 &	AY313758
<i>L. sp. T</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Gunung Karua	S 02 54.130 E 119 41.840	AMNH 167195	AY313760
<i>L. sp. T</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Gunung Karua	S 02 54.130 E 119 41.840	AMNH 167196	
<i>L. sp. T</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Gunung Karua		LSUMZ 81747	
<i>L. sp. T</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Tawaeli-Toboli Road	S 00 44.075 E 119 59.192	AMNH 167197	AY313759
<i>L. sp. T</i>	Indo., Sulawesi Isl., Sulawesi Tenggara Prov.	Tawaeli-Toboli Road	S 00 44.075 E 119 59.192	AMNH 167198	
<i>L. sp. V complex 1</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167199	AY313737
<i>L. sp. V complex 1</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167201	
<i>L. sp. V complex 1</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Tangkoko N. P.	N 01 34.205 E 125 09.416	AMNH 167200	
				AMNH-FS 16105, no voucher	
<i>L. sp. V complex 1</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Bogani Nani Wartabone N. P.	N 00 33.096 E 121 58.129		AY313738
<i>L. sp. V complex 1</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Near Bogani Nani Wartabone N. P.	N 00 34.004 E 123 53.272	AMNH 167202	
<i>L. sp. V complex 1</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Toraut, near Bogani Nani Wartabone N. P.	S 00 33.72 E 123 54.23	MZB Amph.8108	

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<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Binanggi	S 00 45.340 E 120 05.420	LSUMZ 84226	AY313751
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Tawaeli-Toboli Road	S 00 44.075 E 119 59.192	AMNH 167203	
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Tawaeli-Toboli Road	S 00 44.075 E 119 59.192	AMNH 167204	AY313750
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Desa Kebun Kopi, Tawaeli/Toboli Road		MZB Amph.8089	AY313756
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Desa Kebun Kopi, Tawaeli/Toboli Road		LSUMZ 84216	AY313755
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Garumba, near Tawaeli	S 00 43.63 E 119 55.30	JAM 3529†	AY313753
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Lemo	S 00 26.449 E 119 58.978	AMNH 167205	AY313754
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Tengah Prov.	Simoro, Biromaru	S 01 15.570 E 119 58.220	LSUMZ 84215	
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Marisa	N 00 33.096 E 121 58.129	AMNH 167206	AY313752
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Marisa	N 00 33.096 E 121 58.129	AMNH 167207	
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Marisa	N 00 33.096 E 121 58.129	AMNH 167208	
<i>L. sp. V complex 2</i>	Indo., Sulawesi Isl., Sulawesi Utara Prov.	Marisa	N 00 33.096 E 121 58.129	AMNH 167209	
<i>L. visayanus</i>	Phil., Panay Isl, Antique Prov.	Mun. Valdarama, Barangay San Agustin, Mt. Baloy	N 11 1, E 122 7.7	TNHC 56337	AY313720
<i>L. visayanus</i>	Phil., Negros Isl., Negros Oriental Prov.	Mun. Valencia, Barangay Bongabong, Mt. Talinis	N 09 36.4 E 124 4.5	TNHC 61911	AY313719
<i>L. visayanus</i>	Phil., Negros Isl., Negros Oriental Prov.	Mun. Simulan, Barangay Janay-janay, Lake Balinsasayo	N 09 21.8 E 123 4.3	TNHC 61921	
<i>L. woodworthi</i>	Phil., Luzon Isl., Quezon Prov.	Mun. Tayabas, Barangay Lalo, Mt. Banahao	N 14 3.02 E 121 32.46	PNM 7445	AY313708
<i>L. woodworthi</i>	Phil., Luzon Isl., Laguna Prov.	Mun. Los Baños, Barangay Batong Malake, Mt. Makiling	N 14 9.30 E 121 14.08	PNM 7600	AY313707
<i>L. woodworthi</i>	Phil., Luzon Isl., Quezon Prov.	Mun. Atimonan, Barangay Malinao Ilaya	N 13 59.93, E 121 48.79	PNM 7832/TNHC 61942	AY313712
<i>L. woodworthi</i>	Phil., Luzon Isl., Albay Prov.	Mun. Tabaco, Barangay Bongabong	N 13 21.7 E 123 43.7	TNHC 61916	AY313711
<i>L. woodworthi</i>	Phil., Luzon Isl., Camarines Sur Prov.	Mun. Naga City, Barangay Panicuason, Mt. Isarog	N 13 39.3, E 123 23	TNHC 61922	AY313710
<i>L. woodworthi</i>	Phil., Luzon Isl., Albay Prov.	Mun. Tiwi, Barangay Banhao, Mt. Malinao	N 13 27.5, E 123 10.6	TNHC 61915	
<i>L. woodworthi</i>	Phil., Luzon Isl., Albay Prov.	Mun. Malinao, Barangay Tagoytoy, Mt. Malinao	N 13 24.8 E 123 35.8	TNHC 61918	
<i>L. woodworthi</i>	Phil., Luzon Isl., Sorsogon Prov.	Mun. Irosin, Barangay San Roque, Mt. Bulusan	N 12 45.2, E 124 8.0	TNHC 61919	AY313709
<i>L. woodworthi</i>	Phil., Luzon Isl., Sorsogon Prov.	Mun. Irosin, Barangay San Roque, Mt. Bulusan	N 12 45.2, E 124 8.0	TNHC 61920	

Sharon B Emerson field catalog.

Rafe M Brown field catalog deposited in PNM.

& Rafe M Brown field catalog deposited in MZB.

* John W Ferner field catalog number deposited in CMNH.

† Jimmy A. McGuire field catalog number deposited in MZB.

Abbreviations: Phil. = Philippines, Indo. = Indonesia, Mun. = Municipality, Isl. = Island, Mt. = Mountain, N. P. = National Park, Dist. = District, and Prov. = Province.