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## Phylogeography and historical demography of *Polypedates leucomystax* in the islands of Indonesia and the Philippines: Evidence for recent human-mediated range expansion?

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## ABSTRACT

Southeast Asia's widespread species offer unique opportunities to explore the effects of geographical barriers to dispersal on patterns of vertebrate lineage diversification. We analyzed mitochondrial gene sequences (16S rDNA) from a geographically widespread sample of 266 Southeast Asian tree frogs, including 244 individuals of *Polypedates leucomystax* and its close relatives. Our expectation was that lineages on island archipelagos would exhibit more substantial geographic structure, corresponding to the geological history of terrestrial connectivity in this region, compared to the Asian mainland. Contrary to predictions, we found evidence of numerous highly divergent lineages from a limited area on the Asian mainland, but fewer lineages with shallower divergences throughout oceanic islands of the Philippines and Indonesia. Surprisingly and in numerous instances, lineages in the archipelagos span distinct biogeographical provinces. Phylogeographic analyses identified four major haplotype clades; summary statistics, mismatch distributions, and Bayesian coalescent inference of demography provide support for recent range expansion, population growth, and/or admixture in the Philippine and some Sulawesi populations. We speculate that the current range of *P. leucomystax* in Southeast Asia is much larger now than in the recent past. Conversion of forested areas to monoculture agriculture and transportation of agricultural products between islands may have facilitated unprecedented population and range expansion in *P. leucomystax* throughout thousands of islands in the Philippine and Indonesian archipelagos.

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## 1. Introduction

Southeast Asia, the Malay Peninsula, and the island archipelagos of the Philippines and Indonesia comprise a zoogeographic region characterized by striking biogeographic boundaries and fine-scale faunal endemism (Brown and Guttman, 2002; Evans et al., 2003a, 2008; Brown and Diesmos, 2009; Esselstyn et al., 2009). Numerous studies have documented the prevalence of cryptic diversity (species, evolutionary significant units for conservation, highly

divergent genetic lineages) in widespread species of Southeast Asian amphibians (i.e., Evans et al., 2003a; Brown et al., 2008; Ron and Brown, 2008; Stuart and Bain, 2008; Inger et al., 2009; Matsui et al., 2010; Chan and Grismer, 2010; McLeod, 2010). Other studies have emphasized that levels of cryptic diversity may be much higher than currently appreciated (e.g., Bickford et al., 2007), potentially exacerbating an already acute Asian conservation crisis (Sodhi et al., 2008; Rowley et al., 2009). Cryptic species are so prevalent that investigators have questioned whether *any* "widespread" Southeast Asian amphibian species are in fact single evolutionary lineages (Stuart et al., 2006). Indeed, the current *a priori* expectation in evolutionary, ecological, and conservation circles is to assume that most, if not all, geographically widespread Southeast Asian species

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are complexes of morphologically cryptic lineages (Stuart et al., 2006; Bain et al., 2008), especially when their range spans the archipelago portions of western Indonesia (the Sunda Shelf), central Indonesia (Wallacea), and the Philippines (Hall, 2002).

Continents, being larger than islands, have the capacity to support species with broad geographic ranges and limited geographic structure (review: Lomolino et al., 2006). In contrast, island archipelagos may support species with small ranges and pronounced intraspecific genetic variation if they span multiple islands (Wright, 1950; Inger, 1954, 1966, 1999; Schmidt et al., 1995; Evans et al., 1999; Brown and Guttman, 2002; Campbell et al., 2004; Inger et al., 2009). Recent molecular phylogenetic and phylogeographic studies have provided more detail about the role of islands in diversification and in particular about the “permeability” of Southeast Asia’s major biogeographic barriers to dispersal of different lineages. For example, a recent phylogenetic study concluded that a widely recognized biogeographic barrier—Wallace’s Line—was crossed multiple times in the evolutionary history of fanged frogs (Evans et al., 2003a). This and other studies demonstrated that some groups of amphibians (Vences et al., 2003; Brown, 2009; Brown and Diesmos, 2009; Brown et al., 2009; Jones and Kennedy, 2008; Esselstyn et al., 2010) defy formidable biogeographical boundaries recognized by early zoogeographers (Wallace, 1860, 1876; Huxley, 1868).

Several widespread species of frogs found throughout the mainland and islands of Southeast Asia provide compelling systems with which to investigate the impact of habitat fragmentation and connectivity on biological diversification. One example is the widespread Asian tree frog, *Polypedates leucomystax*, a species ostensibly distributed from India to eastern Indonesia (Taylor, 1962; Inger, 1999; Dutta and Manamendra-Arachchi, 1996). The species has a complex synonymy list (Brown, 2007; Frost, 2009), reflecting a long history of taxonomic confusion and varying levels of recognition of its morphologically distinct populations. For the

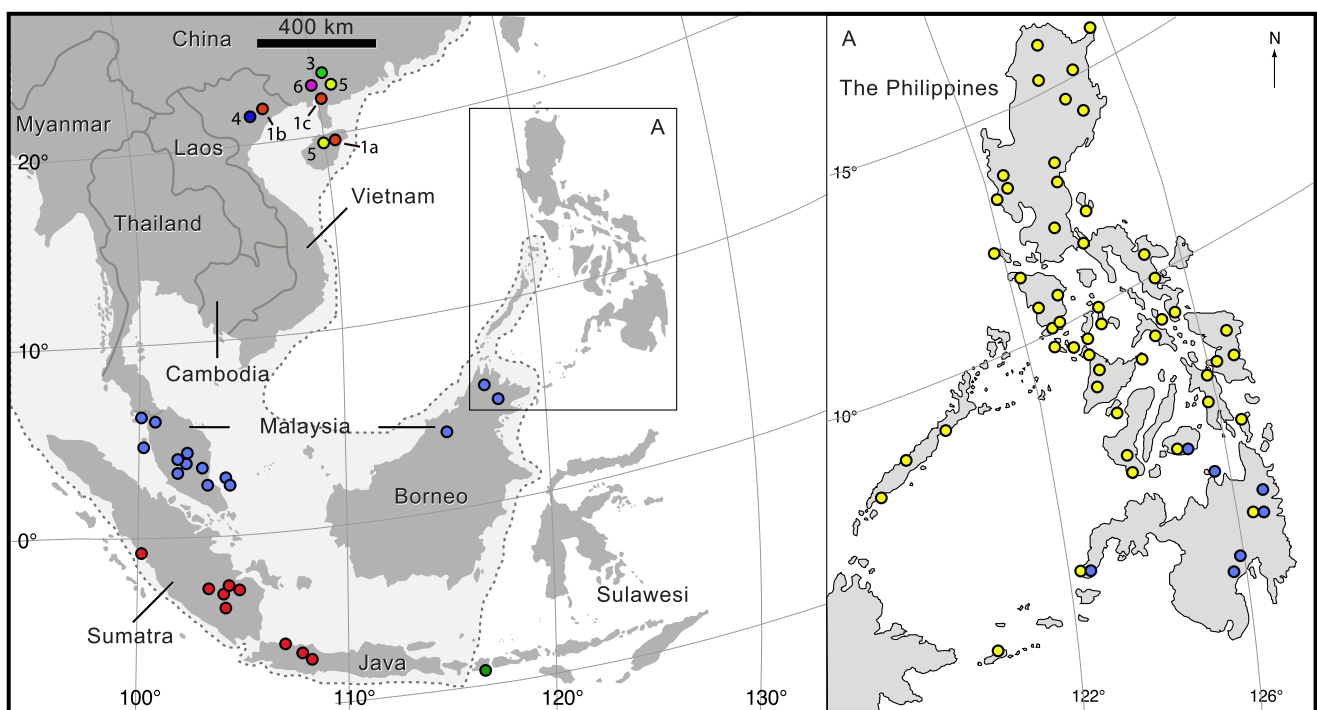
last half-century, many workers have assumed that this species would eventually be shown to represent a complex of morphologically conservative or “cryptic” species (Inger, 1999; Inger et al., 1999; Narins et al., 1998). In this paper, we take a first step towards examining genetic variation the insular populations of *P. leucomystax*. We examined phylogeographic relationships among 121 populations (sampling localities) and 244 individuals of the widespread species *P. leucomystax* and close relatives from throughout its distribution in the island archipelagos in Southeast Asia and a limited part of its range on the Asian mainland (parts of Peninsular Malaysia, northern Vietnam, and southern China).

Our major objectives are to (1) qualitatively compare genetic diversity within this species in different portions of its range, including mainland and archipelago populations, (2) assess whether population structure in *P. leucomystax* is consistent with the geological history of isolation and connectivity of Southeast Asia’s mainland and island regions, and (3) test whether genetic differentiation in *P. leucomystax* populations is consistent with demographic or range expansion.

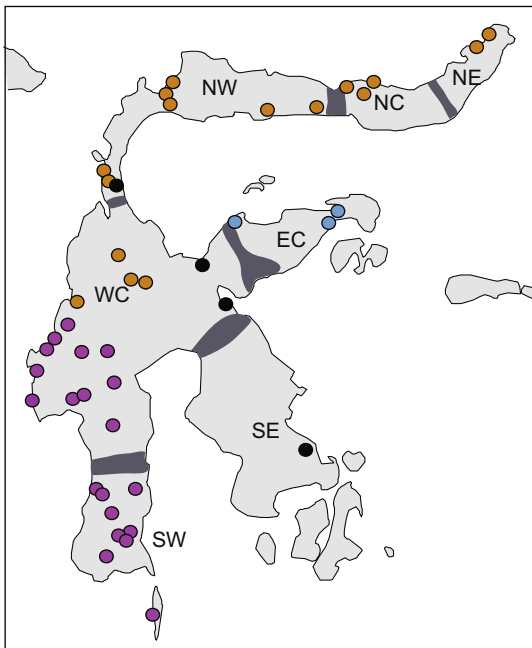
## 2. Materials and methods

### 2.1. Geographic sampling

We sampled 266 individuals, including 22 outgroup samples assignable to *Rhacophorus dennysi*, *Polypedates otitophus*, *P. colletti*, and *P. macrotis*, an additional 22 samples tentatively identified as *P. megacephalus*, *P. mutus*, and/or *P. leucomystax* from the Asian mainland (see below), and 222 individuals representing 121 insular populations of *P. leucomystax*. Our sampling of *P. leucomystax* and close relatives focused on populations from throughout Indochina (Southeast China, Vietnam, and Hainan Island), the Malay Peninsula and associated islands, the islands of the Sunda Shelf (Borneo, Java,



**Fig. 1.** Map of Southeast Asia with haplotype diversity of island populations of *P. cf. leucomystax* and related mainland congeners (putatively assigned to *P. cf. leucomystax*, *P. cf. mutus*, and *P. cf. megacephalus*) represented by different colored circles (numbers correspond to haplotype clades in Appendix A). See Fig. 2 for Sulawesi sampling and Figs. 3 and 4 for relationships. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** Map of Sulawesi with four main haplotype groups denoted by different colors. See Figs. 3 and 4 for relationships. Dark gray bars denote positions of geographical barriers to dispersal for Sulawesi monkeys and toads (Evans et al., 2003b, 2008). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Sumatra), islands on the periphery of the Sunda Shelf (Sulawesi, Tawitawi, Palawan, Mindanao, and Lombok), and the oceanic islands of the Philippines and eastern Indonesia (Fig. 1). Particularly intensive sampling targeted all the Pleistocene Aggregate Island Complexes in the Philippines (Brown and Diesmos, 2002, 2009), and most of the biogeographic subprovinces (Evans et al., 2003b) of Sulawesi (Fig. 2). Tissue samples were flash-frozen in liquid nitrogen, or immersed in  $\geq 90\%$  ethanol or tissue buffer, then stored at  $-80^\circ\text{C}$ . Most specimens are deposited in the Natural History Museum of the University of Kansas (KU), the National Museum of the Philippines (PNM), the Texas Memorial Museum of the University of Texas–Austin (TNHC), the Museum of Vertebrate Zoology of the University of California–Berkeley (MVZ), the Museum Zoologicum Bogoriense (MZB) or are temporarily deposited at Institut Teknologi Bandung, to be later transferred to MZB (Appendix A).

## 2.2. DNA extraction, amplification, purification, and sequencing

We used a non-commercial guanidine thiocyanate method (Esselstyn et al., 2008) to extract DNA from liver samples preserved in 95% ethanol. Although some domains in mitochondrial DNA show more variation, we sequenced all samples for the 16S rRNA mitochondrial gene fragment because this region has been used more often by phylogeographers working with Asian anurans. Two primers were used to amplify an 839 bp region spanning most of the 16S ribosomal RNA gene via polymerase chain reaction: 5' to 3': 16Sc GTRGGCCTAAAAGCAGCCAC and 16Sd CTCGGTCTGACTCAGATCACGTAG (Moriarty and Cannatella, 2004); PCR thermal conditions followed Evans et al. (2003a) and Moriarty and Cannatella (2004). Samples were purified using Exosap purification protocols (USB Corp., Cleveland, OH, USA). Sequencing reactions were conducted with identical undiluted PCR primers, using ABI Big Dye terminator chemistry (Perkin-Elmer, Boston, MA, USA) and Sephadex clean-up (GE Healthcare, Uppsala, Sweden). Sequencing was performed on an ABI 3130xl automated PRISM sequencer (Applied

Biosystems, Foster, CA, USA). All sequences are deposited in GenBank (Accession Nos. HM770125–HM770389).

## 2.3. Sequence alignment and phylogenetic analyses

We sequenced the targeted gene region, assembled contigs in Sequencher 4.5 (Genecodes, Ann Arbor, MI, USA), and initially aligned the consensus sequences using MUSCLE (Edgar, 2004). The alignment was then adjusted by eye in the program Se-AL (Rambaut, 1996). Ambiguously aligned regions were defined as a character set for possible exclusion using MacClade 4.0 (Maddison and Maddison, 2000); exclusion of these positions resulted in the removal of seven autapomorphic nucleotide insertions found in outgroup species. The block of aligned sequences was then trimmed so that beginning and end regions were removed and all individuals had complete data. Due to a high number of identical haplotypes from populations where larger sample sizes were available, we used Collapse v1.2 (Posada: available at <http://darwin.uvigo.es/software/collapse.html>) to reduce our dataset by eliminating haplotypes that were duplicated within populations, resulting in a final matrix with 153 samples.

We used the Akaike Information Criterion as implemented in Modeltest 3.7 to select a model of sequence evolution (Posada and Crandall, 1998; Posada and Buckley, 2004) which was then used in all model-based phylogenetic inference. We treated the 16S fragment as a single data partition in all analyses.

A maximum-likelihood estimate of the phylogeny was obtained using GARLI v0.952 (Zwickl, 2006) under a GTR+I+ $\Gamma$  (general time reversible model with Gamma distributed substitution rates and a proportion of the sites invariable; model parameters estimated during the search). To avoid local optima, 100 independent searches were performed, each starting with a random tree. Each search was terminated after 500,000 generations with no significant topological improvement. The solution with the best likelihood from these 100 searches was selected as our maximum-likelihood estimate. Statistical support for this topology was obtained by running 1000 bootstrap replicates (Felsenstein, 1985) in GARLI with the same settings, except that the termination criterion was reduced to 10,000 generations with no significant topological improvement. We considered branches receiving  $>70\%$  bootstrap support to be well-supported (Hillis and Bull, 1993; see also Wilcox et al., 2002).

A Bayesian estimate of phylogeny was obtained with MrBayes v3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) and the same GTR+I+ $\Gamma$  model of sequence evolution. Four independent Markov chain Monte Carlo searches were run for 20 million generations, sampled every 2000 generations, each with four chains, a temperature of 0.2, and default priors. To assess stationarity, we plotted sampled parameter values and  $-\ln$  likelihood scores from the cold Markov chain against generation time and compared the four independent runs using Tracer v1.4 (Rambaut and Drummond, 2007). We also plotted the cumulative and non-overlapping split frequencies of the 15 most variable nodes, and compared split frequencies among independent runs using Are There Yet? (AWTY; Wilgenbusch et al., 2004). All samples reached stability within 500,000 generations and, to be conservative, 1 million generations (500 trees) were discarded from each run as burn-in. The topology and posterior probabilities (PP) were then summarized separately from the remaining 19 million generations (9500 trees) per run. We considered topologies with posterior probabilities  $\geq 0.95$  to be well-supported (Wilcox et al., 2002).

## 2.4. Analyses of geographic and population structure

To assess general patterns of genetic diversity within clades, we calculated the numbers of haplotypes ( $N$ ), haplotype diversity

( $h$ ; Nei, 1987), numbers of polymorphic sites, and nucleotide diversity ( $\pi$ ; Nei and Tajima, 1981) using DNASP 4.0 (Rozas et al., 2003) and Arlequin 3.1 (Excoffier et al., 2005) for each major lineage of *P. leucomystax*.

We explored hierarchical relationships at the population level using the program TCS 1.18 (Clement et al., 2000) to link haplotypes into a statistical parsimony network. TCS uses the relationship of inferred ancestral (interior) haplotypes relative to younger (tip) haplotypes to make inferences about spatial patterns of genetic variation. A hierarchical nesting structure of the haplotype network was then inferred using the methods outlined in Templeton et al. (1987) and Templeton and Sing (1993). Because our goal was simply to explore our data for patterns of hierarchical geographic structure, and because the biogeographic inference step of Nested Clade Analysis has been criticized on a variety of grounds (Knowles, 2004, 2008; but see Templeton, 2009), we implemented this approach as a qualitative tool to identify the geographical basis of molecular variation.

Analyses of molecular variation (AMOVAs; Excoffier et al., 1992) were conducted on sequence data for *P. leucomystax* on island and selected (Peninsular Malaysian) adjacent mainland populations, in an effort to explore the amount of genetic variation explained among and between the major island archipelagos sampled, and to assess the most probable subdivision of genetic variation among populations. All AMOVAs were completed with 1000 permutations in Arlequin 3.1 (Excoffier et al., 2005). Analyses were conducted to elucidate the amount of genetic variation that could be explained among and between the clades revealed by the phylogenetic analysis and haplotype networks (see Section 3): northern Sunda Region, southern Sunda Region, northern Philippines, and Sulawesi (Appendix A), and within-region biogeographic subdivisions (Philippine Pleistocene Aggregate Island Complexes, PAICs; Brown and Diesmos, 2002, 2009; or Sulawesi Areas of Endemism, AOE; Evans et al., 2003a,b).

### 2.5. Demographic inference

We assessed the four major regional lineages identified in the phylogenetic analyses and haplotype networks for evidence of recent change in effective population size. We therefore calculated mismatch distributions in Arlequin 3.1, which assumes an infinite sites model of selectively neutral nucleotide substitutions and assesses significance via coalescent simulations of a large, neutrally evolving population of constant size (Slatkin and Hudson, 1992; Rogers and Harpending, 1992). This approach involves the assessment of a mismatch distribution for ragged and/or multimodal distributions, which could stem from a structured population, versus smooth or unimodal, which is indicative of possible recent population expansion or sudden panmixia (Harpending et al., 1998). We also employed Fu's  $F_s$  neutrality test (Fu, 1997) as an assessment of possible population expansion. This assumes neutrality and potentially diagnoses a recent population expansion via a highly negative value of  $F_s$ . Finally, we calculated Tajima's  $D$  (implemented as a test for selective neutrality), and Ramos and Rozas  $R_2$  statistics (Ramos-Onsins and Rozas, 2002) as additional indicators of potential population expansion.

Because  $F_s$  and  $R_2$  are summary statistics (based on distributions of haplotypes and numbers of segregating sites) they do not use all of the historical information contained in DNA sequence variation (Galbreath et al., 2009). Alternatively, we attempted to assess changes in demographic growth of effective population size over the history of each major lineage by applying Bayesian skyline analyses (Drummond et al., 2005) in BEAST 1.4.7 (Drummond and Rambaut, 2006, 2007) to each of the four regional lineages (as above). We approximated the posterior distribution of effective

population size (from the original, unreduced dataset) over intervals of the phylogeny in an attempt to diagnose population median effective size fluctuations over time for each of the four clades (as above), and for all *P. leucomystax* for each group identified in the phylogeny and haplotype network. For each of these five analyses we chose the appropriate model of sequence evolution with AIC in MODELTEST (Posada and Crandall, 1998), and generated input files with BEAUTi, using the closest available models with greater complexity. We ran analyses for 10 million steps, using default parameters, sampling every 1000 steps, and discarded the first 10% of samples as conservative burn-in. Each analysis was conducted twice with different random seeds, and results then were combined in LOGCOMBINER 1.4.7 (after burn-in) after examining convergence diagnostics in TRACER 1.4 (Rambaut and Drummond, 2007).

## 3. Results

### 3.1. Sequence variation

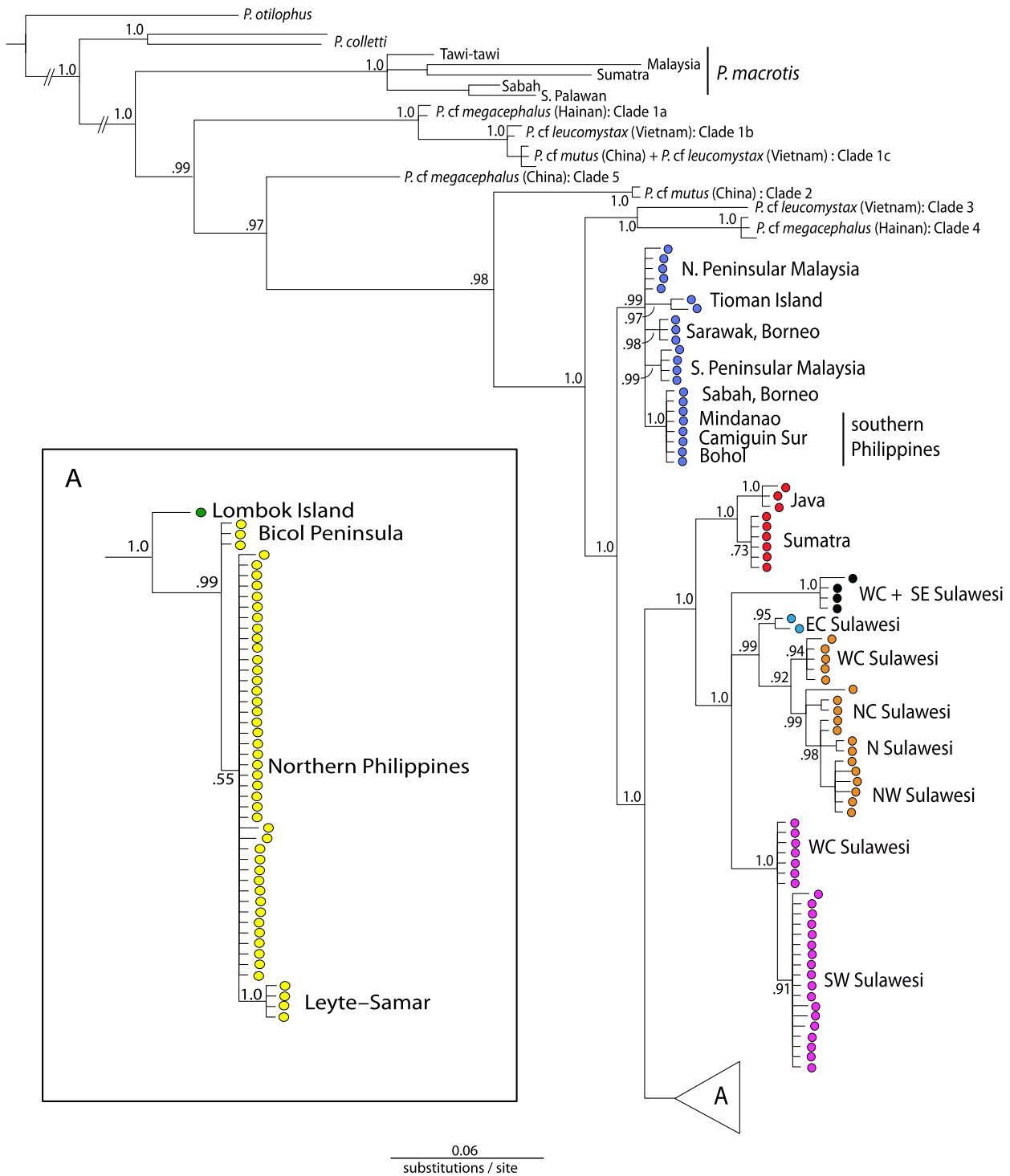
The complete, aligned matrices contain 266 sequences of the 16S ribosomal RNA mitochondrial gene region, spanning a 906-bp fragment. Following initial unrooted analyses, and assuming the root of the tree does not lie within Philippine *Polypedates*, we polarized the tree using samples of *R. dennysi*, *Polypedatus colletti*, and *P. otlophus*. Within the mtDNA gene sequences, 314 variable, 592 constant, and 242 parsimony-informative characters were observed. Our dataset was virtually complete, containing missing fragments for only two samples, both of which were removed by elimination of redundant haplotypes.

### 3.2. Phylogeographic relationships

Likelihood and Bayesian analyses produced identical topologies and qualitatively comparable branch lengths (Fig. 3). Differences involved only minor rearrangements of some terminals (individual samples).

Two hundred and twenty-two of these sequences were ingroup samples from island populations of *P. leucomystax* (Appendix A). Although identification of the outgroup species *R. dennysi*, *P. colletti*, *P. otlophus*, and *P. macrotis* was reliable and straightforward (because of their distinctive morphology; Inger and Stuebing, 1989, 1997; Inger et al., 1999), identification of mainland lineages closely related to *P. leucomystax* was more problematic. Based on morphology and currently available species diagnoses (Inger, 1954, 1966; Matsui et al., 1986; Manthey and Grossman, 1997; Malkmus et al., 2002; Fei, 1999; Fei et al., 2000), the mainland lineages are putatively referable to *P. cf. megacephalus*, *P. cf. mutus*, and *P. cf. leucomystax*. However, because we only were able to include samples of one of these species from its type locality (*P. leucomystax*, type locality Java, Indonesia) and type locality specimens and sequences of *P. mutus* and *P. megacephalus* (N'Chang Yang, northern Myanmar; and Hong Kong, China, respectively) are unavailable, we attempt no taxonomic actions at this time. In fact, it is clear that current diagnoses available for mainland populations of *P. cf. megacephalus*, *P. cf. mutus*, and *P. cf. leucomystax* require future revision. Because the identities of these lineages are ancillary to our questions, and because we do not seek to evaluate the taxonomy of this group at this time, the problematic identification of these lineages will not be considered further.

Mainland populations tentatively referred to *Polypedates cf. megacephalus*, *P. cf. mutus*, and *P. cf. leucomystax* show low levels of variation within sampling localities but are highly variable between localities (Figs. 1 and 3). The large haplotype clade



**Fig. 3.** Phylogeographic relationships among island populations of *P. leucomystax*, related mainland lineages (putatively assigned to *P. leucomystax*, *P. mutus*, and *P. megacephalus*) and outgroups (*P. macrotis*, *P. colletti*, *P. otlophus*, and *Rhacophorus dennysi* [deleted for simplicity]) inferred from Bayesian analysis of 16S ribosomal RNA mitochondrial gene sequences. Bayesian posterior probability values are included above internodes.

containing the type locality (Java, Indonesia) that we confidently identify as true *P. leucomystax* has low levels of divergence throughout the island populations (all pairwise uncorrected differences less than 4%; Table 2). Samples of *P. leucomystax* fall into the following four major haplotype clades as identified by genealogical analyses and parsimony networks (Figs. 1, 3, and 4): (1) the southern Sunda Region (Java–Sumatra) clade, (2) a northern Sunda Region (Peninsular Malaysia, northern Borneo, and southern

Philippines) clade, (3) a Sulawesi clade, and (4) a widespread northern Philippine clade that is the sister taxon to a divergent haplotype represented by a single sample from Lombok Island (Lesser Sunda islands, Indonesia; Fig. 1). Neither the Sunda Region nor Philippine *P. leucomystax* are monophyletic with respect to haplotypes from other geographic regions (i.e., both regions are characterized by two haplotype clades that are not each other's closest relatives). Unlike in previous studies of amphibians known

to us (e.g., Evans et al., 2003a; Inger et al., 2009), the Sunda Region is composed of a northern group and a southern group (Figs. 1 and 3). Additionally, unlike other studies that have shown multiple lineages geographically structured on Pleistocene Aggregate Island Complexes (Brown et al., 2000; Brown and Diesmos, 2009), or clades structured on the west and east Philippine island arcs (Brown and Guttman, 2002; Brown et al., 2009), we found evidence of two groups of haplotypes that are not each others' closest relatives inhabiting the same PAIC. One is distributed throughout the archipelago and the other is restricted to the Mindanao faunal region (Fig. 1). Haplotypes from these two weakly divergent groups have been found in syntopy in populations inhabiting the same microhabitat in at least three localities (Bohol, eastern Mindanao, and the Zamboanga Peninsula of western Mindanao; Fig. 1). The widespread Philippine haplotype group exhibited virtually no geographic genetic structure; the Sunda Region populations exhibited intermediate levels of genetic structure (partitioned among islands); and the monophyletic Sulawesi haplotype clade exhibited greater genetic variation (Figs. 1–3) divided among some of the island's peninsulas (Evans et al., 2003b).

### 3.3. Geographic and population structure

We identified 39 unique haplotypes among the Philippines, Malaysia, Borneo, Sulawesi, Sumatra, Java, and Lombok (Figs. 3, 4 and Table 1). As mentioned these fall into a northern Sunda Region clade (six distinct haplotypes and 20 polymorphic sites), a southern Sunda Region clade (five haplotypes with six polymorphic sites), Sulawesi (20 haplotypes and 151 polymorphic sites) and the Philippines + Lombok (eight haplotypes and 13 polymorphic sites). Across these four clades, mean number of pairwise nucleotide differences ( $k$ ), haplotype diversity ( $h$ ), and percent nucleotide diversity ( $\pi$ ) are all greatly reduced in Philippine populations (Table 1) despite the large numbers of samples sequenced (77 northern Philippine haplotype individuals + 11 northern Sunda Region haplotype clade members from the Mindanao PAIC).

Our analyses of molecular variance (AMOVAs) (Table 3) detected significant geographic structure in hierarchically partitioned populations of *P. leucomystax*. Partitioning of genetic diversity differed between the four haplotype clades inferred by the phylogenetic and haplotype-network analyses. The southern Sunda Region, for example, had greater variation structured among islands (e.g., Java versus Sumatra) whereas the northern Sunda Region clade and Sulawesi had greater portions of the total variance explained by within-PAICs and within-Areas of Endemism differences, respectively. The Philippines exhibited a slightly greater portion of the total genetic variance structured among PAICs than within these island-group platforms (Table 3).

The 95% haplotype network procedure grouped haplotypes into the same major clades of *P. leucomystax* revealed by phylogenetic analysis (Fig. 3), resulting in fifteen 1-step groups, six 2-step groups, and one 3-step group (Fig. 4). The widespread Philippine haplotype clade has the highest outgroup probability of 22.6% and consists of seven distinct haplotypes with minimal divergence between each. Eight changes away from the Philippine group is a haplotype from Lombok. Eight changes away from the Lombok haplotype is the northern Sunda Region group, consisting of samples from Malaysia, Borneo, and the Mindanao PAIC (Philippines). The southern Sunda Region group consists of haplotypes from Sumatra (two identifiable haplotypes) and Java (three). The island of Sulawesi has the highest level of haplotype diversity with 20 distinct haplotypes in four major groupings. One clade consists of haplotypes from the northern peninsula

**Table 1**

Summary of island archipelago *P. leucomystax* sampling, major lineages/haplotype clades, numbers of individuals ( $N$ ), numbers of mtDNA haplotypes ( $N_h$ ), numbers of polymorphic sites ( $P_N$ ), mean number of pairwise nucleotide differences ( $k$ ), haplotype diversity ( $h$ ), and nucleotide diversity ( $\pi$ ). See Appendix A for full details of sampling and a list of all 266 samples included.

Region/clade	$N$	$N_h$	$P_N$	$k$	$h$	Nucleotide diversity ( $\pi$ )
Northern Sundas	44	9	20	7.043 ± 3.37	0.775 ± 0.04	0.0088 ± 0.0046
Southern Sundas	17	5	6	1.681 ± 1.03	0.574 ± 0.13	0.0021 ± 0.0014
Sulawesi	75	20	151	16.159 ± 7.28	0.809 ± 0.04	0.0199 ± 0.0099
Philippines	77	7	13	0.487 ± 0.42	0.220 ± 0.06	0.0006 ± 0.0006
All samples	213	38	172	16.915 ± 7.55	0.860 ± 0.02	0.0209 ± 0.0103

**Table 2**

Uncorrected 16S gene sequence divergence (%) among and within mitochondrial gene lineages of Southeast Asian island archipelago *P. leucomystax* and close relatives. Percentages on the diagonal represent within-clade genetic diversity (bolded for emphasis).

	<i>P. colletti</i>	<i>P. macrotis</i>	<i>P. cf. megacephalus</i>	<i>P. cf. mutus</i>	<i>P. cf. leucomystax</i> (China + Vietnam)	<i>P. leucomystax</i> (Sulawesi)	<i>P. leucomystax</i> (Southern Sundas)	<i>P. leucomystax</i> (Northern Sundas)	<i>P. leucomystax</i> (Philippines)
<i>P. colletti</i>	<b>0.0–5.0</b>								
<i>P. macrotis</i>	10.8–11.9	<b>0.0–4.0</b>							
<i>P. cf. megacephalus</i>	10.4–12.7	7.3–10.3	<b>0.1–6.9</b>						
<i>P. cf. mutus</i>	10.2–13.0	7.8–10.3	0.0–7.9	<b>0.0–7.9</b>					
<i>P. cf. leucomystax</i> (China + Vietnam)	10.3–13.0	7.5–10.6	0.0–8.0	0.0–8.5	<b>0.0–8.7</b>				
<i>P. leucomystax</i> (Sulawesi)	10.0–12.9	9.0–10.8	2.6–8.4	2.7–9.3	2.6–9.4	<b>0.0–2.2</b>			
<i>P. leucomystax</i> (Southern Sundas)	10.0–12.8	9.9–10.8	3.2–7.9	3.3–8.9	3.0–9.0	1.4–2.0	<b>0.0–0.5</b>		
<i>P. leucomystax</i> (Northern Sundas)	9.8–12.9	9.3–10.5	2.5–8.2	2.6–9.2	2.5–9.3	1.5–3.2	1.4–2.2	<b>0.1–2.1</b>	
<i>P. leucomystax</i> (Philippines)	10.1–12.9	9.3–10.6	3.0–8.2	3.1–9.2	3.0–9.3	1.2–3.2	1.6–2.2	0.0–2.1	<b>0.1–1.4</b>

**Table 3**  
Results of two-level Analysis of Molecular Variance (AMOVA) of genetic differences in mtDNA sequences of island archipelago populations of *P. leucomystax*. Entries include the percentage of total variance explained by haplotype clade and by geographic partitioning within these groups (i.e., Java versus Sumatra for the southern Sunda Region), Pleistocene Aggregate Island Complexes (Philippines) or Areas of Endemism (Sulawesi).

Region/ haplotype clade	Among islands/PAICs/ AOEs (%)	Within islands/ PAICs/ AOEs (%)	<i>p</i> -value
Northern Sunda Region	37.36	62.64	<0.0001
Southern Sunda Region	90.06	9.94	<0.0001
Sulawesi	38.59	61.41	<0.0001
Philippines	57.91	42.09	<0.0001
All samples	58.24	41.76	<0.0001

and the west-central region. A small haplotype clade consists of samples from the eastern peninsula; an additional group contains haplotypes from the west-central core and southeastern peninsula. Finally, a large haplotype group contains samples from the southwestern peninsula and southern portions of the west-central core (see also Figs. 2 and 3) including some fixed differences between these regions.

### 3.4. Recent population expansion in the Philippines

Evaluating the hypothesis of stable population structure per region identified by phylogenetic analyses and haplotype networks demonstrated a statistically significant difference between the Philippine haplotype clade and the other four lineages of *P. leucomystax*. Regardless of method used (summary statistics or Bayesian inference of demography), we detected the signature of recent population expansion in the Philippines.

Mismatch distributions (Fig. 5) are relatively ragged and multimodal in the northern Sundas, southern Sundas, and Sulawesi, departing from the model of rapid population expansion and suggesting structured, demographically stable populations. In contrast, simulated versus observed pairwise differences in the Philippines (plus its sister haplotype from Lombok Island) are

nearly identical, consistent with the hypothesis of recent range expansion (although *T* and Harpending's Raggedness Index are non-significant unless all samples are pooled; Table 4). Tajima's *D* indicates marginal departures from expectations of neutrality and demographic stability for the northern Sunda Region clade and Sulawesi (Table 4), with only the northern Philippines haplotypes resulting in highly significant ( $p = 0.003$ ) values. Similarly Fu's *F<sub>s</sub>* is positive or close to zero and non-significant in all regional groupings (including when all samples are combined) except the Philippines where it is large, negative and significant ( $p = 0.011$ ), rejecting the hypothesis of constant population size and consistent with the hypothesis of recent range expansion. Additionally, Ramos-Onsins and Rozas' *R<sub>2</sub>* statistics were small and positive, but only in the Philippine haplotype clade was the observed value statistically significant ( $p = 0.02$ ).

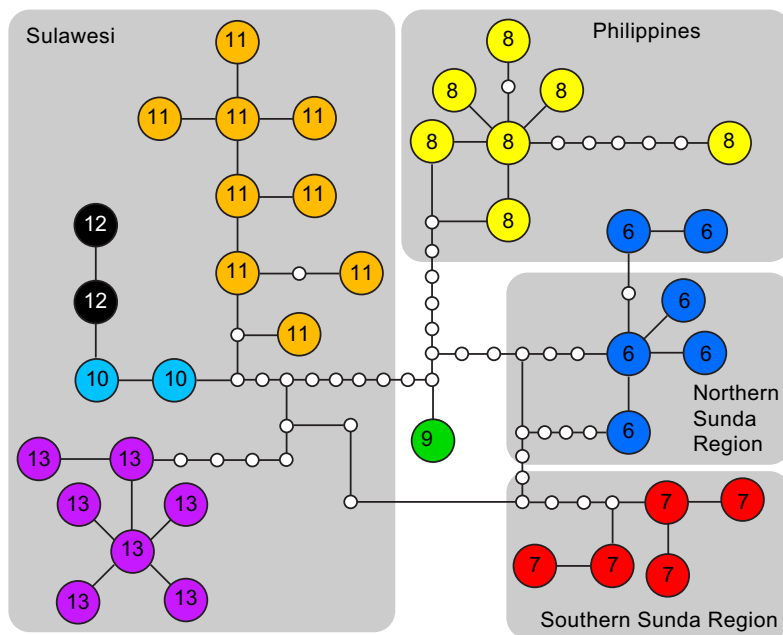
Coupled with lower levels of haplotype diversity, polymorphic sites, and nucleotide diversity (Table 1), these results indicate a marked departure from expectations based on a null model of constant population size for the Philippines.

Bayesian skyline plots revealed a complex demographic history in island archipelago populations of *P. leucomystax* (Fig. 6). In contrast to the two Sunda Region clades that demonstrated a relatively stable effective population estimate over time with a slight decline near the present, both Sulawesi and the northern Philippines clades showed clear signatures of recent population expansion and constant population growth over the most recent time interval. When all *P. leucomystax* samples were pooled to include all 222 insular samples of *P. leucomystax*, a clear pattern of population growth and recent expansion was revealed in a manner near identical to that detected in the Philippines and Sulawesi haplotype clades (not shown).

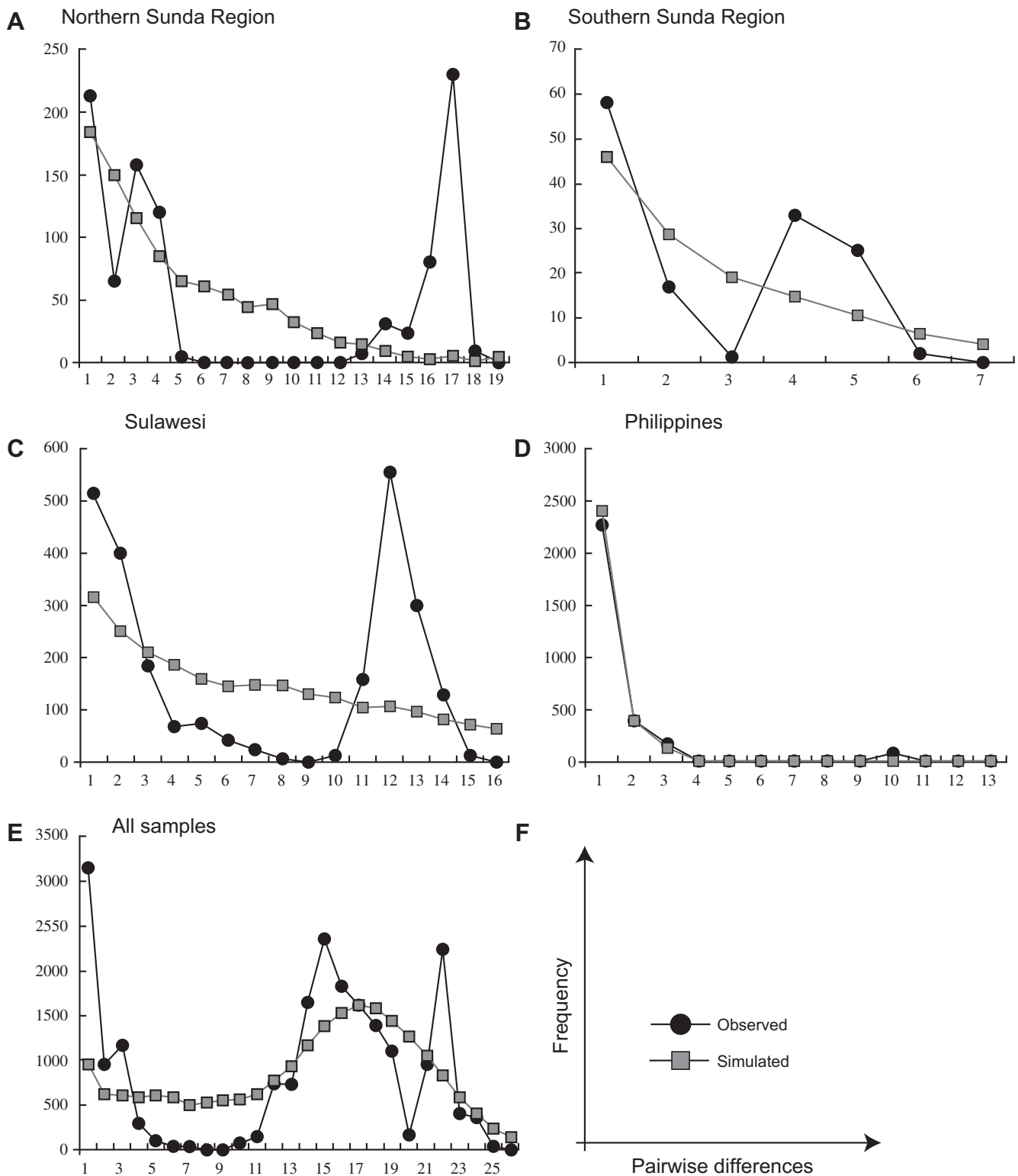
## 4. Discussion

### 4.1. Geographic distribution of lineage diversity

The general pattern of *Polypedates* lineage diversity elucidated in this study was unexpected and contrary to some expectations de-



**Fig. 4.** Minimum spanning 95% connection probability statistical parsimony haplotype network for Southeast Asian island archipelago populations of *P. leucomystax*, depicting hierarchical relationships among the four haplotype clades (northern and southern Sunda Region clades, the Philippines, Sulawesi). Haplotype No. 9 represents a single sample from Lombok Island, Indonesia. See Appendix A for full locality data.



**Fig. 5.** Observed frequencies of pairwise nucleotide differences among sequences (black circles) and expected frequencies under a model of sudden population expansion (see key; gray squares) (Rogers and Harpending, 1992). Mismatch distributions depict frequencies of pairwise differences for: (A) the northern Sunda Region (Peninsular Malaysia, northern Borneo, and the southern Mindanao faunal region), (B) the southern Sunda Region (Java and Sumatra Islands, Indonesia), (C) Sulawesi Island, (D) the Philippines + Lombok Island (Indonesia) samples, and (E) all samples of *P. leucomystax*.

rived from phylogeographic studies on continents and islands (Avice, 2000; Avice et al., 1987). One expectation was that the comparatively contiguous Asian mainland and nearby land-bridge is-

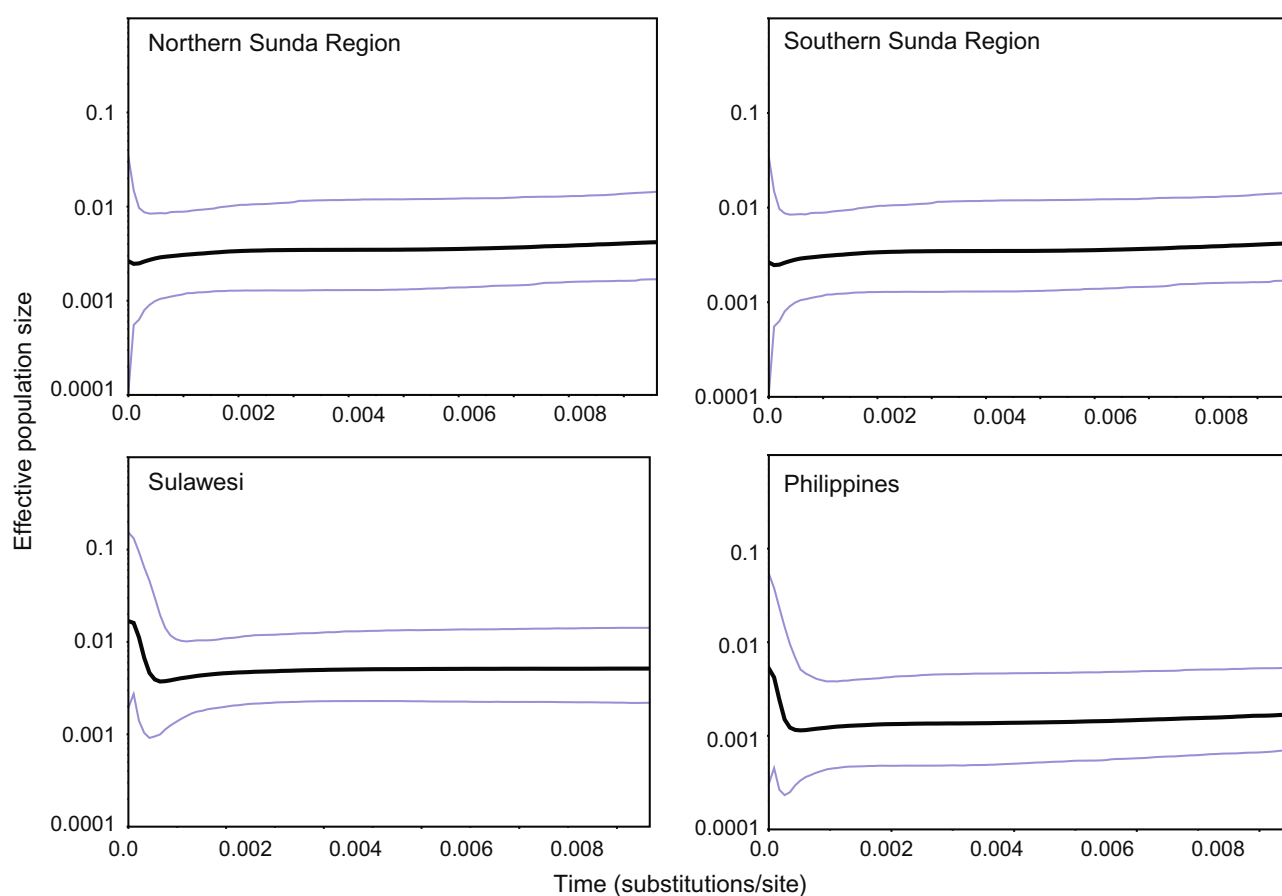
lands (e.g., the Sunda Region, connected as recently as 11,000 ybp) would support less population structure than adjacent oceanic archipelagos in the Philippines and Wallacea, which have a higher

**Table 4**  
Summary statistics and results of tests of population expansion: analysis of mismatch distributions, and substitution model applied to the Bayesian skyline analysis of demographic history. For mismatch distributions,  $T$  is presented along with  $p$ -values for rejection of the sudden expansion model, based on a comparison of the sum of squares of expected and observed distributions (using parametric bootstrapping with 10,000 replicates; Rogers and Harpending, 1992; Excoffier et al., 2005). Additional entries include Harpending's Raggedness Index ( $RI$ ) and  $p$ -values for rejection of the goodness of fit test comparing simulated versus observed distribution raggedness, Tajima's  $D$ , Fu's  $F_s$ , and Ramos-Onsins and Rozas  $R_2$  statistics. All tests were implemented separately for the four groups identified in the parsimony networks and phylogeographic analysis and for all samples of *P. leucomystax* combined (significant  $p$ -values bolded for emphasis).

Region/haplotype clade <sup>a</sup>	$T$	$RI$	Tajima's $D$ ( $p$ -value)	$F_s$ ( $p$ -value) <sup>b</sup>	$R_2$ ( $p$ -value) <sup>b</sup>	Skyline model
Northern Sundas (44)	1.989 (0.050)	0.133 (0.130)	1.7322 ( <b>0.049</b> )	4.281 (0.919)	0.151 (0.112)	GTR+I+ $\Gamma$
Southern Sundas (17)	4.654 (0.220)	0.192 (0.289)	0.1742 (0.424)	-0.2216 (0.444)	0.137 (0.291)	HKY+I
Sulawesi (75)	12.641 (0.070)	0.059 (0.220)	-1.6384 ( <b>0.040</b> )	5.2005 (0.897)	0.097 (0.090)	GTR+I+ $\Gamma$
Philippines (77)	3.000 (0.360)	0.421 (0.220)	-2.2835 ( <b>0.003</b> )	-4.202 ( <b>0.011</b> )	0.056 ( <b>0.010</b> )	GTR+I
All samples (213)	16.920 ( <b>&lt;0.001</b> )	0.030 ( <b>&lt;0.001</b> )	-1.2708 (0.097)	2.2132 (0.741)	0.176 (0.107)	GTR+I+ $\Gamma$

<sup>a</sup> Numbers of haplotypes in parentheses.

<sup>b</sup> Statistical significance for rejecting a null model of constant population size included in parentheses.



**Fig. 6.** Bayesian skyline plots for four major lineages identified by the phylogenetic estimate (Fig. 3) and haplotype networks (Fig. 4). Bold black lines indicate an estimate of median effective population size as a function of time, i.e., scaled by mutation rate; gray lines indicate the 95% upper and lower highest posterior probability interval. The horizontal axis has been scaled to show the same time interval (0.0–0.01 subst./site) for all plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

concentration of permanent or semi-permanent marine barriers. Additionally, populations residing on oceanic archipelagos that have never been connected to the Asian mainland were expected to have diversity partitioned by areas of endemism that have been observed in other taxa (Schmidt et al., 1995; Brown and Guttman, 2002; Evans et al., 2003a,b; Vences et al., 2003). These qualitative expectations reflect the conventional assumptions of anuran biogeographers over the last few centuries based on worldwide studies (Noble, 1931; Savage, 1973; Duellman and Trueb, 1994; Lomolino et al., 2006).

For example, although a continental mainland would be expected to have some geographic and ecological barriers to dispersal, continental biogeographic barriers generally should be fewer for a typical terrestrial vertebrate compared to archipelagos. A greater portion of continental barriers (mountain ranges, valleys, rivers, arid zones) might conceivably function as diffuse filter barriers rather than absolute faunistic boundaries, such as an ocean channel, across which amphibians rarely disperse (Duellman and Trueb, 1994; Stebbins and Cohen, 1995; Vences et al., 2003). Additionally, exten-

sive freshwater drainages that characterize continental systems would be expected to facilitate amphibian dispersal on the mainland by acting as dispersal corridors (Inger, 1999, 2003; Duellman and Trueb, 1994). In contrast, many biogeographers suspect that overseas dispersal is exceedingly unlikely for amphibians (Noble, 1931; Duellman and Trueb, 1994; Stebbins and Cohen, 1995; Brown, 2009). Indeed this is one of the reasons that amphibians are often considered excellent model systems for vicariance scenarios, especially for studies of island biogeography (including “habitat islands”) (Duellman and Trueb, 1994; Brown, 1997; Inger and Voris, 2001; Vences et al., 2003).

Contrary to our expectations, on the Asian mainland we found highly divergent haplotype clades, sometimes in sympatry (as was predicted by Stuart et al., 2006; Inger et al., 2009). These lineages may represent distinct but uncharacterized species and further taxonomic work is needed to resolve the possibility of cryptic biodiversity in mainland *Polypedates*. In contrast, the nearby land-bridge islands of the Sunda Shelf (Fig. 1), and distant oceanic islands of the Philippines and Indonesia are inhabited by genetically uniform populations, with minimal geographic structure—at least with respect to mitochondrial variation. Mitochondrial DNA has a much higher mutation rate than autosomal DNA (e.g., Haag-Liatard et al., 2008), and our surveys of autosomal DNA variation across multiple populations of *P. leucomystax* recovered low levels of variation as well (data not shown). Taken together, this suggests that the genetic homogeneity observed in mitochondrial DNA is likely echoed in other parts of the genome.

Our mainland sampling comes from two regions (southern Peninsular Malaysia and northern Vietnam/southern China) with relatively small geographic extent, so we are unable to fully evaluate the prediction that Asia’s mainland lineages might be geographically widespread. Comparisons among major regions of Southeast Asia (mainland, the Sunda Region, Wallacea, and the Philippines) suggests this complex has been broadly distributed for long enough for mutation and isolation to produced regionally distinctive variation. However, genetic uniformity across dozens of Sundaland and Philippine islands is in striking contrast to the pattern of 2–4 highly divergent sympatric lineages that co-occur at each site sampled on the Asian mainland, implicating other factors, such as humans in the recent biogeography of this species (see below).

#### 4.2. Phylogeographic relationships and demography of *P. leucomystax* in Southeast Asia

Our data are consistent with the hypothesis of multiple dispersal events of *P. leucomystax* to Asian archipelagos, and subsequent recent expansion of a few populations, although it is possible that aspects of this pattern could emerge from one or a limited number of dispersal event(s) of a polymorphic ancestor. One *P. leucomystax* mtDNA lineage occurs throughout the Malaysian Peninsula, northern Borneo, and the southern Philippine islands of Mindanao and Bohol (Fig. 1). Another lineage gave rise to populations sampled on Sumatra, Java, Bali, and Sulawesi, including moderate levels of divergence among populations on Sulawesi (Fig. 1). A third lineage occurs on the Philippines and the Indonesian Island of Lombok, which occurs just east of Wallace’s Line in the Lesser Sunda Islands of Wallacea. We suspect that the first major lineage may also occur on other islands in the Mindanao Faunal Region (Dinagat, Siargao, Basilan, Samar, Leyte, etc.). The first lineage occurs in sympatry through wide portions of its range in the southern Philippines with the third lineage. The Philippine portion of the third lineage is genetically nearly uniform (consisting of seven, minimally divergent haplotypes; Table 1) and lacks significant signal of population structure across its wide distribution.

One of our most surprising results is the finding that the recently expanded haplotype clade in the Philippines is endemic to this archipelago, and only moderately divergent (1.9%) from its sister lineage on Lombok, an island that lies far to the south of the Philippines (Figs. 1, 3, and 4). Interestingly, the Makassar Strait flows south from the Philippine archipelago, between Sulawesi and Borneo, and towards the Lesser Sunda Islands (to the Javan Sea), suggesting a possible route for rafting of an ancestral population of *P. leucomystax* to Lombok. The Philippine haplotype clade is not simply the result of recent invasion of the Philippines from the northern Sunda Region or some other adjacent region. Rather, the Philippine lineage is moderately divergent (Fig. 3), separated from related haplotypes by unique mutational steps (Fig. 4), and as far as we know, endemic to the Philippines (with the exception of a recent introduction into Japan; Kuraishi et al., 2009). Summary statistics and mismatch distributions depict the presence of structured, relatively stable populations of *P. leucomystax* in the northern Sunda Region, the southern Sunda Region, and Sulawesi, and most reject models of stable demographic configuration for the central and northern Philippines (Table 3 and Fig. 5), for which genetic diversity is reduced to a genetically homogenous population constituting a single cluster of seven minimally divergent haplotypes (Table 1) across a wide geographical range. Thus, we view the northern Philippine haplotype clade as a occurring naturally in this region, but recently expanded in range across the entirety of the archipelago, despite many dozens of marine barriers to dispersal. A similar argument applies to diverged lineages found only on Sulawesi, some of which correspond to areas of genetic endemism found in other species.

Our coalescent-based Bayesian demographic analyses detected signal of recent effective population size expansion (although with large variances around parameter estimates) in the Philippine clade and Sulawesi, whereas the other two regions (northern and southern Sunda Regions) exhibited apparently stable or slightly declining estimated effective population size (Fig. 6). Thus, the coalescent methods produce results similar to those generated by demographic summary statistics. An interesting incongruence among results from different analyses was recovered in populations from Sulawesi, for which summary statistics all indicate stable population structure but the Bayesian skyline analysis infers recent demographic growth. One pattern on Sulawesi involves both geographically partitioned genetic structure (Figs. 2 and 3) in part conforming to AOE’s defined by Evans et al. (2003a,b, 2008) but also including two widespread haplotypes across most of northern, central, and southwestern portions of the island (Fig. 2). The widespread distribution of these two minimally divergent haplotypes may thus be the result of recent population growth and steady demographic expansion detected by coalescent-based analyses. We note that western and southwestern Sulawesi are regions of the island that have experienced some of the most extensive habitat conversions as forests have been cleared for massive oil palm plantations (R.M.B., J.A.M., and B.J.E., personal observations). We suspect that this kind of habitat alteration may have facilitated the spread of the two widespread haplotypes of *P. leucomystax* on Sulawesi.

How could single haplotype clades have become so prevalent, overcome so many barriers to dispersal, and spread across many hundreds of islands in the Philippines and other biogeographically isolated portions of the Sunda Region and Wallacea? Biological invasions are facilitated by life history characteristics of hardy, strong-dispersing species, often with high fecundity. Typically, such species enter regions where they have no former evolutionary history, and experience release from predation pressures and competitors, and often undergo unchecked population expansion and geographic dispersion (Nentwig, 2008; Lockwood et al., 2009). However, it is clear that *P. leucomystax* has a natural history in

the archipelagos of Southeast Asia and is not a recently introduced species (this study; Ota et al., 2004; Diesmos et al., 2006). Accordingly, we find it unlikely that an invasive species syndrome explains the recent expansion and success of the Philippine or Sulawesi populations of *P. leucomystax*. Instead, we speculate that recent population expansion of *P. leucomystax* is related to the last 400 years of land use and habitat modification by humans. For centuries, but particularly since the industrial revolution, unchecked exploitation of Philippine and Indonesian natural resources, logging and large-scale monoculture agriculture has resulted in the conversion of nearly all low elevation natural habitats throughout the archipelago to open land, characterized by second and third growth scrubby vegetation or flooded rice fields (the preferred habitat of *P. leucomystax*). Originally more than 85% forested, the Philippines for instance now retains only 4–8% forest cover (Catibog-Sinha and Heaney, 2006; Brown and Diesmos, 2009), and rates of forest removal exceed those virtually anywhere on the planet (Bawa et al., 1990; Collins et al., 1991). Forest removal has previously been identified as the most likely cause of reductions in species richness in the Philippines (Brown and Alcalá, 1963, 1986; Catibog-Sinha and Heaney, 2006; Brown and Diesmos, 2009) but some species thrive in disturbed open habitats (Brown and Alcalá, 1970, 1986; Alcalá and Brown, 1998; Diesmos et al., 2006). In addition to being present in all habitat types including the most disturbed areas, *P. leucomystax* is frequently transported between islands in agricultural shipments of rice, bananas, coconuts, sugarcane and oil palm (personal observations). Consistent with this interpretation, for example, a recent study (Kuraishi et al., 2009) documented the introduction of Philippine *P. leucomystax* into Japan, followed by subsequent range expansion (see also Ota et al., 2004). Brown and Alcalá (1970) suggested that the ubiquitous presence of *P. leucomystax* on virtually all islands they surveyed was a consequence of recent artificial transportations. We concur, and suspect that *P. leucomystax* is now present on most of the Philippines' 7000+ islands due to unprecedented habitat conversion, removal of original forests, and human-mediated dispersal, resulting in archipelago-wide genetic admixture.

Caution is warranted for our interpretation of results of these demographic analyses. Our skyline analyses were based on a single mitochondrial gene that, as a single draw from the coalescent, is subject to random variation, deep coalescence, and lineage sorting, and additionally, this marker is probably subject to natural selection (Edwards and Beerli, 2002; Galtier et al., 2009). Due to the extremely shallow nature of divergences considered here (Table 2), we were unable to use additional loci for our population inferences; several nuclear loci that we screened were invariant across *P. leucomystax* and its close relatives and were deemed uninformative for this study. However, as genomic resources become available in the future, multi-locus approaches have the potential to generate more accurate estimates of population parameters, providing a higher resolution understanding of the evolutionary history of this species. Despite the limitations of our single-locus approach, our general results are corroborated by population summary statistical approaches and coalescent-based demographic inference. Additionally, agreement between the Bayesian inference of recent population expansion and our empirical observations of habitat conversion associated with widespread clades of invariant haplotypes provides further support for our interpretations with respect to the Philippines and Sulawesi.

#### 4.3. Taxonomic implications for *P. leucomystax*?

Many biologists over the past century have noted conspicuous, geographically based, morphological variation in the Southeast

Asian island archipelago populations of *P. leucomystax*. Many of the size and color variants have been named by taxonomists and subsequently synonymized, including no fewer than six formal species epithets that at one time referred to populations from Java, northern Borneo, northern Philippines, Palawan Island (Philippines), Sumatra, Papua, and Sulawesi (Inger, 1954, 1966; Frost, 2009; Brown, 2007). For example, in the Philippines, Taylor (1920, 1922) recognized one widespread species (*P. leucomystax*) and another as endemic to the Sulu Archipelago (*P. linki*). Inger (1954) recognized three forms including a subspecies distributed throughout the country (*P. leucomystax quadrilineatus*), a subspecies endemic to Palawan (*P. leucomystax linki*), a form endemic to Samar Island (*P. hecticus*), and another from southern Palawan and the Sulu archipelago (*P. macrotis*). Brown and Alcalá (1994), Alcalá and Brown (1998), and Brown (2007) recognized the former two under a single name (*P. leucomystax leucomystax*; males with vocal sacs, dorsum and lateral surfaces variable), and retained *P. hecticus* and *P. macrotis* (males lack vocal sacs; dark stripe on lateral surfaces of body). Our results contradict these and other taxonomic hypotheses and suggest subdivisions of *P. leucomystax* not previously conceived by herpetologists. We suggest that the recognition of the morphologically distinct *P. macrotis* (Borneo, Sumatra, southern Palawan Island, and the Sulu Archipelago) is warranted, but we do not support the recognition of a distinct species from Samar Island (*P. hecticus*). If one were to partition *P. leucomystax* to the finest scale possible and assign available names to biogeographic and phylogenetic units, one might recognize Clade 7 (Fig. 4) as true *P. leucomystax* (type locality Java). Using our results as a guide (and if these hypotheses were corroborated by morphological and/or acoustical data), one might recognize another taxon in the northern Sunda Region and southern Philippines (our Clade 6), a taxon endemic to Sulawesi (for which the name *P. celebensis* may be available), a taxon from the Lesser Sunda Islands of Indonesia (represented here by a single specimen from Lombok), and a possible taxon distributed throughout the Philippines (for which the name *quadrilineatus* may be available). However, we would not advocate such a fine taxonomic approach until a comprehensive analysis of morphological variation is conducted throughout the range of all populations (including those on the Asian mainland) as we have collected syntopic, morphologically indistinguishable frogs in the southern Philippines that have now been genetically identified as possessing divergent haplotypes. In addition to populations from the islands of Southeast Asia, mainland populations currently referred to *P. cf. leucomystax*, *P. cf. megacephalus*, and *P. cf. mutus* will require revision with a similarly comprehensive approach, using morphology, ecological characteristics, advertisement calls, and additional molecular data.

## 5. Conclusions

Contrary to expectations, our data demonstrate that Southeast Asian mainland *Polypedates* are composed of numerous, highly divergent mitochondrial gene lineages, and that adjacent island archipelago populations are lineage depauperate over a wide geographic area. Phylogeographic analyses and haplotype networks suggest that in the relatively recent geological past (based on low molecular divergence), a natural dispersal event gave rise to *P. leucomystax* in the Philippines. Contrary to biogeographical expectations, summary statistics and demographic inference suggest a subsequent spread across the archipelago's marine barriers; similar evidence was recovered for dispersal across biogeographical barriers on Sulawesi. Although Pleistocene sea-level reductions and aggregate island formation may have contributed to such a process, it is unlikely that dispersal among all PAICs (and many islands that were not connected to one an-

other during the Pleistocene) and apparent archipelago-wide panmixia would have been facilitated by sea-level oscillations of the Pleistocene. Rather, we find it more plausible that habitat modification on a massive scale in Southeast Asia, including near complete removal of native forests, conversion of all arable land to agriculture, plus extensive inter-island shipping of agricultural goods are the causes of the apparent archipelago-wide panmixia in *P. leucomystax* across some of the world's most formidable biogeographical barriers. Together, our results strongly contradict expected patterns derived from the geological history of this region and suggest that the expectation of cryptic diversity should be evaluated on a taxon-by-taxon basis.

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### Appendix A

Species, samples, clade designations, field numbers, museum catalog numbers, general locality (Country), biogeographic region (Area of Endemism or Pleistocene Aggregate Island Complex; Brown and Diesmos, 2002, 2009; Evans et al., 2003a,b), and specific locality for all samples included in this study. GPM = specimen deposited in the Guangxi Province Museum, Nanning, China; PNM = specimen deposited in the National Museum of the Philippines; ITB = specimen deposited in the Institut Teknologi Bandung; MZB = specimen deposited in the Museum Zoologicum Bogoriense, Indonesia; MVZ = specimens deposited at the Museum of Vertebrate Zoology, University of California, Berkeley.

Appendix A

Taxon	Clade	Field No.	Catalog No.	Country	AOE/PAIC	Island/landmass	Specific locality
<i>Polypedates cf. leucomystax</i>	Clade 1a		MVZ 236721	China	Mainland Asia	Hainan Isl.	Bawangling
<i>Polypedates cf. leucomystax</i>	Clade 1a		MVZ 236715	China	Mainland Asia	Hainan Isl.	Bawangling
<i>Polypedates cf. leucomystax</i>	Clade 4		MVZ 236720	China	Mainland Asia	Hainan Isl.	Bawangling
<i>Polypedates cf. leucomystax</i>	Clade 4		MVZ 236719	China	Mainland Asia	Hainan Isl.	Bawangling
<i>Polypedates cf. leucomystax</i>	Clade 4		MVZ 236716	China	Mainland Asia	Hainan Isl.	Bawangling
<i>Polypedates cf. megacephalus</i>	Clade 1a		LSUHC 4220	China	Mainland Asia	Hainan Isl.	Wuzhi Shan
<i>Polypedates cf. megacephalus</i>	Clade 4		LSUHC 4155	China	Mainland Asia	Hainan Isl.	Eight-kilometer NW of Shi Yun
<i>Polypedates cf. leucomystax</i>	Clade 1b		MVZ 226451	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 1b		MVZ 232164	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, E of Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 1b		MVZ 226388	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 1b		MVZ 226440	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 1b		MVZ 226439	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 1b		MVZ 232163	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, E of Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 4		MVZ 226407	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 4		MVZ 232165	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, E of Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 4		MVZ 226396	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, Tam Dao
<i>Polypedates cf. leucomystax</i>	Clade 4		MVZ 223834	Vietnam	Mainland Asia	Mainland Asia	Vinh Phuc Province, Vin Yen District, Tam Dao
<i>Polypedates cf. mutus</i>	Clade 1c	KUFS 354	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Shiwandashang Nature Reserve, near Fulong Town
<i>Polypedates cf. mutus</i>	Clade 1c	KUFS 358	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Shiwandashang Nature Reserve, near Fulong Town
<i>Polypedates cf. mutus</i>	Clade 1c	JMG 262	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Canton Jing Xin, Provincial Nature Reserve, Nian We Station
<i>Polypedates cf. mutus</i>	Clade 2	JMG 310	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Canton Jing Xin, Provincial Nature Reserve, Nian We Station
<i>Polypedates cf. mutus</i>	Clade 3	JMG 308	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Canton Jing Xin, Provincial Nature Reserve
<i>Polypedates cf. mutus</i>	Clade 2	JMG 302	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Canton Jing Xin, Provincial Nature Reserve
<i>Polypedates cf. mutus</i>	Clade 4	KUFS 360	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Shiwandashang Nature Reserve, near Fulong Town
<i>Polypedates cf. megacephalus</i>	Clade 2	JMG 301	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Canton Jing Xin, Provincial Nature Reserve
<i>Polypedates cf. megacephalus</i>	Clade 2	JMG 287	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Canton Jing Xin, Provincial Nature Reserve, Nian We Station
<i>Polypedates cf. megacephalus</i>	Clade 4	KUFS 026	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Nanning City, People's Park
<i>Polypedates cf. megacephalus</i>	Clade 5	JMG 313	GPM	China	Mainland Asia	Mainland Asia	Guangxi Province, Canton Jing Xin, Provincial Nature Reserve
<i>Polypedates leucomystax</i>	Clade 6	HKV 35266	FMNH 231040	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sabah, Lahad Datu District, Danum Valley Research Center
<i>Polypedates leucomystax</i>	Clade 6	HKV 35268	FMNH 231041	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sabah, Lahad Datu District, Danum Valley Research Center
<i>Polypedates leucomystax</i>	Clade 6	RFI 43700	FMNH 239159	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sabah, Tenom District, Crocker Range National Park, Purlon Camp, Area III
<i>Polypedates leucomystax</i>	Clade 6	RFI 44349	FMNH 239162	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sabah, Tenom District, Crocker Range National Park, Purlon Camp, Area III
<i>Polypedates leucomystax</i>	Clade 6	HKV 39017	FMNH 244921	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sabah, Lahad Datu District, Danum Valley Research Center
<i>Polypedates leucomystax</i>	Clade 6	HKV 39019	FMNH 244922	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sabah, Lahad Datu District, Danum Valley Research Center
<i>Polypedates leucomystax</i>	Clade 6	RFI 51330	FMNH 267973	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sarawak, Bintulu District, Samarakan Nursery
<i>Polypedates leucomystax</i>	Clade 6	RFI 51335	FMNH 267975	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sarawak, Bintulu District, Samarakan Nursery
<i>Polypedates leucomystax</i>	Clade 6	RFI 51450	FMNH 267978	Malaysia	Sunda Shelf	Borneo Isl.	East Malaysia, Sarawak, Bintulu District, Samarakan Nursery
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 4779	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Johor, Pulau Tinggi, Pasir Panjang Waterfall Trail
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 4780	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Sungai Lembing Logging Camp
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 4972	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Sungai Lembing Logging Camp
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 4973	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Sungai Lembing Logging Camp
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 5909	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Kedah, Jerai
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 6031	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Kedah, Jerai
<i>Polypedates leucomystax</i>	Clade 6		FRIM 1140	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia
<i>Polypedates leucomystax</i>	Clade 6	JAM 1868	TNHC 56671	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pulau Tioman
<i>Polypedates leucomystax</i>	Clade 6	JAM 1869		Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pulau Tioman
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 3845	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pulau Tioman, Tekek-Juara Trail
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 6102	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pekan
<i>Polypedates leucomystax</i>	Clade 6		LSUHC 6609	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Selangor, Genting Highlands



Appendix A (continued)

Taxon	Clade	Field No.	Catalog No.	Country	AOE/PAIC	Island/landmass	Specific locality
<i>Polypedates leucomystax</i>	Clade 8	RMB 3343	PNM	Philippines	Luzon PAIC	Luzon Isl.	Area = "Mapga" Camarines Sur Province, Municipality of Naga City, Barangay Panicusason, Mt. Isarog National Park
<i>Polypedates leucomystax</i>	Clade 8	RMB 3407	TNHC 62846	Philippines	Luzon PAIC	Luzon Isl.	Camarines Sur Province, Municipality of Naga City, Barangay Panicusason, Mt. Isarog National Park
<i>Polypedates leucomystax</i>	Clade 8	RMB 3537	TNHC 62849	Philippines	Luzon PAIC	Luzon Isl.	Albay Province, Municipality of Tiwi Barangay Banhaw Sitio Purok 7, Mt. Malinao
<i>Polypedates leucomystax</i>	Clade 8	RMB 3538	TNHC 62850	Philippines	Luzon PAIC	Luzon Isl.	Albay Province, Municipality of Tiwi Barangay Banhaw Sitio Purok 7, Mt. Malinao
<i>Polypedates leucomystax</i>	Clade 8	RMB 3814	TNHC 62852	Philippines	Luzon PAIC	Luzon Isl.	Albay Province, Municipality of Malinao, Barangay Tagoytoy, Sitio Kumangking, Mt. Malinao
<i>Polypedates leucomystax</i>	Clade 8	RMB 3815	TNHC 62853	Philippines	Luzon PAIC	Luzon Isl.	Albay Province, Municipality of Malinao, Barangay Tagoytoy, Sitio Kumangking, Mt. Malinao
<i>Polypedates leucomystax</i>	Clade 8	RMB 3886	TNHC 62855	Philippines	Luzon PAIC	Luzon Isl.	Albay Province, Municipality of Malinao, Barangay Tagoytoy, Sitio Kumangking, Mt. Malinao
<i>Polypedates leucomystax</i>	Clade 8	RMB 3887	TNHC 62856	Philippines	Luzon PAIC	Luzon Isl.	Albay Province, Municipality of Malinao, Barangay Tagoytoy, Sitio Kumangking, Mt. Malinao
<i>Polypedates leucomystax</i>	Clade 8	RMB 4013	PNM	Philippines	Luzon PAIC	Luzon Isl.	Sorsogon Province, Municipality of Irosin, Barangay San Roque, Mt. Bulusan
<i>Polypedates leucomystax</i>	Clade 8	RMB 4014	PNM	Philippines	Luzon PAIC	Luzon Isl.	Sorsogon Province, Municipality of Irosin, Barangay San Roque, Mt. Bulusan
<i>Polypedates leucomystax</i>	Clade 8	RMB 4145	PNM	Philippines	Luzon PAIC	Luzon Isl.	Rizal Province, Municipality of Tanay, Barangay Sampaloc
<i>Polypedates leucomystax</i>	Clade 8	RMB 4146	PNM	Philippines	Luzon PAIC	Luzon Isl.	Rizal Province, Municipality of Tanay, Barangay Sampaloc
<i>Polypedates leucomystax</i>	Clade 8	RMB 4207	PNM	Philippines	Luzon PAIC	Luzon Isl.	Cagayan Province, Municipality of Peña Blanca, Callao Caves
<i>Polypedates leucomystax</i>	Clade 8	RMB 4208	PNM	Philippines	Luzon PAIC	Luzon Isl.	Cagayan Province, Municipality of Peña Blanca, Callao Caves
<i>Polypedates leucomystax</i>	Clade 8	RMB 4225	PNM	Philippines	Luzon PAIC	Luzon Isl.	Cagayan Province, Municipality of Gutturaran, Barangay Nassiping
<i>Polypedates leucomystax</i>	Clade 8	RMB 4236	PNM	Philippines	Luzon PAIC	Luzon Isl.	Cagayan Province, Municipality of Santa Anna, Barangay Palauti Palauti Isl. (N of Luzon Isl.)
<i>Polypedates leucomystax</i>	Clade 8	RMB 4237	PNM	Philippines	Luzon PAIC	Luzon Isl.	Cagayan Province, Municipality of Santa Anna, Barangay Palauti Palauti Isl. (N of Luzon Isl.)
<i>Polypedates leucomystax</i>	Clade 8	RMB 4252	PNM	Philippines	Luzon PAIC	Luzon Isl.	Anna, Barangay Palauti
<i>Polypedates leucomystax</i>	Clade 8	RMB 4479	PNM	Philippines	Luzon PAIC	Luzon Isl.	Cagayan Province, Municipality of Claveria, Barangay Mabnang, Mabnang Falls
<i>Polypedates leucomystax</i>	Clade 8	RMB 4504	PNM	Philippines	Luzon PAIC	Luzon Isl.	Zambales Province, Municipality of Olongapo, Bubic Bay Metropolitan Area Naval Base, "Nav-Mag" Area, Ilanin Forest
<i>Polypedates leucomystax</i>	Clade 8	RMB 4611	FMNH 266272	Philippines	Luzon PAIC	Luzon Isl.	Zambales Province, Municipality of Olongapo, Bubic Bay Metropolitan Area Naval Base, "Nav-Mag" Area, Ilanin Forest
<i>Polypedates leucomystax</i>	Clade 8	CDS 0008	FMNH 266269	Philippines	Luzon PAIC	Luzon Isl.	Zambales Province, Municipality of Palauig, Barangay Dampay, Sitio Salaza Mt. High Peak
<i>Polypedates leucomystax</i>	Clade 8	CDS 1032	KU 302459	Philippines	Luzon PAIC	Polillo Isl. (SE of Luzon)	Salaza Mt. High Peak
<i>Polypedates leucomystax</i>	Clade 8	CDS 1033	KU 302460	Philippines	Luzon PAIC	Polillo Isl. (SE of Luzon)	Quezon Province, Municipality of Polillo, near Polillo Town
<i>Polypedates leucomystax</i>	Clade 8	ACD 1314	PNM	Philippines	Luzon PAIC	Luzon Isl.	Quezon Province, Municipality of Polillo, near Polillo Town
<i>Polypedates leucomystax</i>	Clade 8	CDS 0061	KU 302450	Philippines	Mindanao PAIC	Camiguin Isl.	Laguna Province, Municipality of Los Baños, Barangay Batong Malaki, Mt. Maquiling
<i>Polypedates leucomystax</i>	Clade 8	RMB 2872	PNM	Philippines	Mindanao PAIC	Bohol Isl.	Camiguin Province, Municipality of Mambajao, Barangay Balbagon Bohol Prov., Municipality of Antequera, Baran gay Villa Aurora, Hinambangan Caves
<i>Polypedates leucomystax</i>	Clade 8	RMB 4308	PNM	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of San Jose, Tacloban City, Tacloban City Airport
<i>Polypedates leucomystax</i>	Clade 8	RMB 4370	PNM	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of Baybay, Barangay Guadalupe, Calbiga-a Creek
<i>Polypedates leucomystax</i>	Clade 8	CWL 217	KU 306340	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of Baybay
<i>Polypedates leucomystax</i>	Clade 8	CWL 182	KU 306334	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of Tacloban, NE of Tacloban City
<i>Polypedates leucomystax</i>	Clade 8	CWL185	KU 306337	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of Tacloban, NE of Tacloban City
<i>Polypedates leucomystax</i>	Clade 8	CWL186	KU 306338	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of Tacloban, NE of Tacloban City
<i>Polypedates leucomystax</i>	Clade 8	CWL 180	KU 306332	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of Tacloban, NE of Tacloban City
<i>Polypedates leucomystax</i>	Clade 8	CWL 181	KU 306333	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality of Tacloban, NE of Tacloban City

<i>Polypedates leucomystax</i>	Clade 8	CWL 184	KU 306336	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality Tacloban, NE of Tacloban City
<i>Polypedates leucomystax</i>	Clade 8	CWL 179	KU 306336	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality Tacloban, NE of Tacloban City
<i>Polypedates leucomystax</i>	Clade 8	CWL 183	KU 306335	Philippines	Mindanao PAIC	Leyte Isl.	Leyte Province, Municipality Tacloban, NE of Tacloban City
<i>Polypedates leucomystax</i>	Clade 8	CDS 1811	KU 306359	Philippines	Mindanao PAIC	Samar Island	Northern Samar Province, Municipality of San Jose de Buan, Barangay Poblacion
<i>Polypedates leucomystax</i>	Clade 8	RMB 9978	KU 314650	Philippines	Mindanao PAIC	Mindanao Isl.	Agusan Del Sur Province, Municipality of Bunawan, Barangay San Marcos
<i>Polypedates leucomystax</i>	Clade 8	RMB 9961	KU 314648	Philippines	Mindanao PAIC	Mindanao Isl.	Agusan Del Sur Province, Municipality of San Francisco, Barangay Kainpugan, Agusan Marsh
<i>Polypedates leucomystax</i>	Clade 8	ACD 1400	PNM	Philippines	Mindoro PAIC	Mindoro Isl.	Occidental Mindoro Province, Municipality of Sablayan, Barangay Batong Buhay, Malate, Sitio Palbong
<i>Polypedates leucomystax</i>	Clade 8	RMB 4846	KU 303765	Philippines	Mindoro PAIC	Mindoro Isl.	Occidental Mindoro Province, Municipality of Sablayan, Barangay Burgos, Sitio Posog, Posog River
<i>Polypedates leucomystax</i>	Clade 8	RMB 4847	KU 303766	Philippines	Mindoro PAIC	Mindoro Isl.	Occidental Mindoro Province, Municipality of Sablayan, Barangay Burgos, Sitio Posog, Posog River
<i>Polypedates leucomystax</i>	Clade 8	RMB 4881	KU 303728	Philippines	Mindoro PAIC	Mindoro Isl.	Occidental Mindoro Province, Municipality of Magsaysay, Barangay Nicolas, Sitio Bamban
<i>Polypedates leucomystax</i>	Clade 8	CDS 1192	KU 302421	Philippines	Mindoro PAIC	Mindoro Isl.	Oriental Mindoro Province, Municipality of Bongabong, Barangay Formon, Sitio Pastuhan
<i>Polypedates leucomystax</i>	Clade 8	RMB 4943	KU 303694	Philippines	Mindoro PAIC	Mindoro Isl.	Oriental Mindoro Province, Municipality of Bongabong, Barangay Formon, Sitio Pastuhan
<i>Polypedates leucomystax</i>	Clade 8	RMB 4946	KU 303686	Philippines	Mindoro PAIC	Mindoro Isl.	Oriental Mindoro Province, Municipality of Bongabong, Barangay Formon, Sitio Pastuhan
<i>Polypedates leucomystax</i>	Clade 8	RMB 4947	KU 303687	Philippines	Mindoro PAIC	Mindoro Isl.	Oriental Mindoro Province, Municipality of Bongabong, Barangay Carmundo, Sitio Paypay-ama, Paypay-ama River
<i>Polypedates leucomystax</i>	Clade 8	CDS 0630	KU 302426	Philippines	Mindoro PAIC	Semirara Isl. (SE of Mindoro)	Antique Province, Municipality of Caluya, Barangay Tinoghoc
<i>Polypedates leucomystax</i>	Clade 8	CDS 0631	KU 302427	Philippines	Mindoro PAIC	Semirara Isl. (SE of Mindoro)	Antique Province, Municipality of Caluya, Barangay Tinoghoc
<i>Polypedates leucomystax</i>	Clade 9	CDS 0595	KU 302424	Philippines	Mindoro PAIC	Caluya Isl. (SE of Mindoro)	Antique Province, Municipality of Caluya, Barangay Poblacion
<i>Polypedates leucomystax</i>	Clade 8	CDS 0596	KU 302425	Philippines	Mindoro PAIC	Caluya Isl. (SE of Mindoro)	Antique Province, Municipality of Caluya, Barangay Poblacion
<i>Polypedates leucomystax</i>	Clade 8	CDS 1238	KU 302444	Philippines	Mindoro PAIC	Mindoro Isl.	Oriental Mindoro Province, Municipality of Gloria, Barangay malamig, Sitio tipulo, Balite River
<i>Polypedates leucomystax</i>	Clade 8	CDS 1242	KU 302445	Philippines	Mindoro PAIC	Mindoro Isl.	Oriental Mindoro Province, Municipality of Gloria, Barangay malamig, Sitio tipulo, Balite River
<i>Polypedates leucomystax</i>	Clade 8	RMB 2970	PNM	Philippines	Palawan PAIC	Palawan Isl.	Palawan Province, Municipality of Puerto Princesa, Barangay Irawan, Sitio Tagaud
<i>Polypedates leucomystax</i>	Clade 8	RMB 2971	PNM	Philippines	Palawan PAIC	Palawan Isl.	Palawan Province, Municipality of Puerto Princesa, Barangay Irawan, Sitio Tagaud
<i>Polypedates leucomystax</i>	Clade 8	RMB 2982	PNM	Philippines	Palawan PAIC	Palawan Isl.	Palawan Province, Municipality of Nara, Barangay Estrella, Estrella Falls
<i>Polypedates leucomystax</i>	Clade 8	RMB 3061	PNM	Philippines	Palawan PAIC	Palawan Isl.	Palawan Province, Municipality of Brooke's Point, Barangay Mainit, Mainit Falls
<i>Polypedates leucomystax</i>	Clade 8	RMB 3063	PNM	Philippines	Palawan PAIC	Palawan Isl.	Palawan Province, Municipality of Brooke's Point, Barangay Mainit, Mainit Falls
<i>Polypedates leucomystax</i>	Clade 8	RMB 5119	KU 303733	Philippines	Romblon PAIC	Romblon Isl.	Romblon Province, Municipality of Romblon, Barangay Lunas
<i>Polypedates leucomystax</i>	Clade 8	RMB 5120	KU 303734	Philippines	Romblon PAIC	Romblon Isl.	Romblon Province, Municipality of Romblon, Barangay Lunas
<i>Polypedates leucomystax</i>	Clade 8	CDS 0782	KU 302472	Philippines	Romblon PAIC	Romblon Isl.	Romblon Province, Municipality of Romblon, Barangay Li-O, Takot Cave
<i>Polypedates leucomystax</i>	Clade 8	CDS 0783	KU 302473	Philippines	Romblon PAIC	Romblon Isl.	Romblon Province, Municipality of Romblon, Barangay Li-O, Takot Cave
<i>Polypedates leucomystax</i>	Clade 8	CDS 0803	KU 302423	Philippines	Romblon PAIC	Tablas Isl.	Tablas Province, Municipality of Calatrava, Barangay San Roque
<i>Polypedates leucomystax</i>	Clade 8	RMB 3214	TNHC 62844	Philippines	Visayan PAIC	Negros Isl.	Negros Oriental Province, Municipality of Valencia, Barangay Bongabong, Camp Lookout, Cuernos de Negros Mountain Range, Mt. Talinis
<i>Polypedates leucomystax</i>	Clade 8	RMB 3215	TNHC 62845	Philippines	Visayan PAIC	Negros Isl.	Negros Oriental Province, Municipality of Valencia, Barangay Bongabong, Camp Lookout, Cuernos de Negros Mountain Range, Mt. Talinis
<i>Polypedates leucomystax</i>	Clade 8	RMB 3308	PNM	Philippines	Visayan PAIC	Negros Isl.	Negros Oriental Province, Municipality of Valencia, Sitio Nasuji, PNOC Watershed, Mt. Talinis

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Appendix A (continued)

Taxon	Clade	Field No.	Catalog No.	Country	AOE/PAIC	Island/landmass	Specific locality
<i>Polypedates leucomystax</i>	Clade 8	CDS 0110	KU 302443	Philippines	Visayan PAIC	Negros Isl.	Negros Oriental Province, Municipality of Dumaguete City, Barangay Bantayan, SUAKCREM Marine Laboratory, Agricultural Fields
<i>Polypedates leucomystax</i>	Clade 8	CDS 0281	KU 302439	Philippines	Visayan PAIC	Negros Isl.	Camalandaan, Sitio Banso
<i>Polypedates leucomystax</i>	Clade 8	CDS 0018	KU 302434	Philippines	Visayan PAIC	North Gigante Isl. (N of Pana Isl.)	Iloilo Province, Municipality of Carles, Barangay Asloman
<i>Polypedates leucomystax</i>	Clade 8	CDS 0019	KU 302435	Philippines	Visayan PAIC	North Gigante Isl. (N of Pana Isl.)	Iloilo Province, Municipality of Carles, Barangay Asloman
<i>Polypedates leucomystax</i>	Clade 8	CDS 0214	KU 302452	Philippines	Visayan PAIC	Panay Isl.	Antique Province, Municipality of Pandan, Barangay Duyong
<i>Polypedates leucomystax</i>	Clade 8	CDS 0215	KU 302453	Philippines	Visayan PAIC	Panay Isl.	Antique Province, Municipality of Pandan, Barangay Duyong
<i>Polypedates leucomystax</i>	Clade 8	RMB 1016	TNHC 56336	Philippines	Visayan PAIC	Panay Isl.	Antique Province, Municipality of Valdarrama, Barangay Lublub
<i>Polypedates leucomystax</i>	Clade 8	RMB 1017	TNHC 56338	Philippines	Visayan PAIC	Panay Isl.	Antique Province, Municipality of Valdarrama, Barangay Lublub
<i>Polypedates leucomystax</i>	Clade 8	CDS 0447	KU 302451	Philippines	Visayan PAIC	Ticao Isl.	Masbate Province, Municipality of Monreal, Rejuso Street
<i>Polypedates leucomystax</i>	Clade 8	CDS 0549	KU 302446	Philippines	Visayan PAIC	Guimaras Isl.	Guimaras Province, Municipality of Jordon, Barangay Rizal, Sambulawa
<i>Polypedates leucomystax</i>	Clade 8	CDS 0555	KU 302422	Philippines	Visayan PAIC	Guimaras Isl.	Guimaras Province, Municipality of Jordon, Barangay Rizal, Sambulawa
<i>Polypedates leucomystax</i>	Clade 8	ELR 0231	PNM	Philippines	Sulu PAIC	Tawi-tawi Isl.	Tawi-tawi Province, Sulu Archipelago, Autonomous Region of Muslim Mindanao, Municipality of Laguyin
<i>Polypedates leucomystax</i>	Clade 9	JAM 3211		Indonesia	Lombok	Lombok Isl.	Lombok Island
<i>Polypedates leucomystax</i>	Clade 10	RMB 1625	MZB	Indonesia	East-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Banggai, Kecamatan Pagimana, Desa Siuna, Mt. Tompotika
<i>Polypedates leucomystax</i>	Clade 10	RMB 1696	MZB	Indonesia	East-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Banggai, Kecamatan Pagimana, Desa Siuna, Mt. Tompotika
<i>Polypedates leucomystax</i>	Clade 10	RMB 1446	TNHC 58939	Indonesia	East-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Poso, Kecamatan Ulubongka, Desa Marowo, Dusun Tiga
<i>Polypedates leucomystax</i>	Clade 10	RMB 1458	TNHC 58967	Indonesia	East-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Poso, Kecamatan Ulubongka, Desa Marowo, Dusun Tiga
<i>Polypedates leucomystax</i>	Clade 10	RMB 1512	MZB	Indonesia	East-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Poso, Kecamatan Ulubongka, Desa Marowo, Dusun Tiga
<i>Polypedates leucomystax</i>	Clade 11	RMB 1948	TNHC 59794	Indonesia	Northeast Sulawesi	Sulawesi Isl.	Sulawesi Utara Province, Manado City, Nusantara Dive Center
<i>Polypedates leucomystax</i>	Clade 11	RMB 1949	TNHC 59795	Indonesia	Northeast Sulawesi	Sulawesi Isl.	Sulawesi Utara Province, Manado City, Nusantara Dive Center
<i>Polypedates leucomystax</i>	Clade 11	BSI 0289	MVZ 254983	Indonesia	Northeast Sulawesi	Sulawesi Isl.	Sulawesi Utara Province, Kabupaten Minahasa, Tangkoko Nature Reserve
<i>Polypedates leucomystax</i>	Clade 11	BSI 0366	MVZ 254989	Indonesia	North-central Sulawesi	Sulawesi Isl.	Gorontalo Province, Kabupaten Bone Bolango, Kecamatan Suwawa, Desa Lombongo, Bogani Nani Wartabone National Park
<i>Polypedates leucomystax</i>	Clade 11	BSI 0545	MVZ 254993	Indonesia	North-central Sulawesi	Sulawesi Isl.	Gorontalo Province, Kabupaten Gorontalo, Kecamatan Kuandang, Desa Bubode
<i>Polypedates leucomystax</i>	Clade 11	BSI 0696	MVZ 254999	Indonesia	North-central Sulawesi	Sulawesi Isl.	Gorontalo Province, Kabupaten Gorontalo, Kecamatan Antinggola, Desa Buata
<i>Polypedates leucomystax</i>	Clade 11	BSI 0859	MVZ 255005	Indonesia	North-central Sulawesi	Sulawesi Isl.	Gorontalo Province, Kabupaten Bolmang Utara, Kecamatan Bolang Itang, Desa Ollat
<i>Polypedates leucomystax</i>	Clade 11	BSI 0915	MVZ 255014	Indonesia	North-central Sulawesi	Sulawesi Isl.	Gorontalo Province, Kabupaten Gorontalo, Kecamatan Tibawa, Desa Multonegoro
<i>Polypedates leucomystax</i>	Clade 11	BSI 0959	MVZ 255016	Indonesia	North-central Sulawesi	Sulawesi Isl.	Gorontalo Province, Kabupaten Bohuwata, Kecamatan Marisa, Desa Hulawa
<i>Polypedates leucomystax</i>	Clade 11	RMB 4759	MVZ 255129	Indonesia	Northwest Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Toli-toli Kecamatan, Basi Dondo, Desa Labonu
<i>Polypedates leucomystax</i>	Clade 11	RMB 4784	MVZ 255141	Indonesia	Northwest Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Toli-toli Kecamatan, Toli-toli, Desa Lingadan
<i>Polypedates leucomystax</i>	Clade 11	RMB 4770	MVZ 255138	Indonesia	Northwest Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Toli-toli, Kecamatan, Basi Dondo, Desa Alisang
<i>Polypedates leucomystax</i>	Clade 11	BSI 1279	MVZ 255017	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Donggala, Kecamatan Kulawi, Desa Mataue, Lore Lindu National Park
<i>Polypedates leucomystax</i>	Clade 11	BSI 1506	MVZ 255018	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Donggala, Kecamatan Kulawi, Desa Namo
<i>Polypedates leucomystax</i>	Clade 11	BSI 1800	MVZ 255025	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Donggala, Kecamatan Sirenja, Desa Ombo
<i>Polypedates leucomystax</i>	Clade 11	BSI 1807	MVZ 255027	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Donggala, Kecamatan Sirenja, Desa Ombo

<i>Polypedates leucomystax</i>	Clade 11	BSI 1809	MVZ 255029	Indonesia	West-central Sulawesi	Sulawesi Isl.	Desa Ombo Sulawesi Tengah Province, Kabupaten Donggala, Kecamatan Sirenja, Desa Ombo
<i>Polypedates leucomystax</i>	Clade 11	BSI 1879	MVZ 256090	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Poso, Kecamatan Lore Urara, Desa Wuasa, E of Lore Lindu National Park
<i>Polypedates leucomystax</i>	Clade 11	BSI 1915	MVZ 255046	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Poso, Kecamatan Lore Urara, Desa Wuasa, E of Lore Lindu National Park
<i>Polypedates leucomystax</i>	Clade 11	BSI 2307	MVZ 255066	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Mamuju, Kecamatan Babona, Desa Bolorembo
<i>Polypedates leucomystax</i>	Clade 11	BSI 2334	MVZ 255072	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Mamuju Urara, Kecamatan Babona, Desa Bolorembo
<i>Polypedates leucomystax</i>	Clade 11	JAM 4958	MVZ 255126	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Parigi Moutong, Kecamatan Parigi, Desa Uekali
<i>Polypedates leucomystax</i>	Clade 11	JAM 5052	MVZ 255128	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Parigi Moutong, Kecamatan Parigi, Desa Kolonodale
<i>Polypedates leucomystax</i>	Clade 11	MVZ 239213	MVZ 239213	Indonesia	Southeast Sulawesi	Sulawesi Isl.	Sulawesi Tenggara Province, Kendari City
<i>Polypedates leucomystax</i>	Clade 11	JAM 4865	MVZ 255123	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kecamatan Tawaeli, Desa Kebun Kopi
<i>Polypedates leucomystax</i>	Clade 13	BSI 2384	MVZ 255094	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Mamuju, Kecamatan Kalukku, Desa Bebangga
<i>Polypedates leucomystax</i>	Clade 13	BSI 2402	MVZ 255102	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Mamuju, Kecamatan Kalukku, Desa Tadui
<i>Polypedates leucomystax</i>	Clade 13	BSI 2449	MVZ 255107	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Tengah Province, Kabupaten Mamuju, Kecamatan Kalukku, Desa Keang
<i>Polypedates leucomystax</i>	Clade 13	BSI 2669	MVZ 255111	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Bone, Kecamatan Kahu, Desa Camilo
<i>Polypedates leucomystax</i>	Clade 13	BSI 2673	MVZ 255112	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Bone, Kecamatan Kahu, Desa Camilo
<i>Polypedates leucomystax</i>	Clade 13	BSI 2678	MVZ 255116	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Bone, Kecamatan Kahu, Desa Camilo
<i>Polypedates leucomystax</i>	Clade 13	BSI 2723	MVZ 255117	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Sinjai, Kecamatan Bulupoodo, Desa Lamatiraja
<i>Polypedates leucomystax</i>	Clade 13	BSI 2805	MVZ 255118	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Maros, Kecamatan Cendrana, Desa Rompegading
<i>Polypedates leucomystax</i>	Clade 13	BSI 2923	MVZ 255120	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Gowa, Kecamatan Tompobulu, Kelurahan, Desa Cikoro, Mt. Lompobatang
<i>Polypedates leucomystax</i>	Clade 13	JAM 5133	MVZ	Indonesia	Southwest Sulawesi	Selayar (SW of Sulawesi)	Sulawesi Selatan Province, Kabupaten Selayar, approx. 20 km S. of Benteng
<i>Polypedates leucomystax</i>	Clade 13	JAM 5134	MVZ	Indonesia	Southwest Sulawesi	Selayar (SW of Sulawesi)	Sulawesi Selatan Province, Kabupaten Selayar, approx. 20 km S. of Benteng
<i>Polypedates leucomystax</i>	Clade 13	JAM 5135	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Selayar, approx. 20 km S. of Benteng
<i>Polypedates leucomystax</i>	Clade 13	JAM 5136	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Selayar, approx. 20 km S. of Benteng
<i>Polypedates leucomystax</i>	Clade 13	JAM 5137	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Selayar, approx. 20 km S. of Benteng
<i>Polypedates leucomystax</i>	Clade 13	JAM 5618	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Barru, Kecamatan Barru, Desa Galung
<i>Polypedates leucomystax</i>	Clade 13	JAM 5619	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Barru, Kecamatan Barru, Desa Galung
<i>Polypedates leucomystax</i>	Clade 13	JAM 5620	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Barru, Kecamatan Barru, Desa Galung
<i>Polypedates leucomystax</i>	Clade 13	JAM 5673	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Barru, Kecamatan Barru, Desa Galung
<i>Polypedates leucomystax</i>	Clade 13	JAM 5674	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Soppeng, Kecamatan Talumpoe, Takalasi
<i>Polypedates leucomystax</i>	Clade 13	JAM 5675	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Soppeng, Kecamatan Talumpoe, Takalasi

(continued on next page)

Appendix A (continued)

Taxon	Clade	Field No.	Catalog No.	Country	AOE/PAIC	Island/landmass	Specific locality
<i>Polypedates leucomystax</i>	Clade 13	JAM 5764	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Talulimpo, Takalasi
<i>Polypedates leucomystax</i>	Clade 13	JAM 5765	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Enrekang, Kecamatan Maiwa, Desa Tapong
<i>Polypedates leucomystax</i>	Clade 13	JAM 5766	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Enrekang, Kecamatan Maiwa, Desa Tapong
<i>Polypedates leucomystax</i>	Clade 13	JAM 5767	MVZ	Indonesia	Southwest Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Enrekang, Kecamatan Maiwa, Desa Tapong
<i>Polypedates leucomystax</i>	Clade 13	RMB 2484	MZB Amp 15917	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Tana Toraja, Kecamatan Rindingallo, Desa Awan, Dusun Rantekaru
<i>Polypedates leucomystax</i>	Clade 13	JAM 5792	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Tana Toraja, Kecamatan Rembon, Desa To-Pao, Batusura
<i>Polypedates leucomystax</i>	Clade 13	JAM 5793	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Tana Toraja, Kecamatan Rembon, Desa To-Pao, Batusura
<i>Polypedates leucomystax</i>	Clade 13	JAM 5794	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Tana Toraja, Kecamatan Rembon, Desa To-Pao, Batusura
<i>Polypedates leucomystax</i>	Clade 13	JAM 5795	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Tana Toraja, Kecamatan Rembon, Desa To-Pao, Batusura
<i>Polypedates leucomystax</i>	Clade 13	JAM 5797	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Tana Toraja, Kecamatan Rembon, Desa To-Pao, Batusura
<i>Polypedates leucomystax</i>	Clade 13	JAM 5906	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Selatan Province, Kabupaten Soppeng, Kecamatan Mariowiano, Desa Mariolilau
<i>Polypedates leucomystax</i>	Clade 13	JAM 5919	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Polman, Kecamatan Matande, Polewali-Massawa Road
<i>Polypedates leucomystax</i>	Clade 13	JAM 5998	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Polman, Kecamatan Massawa, Sungai 2
<i>Polypedates leucomystax</i>	Clade 13	JAM 5999	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Polman, Kecamatan Massawa, Sungai 2
<i>Polypedates leucomystax</i>	Clade 13	JAM 6000	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Polman, Kecamatan Massawa, Sungai 2
<i>Polypedates leucomystax</i>	Clade 13	JAM 6252	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Kelurahan Galung
<i>Polypedates leucomystax</i>	Clade 13	JAM 6325	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Majene, Desa Kabiraan
<i>Polypedates leucomystax</i>	Clade 13	JAM 6326	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Majene, Desa Kabiraan
<i>Polypedates leucomystax</i>	Clade 13	JAM 6514	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Tasiu-Tibo Road
<i>Polypedates leucomystax</i>	Clade 13	JAM 6515	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Tasiu-Tibo Road
<i>Polypedates leucomystax</i>	Clade 13	JAM 6550	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Tasiu-Tibo Road
<i>Polypedates leucomystax</i>	Clade 13	JAM 6551	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Tasiu-Tibo Road
<i>Polypedates leucomystax</i>	Clade 13	JAM 6552	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Tasiu-Tibo Road
<i>Polypedates leucomystax</i>	Clade 13	JAM 6596	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Desa Keang
<i>Polypedates leucomystax</i>	Clade 13	JAM 6597	MVZ	Indonesia	West-central Sulawesi	Sulawesi Isl.	Sulawesi Barat Province, Kabupaten Mamuju, Desa Keang
<i>Polypedates macrotis</i>			LSUHC 6096	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pekan
<i>Polypedates macrotis</i>			LSUHC 4076	Malaysia	Sunda Shelf	Peninsular Malaysia	East Malaysia, Sarawak, Lambir Hills National Park
<i>Polypedates macrotis</i>			FMNH 239107	Malaysia	Sunda Shelf	Borneo	Sabah, Sipitang District
<i>Polypedates macrotis</i>			FMNH 239114	Malaysia	Sunda Shelf	Borneo	Sabah, Sipitang District
<i>Polypedates macrotis</i>		DTI 16333	FMNH 266917	Malaysia	Sunda Shelf	Sumatra Isl.	Sarasa Buntah Payakumbuh
<i>Polypedates macrotis</i>		DTI 16338	FMNH 266918	Malaysia	Sunda Shelf	Sumatra Isl.	Sarasa Buntah Payakumbuh
<i>Polypedates macrotis</i>		DTI 16448	Deposited in MZB	Malaysia	Sunda Shelf	Sumatra Isl.	Sarasa Buntah 1 Payakumbuh
<i>Polypedates macrotis</i>		DTI 16513	FMNH 266923	Malaysia	Sunda Shelf	Sumatra Isl.	Sarasa Buntah 1 Payakumbuh
<i>Polypedates macrotis</i>		ELR 0166	PNM	Philippines	Sulu PAIC	Tawi-tawi Isl.	Tawi-tawi Province, Sulu Archipelago, Autonomous Region of Muslim Mindanao, Municipality of Laguyin
<i>Polypedates macrotis</i>		ELR 0177	PNM	Philippines	Sulu PAIC	Tawi-tawi Isl.	Tawi-tawi Province, Sulu Archipelago, Autonomous Region of Muslim Mindanao, Municipality of Laguyin
<i>Polypedates macrotis</i>		ELR 0178	PNM	Philippines	Sulu PAIC	Tawi-tawi Isl.	Tawi-tawi Province, Sulu Archipelago, Autonomous Region of Muslim Mindanao, Municipality of Laguyin
<i>Polypedates macrotis</i>		ELR 0180	PNM	Philippines	Sulu PAIC	Tawi-tawi Isl.	Tawi-tawi Province, Sulu Archipelago, Autonomous Region of Muslim Mindanao, Municipality of Laguyin

Species	ELR	PNM	Philippines	Sulu PAIC	Tawi-tawi Isl.	Location
<i>Polypedates macrotis</i>	ELR 0181	PNM	Philippines	Sulu PAIC	Tawi-tawi Isl.	Tawi-tawi Province, Sulu Archipelago, Autonomous Region of Muslim Mindanao, Municipality of Laguyin
<i>Polypedates macrotis</i>	RMB 3087	PNM	Philippines	Palawan PAIC	Palawan Isl.	Palawan Province, Municipality of Brooke's Point Barangay Mainit, Mainit Falls
<i>Polypedates macrotis</i>	RMB 3088	PNM	Philippines	Palawan PAIC	Palawan Isl.	Palawan Province, Municipality of Brooke's Point Barangay Mainit, Mainit Falls
<i>Polypedates colletti</i>	LSUHC 4063	LSUHC 4063	Malaysia	Sunda Shelf	Peninsular Malaysia	East Malaysia, Sarawak, Niah Cave
<i>Polypedates colletti</i>	LSUHC 4064	LSUHC 4064	Malaysia	Sunda Shelf	Peninsular Malaysia	East Malaysia, Sarawak, Niah Cave
<i>Polypedates colletti</i>	LSUHC 6079	LSUHC 6079	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pekan
<i>Polypedates colletti</i>	LSUHC 6081	LSUHC 6081	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pekan
<i>Polypedates colletti</i>	LSUHC 6097	LSUHC 6097	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pekan
<i>Polypedates colletti</i>	LSUHC 6112	LSUHC 6112	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pekan
<i>Polypedates colletti</i>	LSUHC 6113	LSUHC 6113	Malaysia	Sunda Shelf	Peninsular Malaysia	West Malaysia, Pahang, Pekan
<i>Polypedates otlophus</i>	LSUHC 6155	LSUHC 6155	Malaysia	Sunda Shelf	Peninsular Malaysia	East Malaysia, Sabah, Sepilok Jungle Resort

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