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PHILIPPINE FROGS OF THE GENUS *LEPTOBRACHIUM* (ANURA; MEGOPHRYIDAE): PHYLOGENY-BASED SPECIES DELIMITATION, TAXONOMIC REVIEW, AND DESCRIPTIONS OF THREE NEW SPECIES

Rafe M. Brown[1,2,3,4], Cameron D. Siler[1], Arvin C. Diesmos[2,3], and Angel C. Alcala[3]

[1]*Natural History Museum, Biodiversity Institute and Department of Ecology and Evolutionary Biology; University of Kansas, Dyche Hall, 1345 Jayhawk Blvd, Lawrence, KS 66045-7561, USA*
[2]*Herpetology Section, Zoology Division, National Museum of the Philippines, Padre Burgos Avenue, Ermita 1000, Manila, Philippines*
[3]*Silliman University-Angelo King Center for Research and Environmental Management, Marine Laboratory Building, Bantayan, Dumaguete City 6200, Philippines*

Abstract: We review the Philippine frogs of the genus *Leptobrachuim*. All previous treatments have referred Philippine populations to *L. hasseltii*, a species we restrict to Java and Bali, Indonesia. We use external morphology, body proportions, color pattern, advertisement calls, and phylogenetic analysis of molecular sequence data to show that Philippine populations of *Leptobrachium* represent three distinct and formerly unrecognized evolutionary lineages, and we describe each (populations on Mindoro, Palawan, and Mindanao Island groups) as new species. Our findings accentuate the degree to which the biodiversity of Philippine amphibians is currently underestimated and in need of comprehensive review with new and varied types of data.

Lagom: Pinagbalik aralan namin ang mga palaka sa Pilipinas mula sa genus *Leptobrachium*. Ang nakaraang mga palathala ay tumutukoy sa populasyon *ng L. hasseltii*, ang uri ng palaka na aming tinakda lamang sa Java at Bali, Indonesia. Ginamit namin ang panglabas na morpolohiya, proporsiyon ng pangangatawan, kulay disenyo, pantawag pansin, at phylogenetic na pagsusuri ng molekular na pagkakasunod-sunod ng datos upang maipakita na ang populasyon sa Pilipinas ng *Leptobrachium* ay kumakatawan sa tatlong natatangi at dating hindi pa nakilalang ebolusyonaryong lipi. Inilalarawan din naming ang bawat isa (populasyon sa Mindoro, Palawan, at mga grupo ng isla sa Mindanao) na bagong uri ng palaka. Ang aming natuklasan ay nagpapatingkad sa antas kung saan ang biodibersidad ng amphibians sa Pilipinas sa kasalukuyan ay may mababang pagtatantya at nangangailangan ng malawakang pagbabalik-aral ng mga bago at iba't ibang uri ng datos.

Key words: Asian spadefoot toads; Lineage based species concepts; Mindanao; Mindoro; new species; Palawan; Philippines; Species delimitation.

Asian spadefoot toads, moustache toads, litter frogs, and horned frogs of the family Megophryidae consist of approximately 140 species in 10 genera (*Brachytarsophrys*, *Borneophrys*, *Leptobrachella*, *Leptolalax*, *Leptobrachium*, *Megophrys*, *Ophryophryne*, *Oreolalax*, *Scutiger*, *Xenophrys*). Despite their impressive ecological and morphological diversity, no comprehensive phylogenetic analysis of these taxa has been performed. As a result, the monophyly (and taxonomic validity) of many of these genera remains untested and questionable.

The genus *Leptobrachium* contains 21 species of Chinese, Indochinese, and Southeast Asian taxa, including six species of moustache toads formerly assigned to the genus *Vibrissaphora*: *L. ailaonicum*, *L. boringii*, *L. leishanense*, *L. liui*, *L. ngoclinhense*, and *L. promustache*. For the last 50 yr, herpetologists have recognized two megophryid genera in the Philippines: *Megophrys* and *Leptobrachium* (Alcala, 1986; Alcala and Brown, 1998; Brown, 2007; Brown and Alcala, 1970; Brown and Diesmos, 2002; Diesmos et al., 2002; Inger, 1954; Taylor, 1920).

The name *Leptobrachium hasseltii* (Müller in Tschudi, 1838) has been applied by earlier workers to various populations throughout southern Indochina and the Southeast Asian island archipelagos associated with the edge of the Sunda Shelf (Berry, 1975; Boulenger, 1882, 1894, 1912; Bourret, 1942; Brown, 2007; Inger, 1954, 1966; Smith, 1930; Taylor, 1928, 1962; van Kampen, 1923). Inger (1954) followed earlier works of Taylor (1920, 1921)

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[4] Correspondence: e-mail, rafe@ku.edu

in the recognition of Philippine populations of *Leptobrachium* as conspecific with *L. hasseltii* (type locality: Java). Inger (1966) originally recognized the Bornean populations as *L. hasseltii* and *L. nigrops* but, during intervening years as new data became available, he and others revised this treatment and reassigned Bornean populations to *L. abbotti*, *L montanum*, *L. nigrops*, *L. hendricksoni*, and *L. gunungense* (Inger et al., 1995; Inger and Stuebing, 1997, 1989; Inger and Tan, 1996; Malkmus, 1996; Malkmus et al., 2002; Manthey and Grossman, 1997; Taylor, 1962). Recent taxonomic works suggested restriction of *L. hasseltii* to Java, Bali, and nearby Indonesian islands (Dubois and Ohler, 1998; Iskandar, 1998; Iskandar and Colijn, 2000; Matsui et al., 1999, 2006), but most of these actions have been undertaken with reference to the taxonomic revisions of *Leptobrachium* on Borneo, Indochina, and Peninsular Malaysia. None has specifically addressed the populations in the Philippines, all of which continue to be referred to *L. hasseltii* (Brown, 2007). Other than Iskandar and Colijn's (2002) assertion that Philippine populations may be referable to *L. nigrops*, any taxonomic work accompanied by new data has not been forthcoming. Accordingly, a careful taxonomic assessment of the Philippine populations is still lacking. As presently recognized, *L. hasseltii* has a highly disjunct and biogeographically nonsensical distribution including the Indonesia islands of Java and Bali and the Philippine islands of Palawan, Mindoro, and Mindanao (Fig. 1).

Here we evaluate the status of populations of *Leptobrachium* in the Philippines (Fig. 2) using characters of external morphology, body size and proportions, color pattern, advertisement calls, and molecular sequence data. We find sufficient evidence for the recognition of three species of *Leptobrachium* (each named and described here). Our results further underscore the need for a comprehensive review of Philippine Amphibia within the context of lineage-based species concepts (Brown and Diesmos, 2002; de Queiroz, 1998, 1999; Frost and Hillis, 1990; Simpson, 1961; Wiley, 1978) using new and varied types of data to define species boundaries.

Materials and Methods

Field Work, Sample Collection, and Specimen Preservation

We conducted fieldwork on Mindoro, Palawan, Dumaran, Mindanao, Samar, Leyte, Dinagat, and Bohol islands (Fig. 1) between 1992 and 2008. Specimens (Fig. 2) were collected between 1800 and 2400 h, overanesthetized in aqueous chloretone, dissected for genetic samples (liver preserved in 95% ethanol or flash frozen in liquid nitrogen), fixed in 10% formalin, and eventually (< 2 mo) transferred to 70% ethanol. Newly sequenced specimens are deposited in U.S. and Philippine museum collections (See Acknowledgments and Specimens Examined); where available, voucher information corresponding to data from GenBank sequences is included in Table 1.

Taxon Sampling and Outgroup Selection

Because our primary goal was to estimate species-level relationships of *Leptobrachium* and determine affinities of Philippine populations, we included only single species exemplars or, in the case of Sundaland taxa with disjunct distributions, two or three allopatric samples per species at most. We included most known species of *Leptobrachium*, including taxa formerly referred to *Vibrissaphora* for which tissue samples or Genbank data were available. *Leptobrachium pullum* and *L. buchardi* were not included, as no genetic samples clearly assignable to these taxa were available for inclusion. We included *Oreolalax lichuanensis*, *Leptolalax arayai*, *Ophryophryne microstoma*, *Brachytarsophrys platyparietas*, and *Megophrys aceras* as Asian outgroup taxa and deeply rooted our analysis with oldworld taxa, including a European pelobatid (*Pelobates curtipes*), and two North American scaphiopidids (*Spea multiplicata*, and *Scaphiopus hurterii*).

DNA Extraction, Purification, and Amplification

Total genomic DNA was extracted from tissues (Table 1) using the modified guanidine thiocyanate extraction method of Esselstyn et al. (2008). A fragment of mitochondrial DNA that encodes part of the 16S ribosomal RNA gene (16S) was amplified using the primers

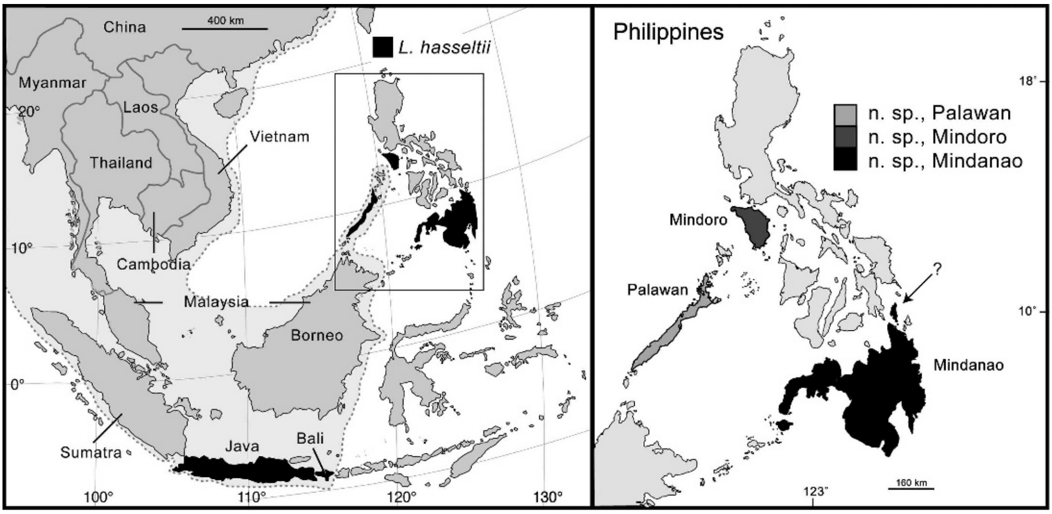

FIG. 1.—Past and present perspectives on the distribution of *Leptobrachium hasseltii*. Past taxonomic treatments have referred highly disjunct populations from Java, Bali (Indonesia), Palawan, Mindoro, and Mindanao (Philippines, inset) all to a single species (left panel). The Sunda Shelf (dashed line) includes the Asian mainland and the islands of Sumatra, Borneo, Java, and Bali, and is associated with the land bridge Philippine island of Palawan. Our revised interpretation (right panel) assigns the Philippine populations to three distinct new species, endemic to the Mindoro, Palawan, and Mindanao faunal regions (denoted with incremental shades of gray) and restricts *L. hasseltii* to Java, Bali, and small surrounding islands. The question mark indicates a single questionable record of *Leptobrachium* from Dinagat Island.

16Sc-L and 16Sd-H (Table 2). For samples difficult to amplify, the nested internal primer 16S.intF1 was designed for this study to replace primer 16Sc-L (Table 2). Additionally, a fragment that encodes part of the NADH deydrogenase subunit 1 gene (ND1) was amplified using a set of external, nested, and internal primers. The external primers 16S and tMet (Wiens et al., 2005) were used to amplify the first target gene fragment. Cycle sequencing reactions were then performed with combinations of nested and internal primers designed to collect complete double stranded sequences.

We used the following thermal cycler profile to amplify target fragments: 4 min at 94 C, followed by 35 cycles of 94 C for 30 sec, 52–53 C for 30 sec, and 72 C for 1 min 30 sec, and a final extension phase at 72 C for 7 min. Amplified products were visualized on 1.0% agarose gels. Amplified products were purified with 1 μL of a 20% solution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) on the following thermal cycler profile: 31 min at 37 C, followed by 15 min at 80 C. Cycle sequencing reactions were run using ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems, Foster City, CA), and purified with Sephadex Medium (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). Purified product was analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Gene sequences were assembled and initially edited using Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Alignment and Phylogenetic Analysis

An initial alignment was produced in Muscle v3.7 (Edgar, 2004), and manual adjustments were made in MacClade 4.08 (Maddison and Maddison, 2005) to minimize informative sites and identify ambiguous regions for exclusion (Moriarty and Cannatella, 2004). In cases of insertions or deletions in the ND1, amino acid codon translations were used to assess sequence homology. For 16S, ambiguously aligned regions were defined as character sets in MacClade and excluded following confirmation that exclusion of these data do not appreciably affect topology or nodal support (not shown). The

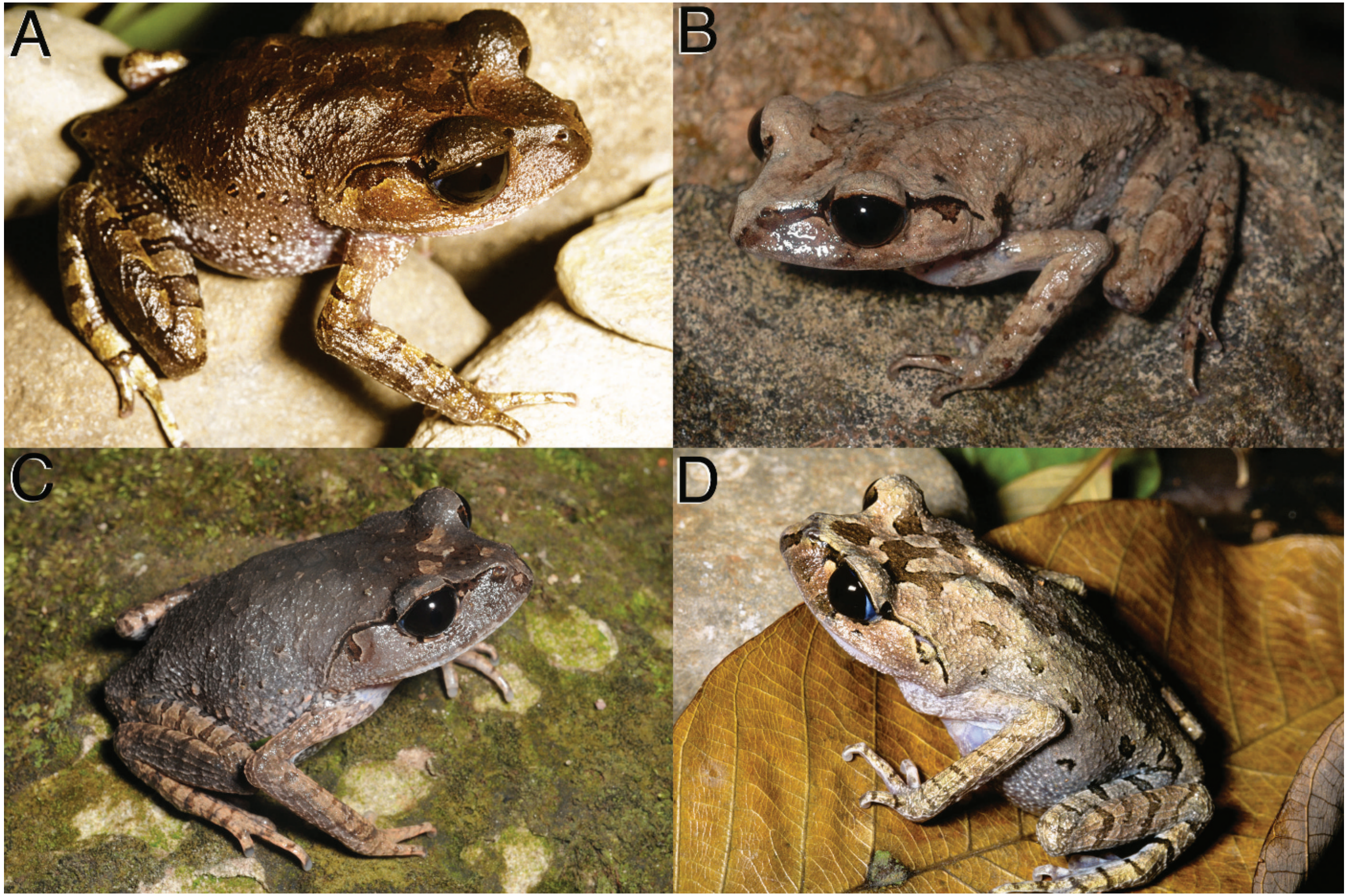

FIG. 2.—Asian spadefoot toads formerly all referred to *Leptobrachium hasseltii*. Specimens in life representing three new species from (A) Mindoro Island (PNM 9559), (B) the Palawan faunal region (KU 309075), and (C) the Mindanao faunal region (PNM 9561), Philippines. (D) *Leptobrachium hasseltii* (specimen from the type locality, Java Island, TNHC 67276) of Java and Bali, Indonesia. Photographs by RMB.

total alignment after exclusion of ambiguous regions was 2,223 mitochondrial characters and consisted of 978 protein-coding, 848 ribosomal, and 397 tRNA characters.

Phylogenetic analyses were conducted using parsimony and likelihood optimality criteria. Parsimony analyses were conducted in PAUP* 4.0 (Swofford, 2002) with gaps treated as missing data and all characters weighted equally. Most-parsimonious trees were estimated using heuristic searches with 1000 random addition-sequence replicates and tree bisection and reconnection (TBR) branch swapping. To assess heuristic support, nonparametric bootstrapping was conducted using 1000 replicates, each with 100 random addition-sequence replicates and TBR branch swapping.

Exploratory maximum likelihood (ML) analyses were conducted in the 2008 version of GARLI 0.96 (Zwickl, 2006). We implemented five independent analyses, each with five initial search replicates. Additional partitioned and non-partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.04 (Stamatakis, 2006). The alignment was partitioned into ribosomal 16S characters codon positions for the protein-coding region of ND1. The three flanking tRNAs (tRNA^{leu}, tRNA^{Ile}, tRNA^{gln}) were analyzed as a single partition. The Akaike Information Criterion (AIC) as implemented in Modeltest v3.7 (Posada and Crandall, 1998) was used to find appropriate models of sequence evolution. The best-fit model for each of the five partitions of the mitochondrial data was the general time reversible (GTR) model, with a proportion of invariable sites (I) and a parameter for variation in rates among sites (Γ). Partitioned ML analyses were then run under the same model ($GTR + I + \Gamma$) with RAxMLHPC v7.04, with 100 replicate best tree inferences. Each inference was performed with the options "-d" to start each search with a random starting tree, and "-fd" to run each analysis with the rapid hill-climbing algorithm implemented in the new version of RAxML v7.04. Clade support was assessed with 1000 bootstrap pseudoreplicates.

Bayesian analyses were performed in MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) under the $GTR + I + \Gamma$ model. The same partitioning strategy used for maximum likelihood analyses was also used for the Bayesian analyses. Searches over tree space were conducted with four runs, each with four chains, and were run for 20×10^6 generations. Trees were sampled every 1000 generations, with 4000 samples discarded as burn-in, this left 16001 post-burnin trees from each run included in the summary. Visual inspection for chain stationarity was conducted within the program Tracer v1.4 (Rambaut and Drummond, 2007). Results were summarized using SumTrees v1.0 (Sukumaran, 2008).

Morphological Data

We collected morphological data from fluid-preserved specimens (see Specimens Examined section; institutional abbreviations follow Leviton et al., 1985). Sex was determined by gonadal inspection when possible, by sexual size dimorphism when obvious, by direct observations of vocalizing behavior in males, and visibility of eggs through the body wall of females. Morphometric data were taken only by RMB (with digital calipers) to minimize interobserver bias (Hayek et al., 2001; Lee, 1982) and we calculated simple univariate summary statistics for males and females separately. Character definitions generally follow Brown and Guttman (2002; based on Inger 1954, 1966) unless otherwise noted. Measurements include: snout–vent length, head length from the tip of the snout to the rear corner of the jaws, head width at the widest point (rear commisure of the jaws), snout length from the tip of the snout to the anterior corner of the eye, interorbital distance at the midpoint of the orbits, eye diameter of the exposed eyeball, inter-narial distance, horizontal tympanic annulus diameter, upper arm length, forearm length, femur length, tibia length from the cloaca to the outer surface of the flexed knee, tarsus length, pes length from the tip of the fourth toe to the base of the inner metatarsal tubercle, manus length from tip of third digit to the base of the outer metacarpal tubercle, first finger length, third finger length, fourth toe length. Other qualitative external characters include color pattern, dermal ornamentation (including

TABLE 1.—Species, sampling localities, museum catalog numbers or voucher specimens, and Genbank accession numbers corresponding to gene sequences included in the phylogenetic analysis. See Rao and Wilkinson (2008), Zheng et al. (2008) and Fu et al. (2007) for additional locality data and voucher information.

Species	Locality	Museum catalog or voucher no.	Genbank no (16S, ND1)
Pelobates cultripes	Western Europe	VUB 0510	AY523760
Scaphiopus hurterii	Texas, North America	DCC 3005	AY523776
Spea multiplicata	North America	JAJ 428	AY523786
Brachytarsophrys platyparietus	China	W0 1395	AY526206
Xenophrys aceras	West Malaysia, Perak, Temengor Forest	LSUHC 7038	GQ995534
Ophryophryne microstoma	China	ZYC 1538	AY561309
Leptolalax arayai	Malaysia, Sabah, Borneo Isl.	None	AY523768
Oreolalax lichuanensis	China	IOZ-CAS 2675 (IZCASH 30004)	EF544237, EF544306
Leptobrachium xanthospilum	Vietnam	ROM 32186	EF544231, EF544300, EF54431
Leptobrachium banae	Vietnam	ROM 32200	EF544229, EF544298,
Leptobrachium hainanensis	Tam Dao, Vietnam	ROM 32176	EF544232, EF544301
Leptobrachium mouhoti	Mondolkiri Prov., Cambodia	FMNH 261758	EF672272
Leptobrachium (Vibrissophora) ngoclinhensis	Ngoc Linh, Vietnam	ROM-Fn 39612	EF544228, EF544297
Leptobrachium (Vibrissophora) promustache	Daweishan, China (type locality)	IOZ-CAS 2904 (IZCASH 30044)	EF544287, EF544240, EF544369
Leptobrachium huashen	Longling, China	SCUM 060633L (IZCASH30048)	EF544239, EF544295
Leptobrachium chapaense	Sa Pa, Vietnam (type locality)	ROM 38038	EF544227, EF544296
Leptobrachium (Vibrissophora) liui	Zhangjiajie, China	CIB-ZYC636	EF544198, EF544346
Leptobrachium (Vibrissophora) leishanensis	Leigongshan, China	ZYC A020, (IZCASH30004)	EF544200, EF544247
Leptobrachium (Vibrissophora) boringiae	Bifengxia, China	IOZ-CAS 2743 (IZCASH30024)	EF544277, EF544211
Leptobrachium (Vibrissophora) ailaonicum	Lao Cai, Vietnam	ROM-Fn 38046	GQ995555
Leptobrachium nigrops		ZMH 9369	GQ995539
Leptobrachium nigrops	West Malaysia, Selangor, Templers Park	LSUHC 6497	GQ995540
Leptobrachium hendricksoni	Forest Research Institute of Malaysia Station, Kepong (near Kuala Lumpor), Peninsular Malaysia	LSUHC 3998	GQ995535
Leptobrachium hendricksoni	Northern Peninsular Malaysia, Kedah, Jerai	LSUHC 5912	GQ995536
Leptobrachium hasseltii	Sukabumi, west Java Isl., Indonesia	TNHC 67276	GQ995537
Leptobrachium hasseltii	Taman Safari Park, near Cibodas, Java Isl., Indonesia	UTA A-53688	GQ995538
Leptobrachium smithi	Sayaboury Prov., Laos	FMNH 258092	GQ995541
Leptobrachium smithi	Thailand	DSM 910, deposited at KU.	GQ995542
Leptobrachium tagbanorum	Palawan Isl., Palawan Province, Municipality of Brookes Point, Mt. Mantalingahan	KU 309463	GQ995550
Leptobrachium tagbanorum	Palawan Isl., Palawan Province, Municipality of Brookes Point, Mt. Mantalingahan	KU 309461	GQ995551

TABLE 1.—Continued.

Species	Locality	Museum catalog or voucher no.	Genbank no (16S, ND1)
Leptobrachium tagbanorum	Palawan Isl., Palawan Province, Municipality of Nara, Estrella Falls	RMB 3025; deposited at PNM	GQ995552
Leptobrachium mangyanorum	Mindoro Isl., Occidental Mindoro Province, Municipality of Sablayan, Mt. Siburan	KU 304401	GQ995553
Leptobrachium mangyanorum	Mindoro Isl., Oriental Mindoro Province, Municipality of Baco, Mt. Halcon	PNM/CMNH-H 879; deposited at CMNH	GQ995554
Leptobrachium mangyanorum	Mindoro Isl., Oriental Mindoro Province, Municipality of Baco, Mt. Halcon	PNM/CMNH-H 881; deposited at CMNH	GQ995556
Leptobrachium lumadorum	Mindanao Isl., Zamboanga City Province, Pasonanca Natural Park,	KU 314148	GQ995549
Leptobrachium lumadorum		ACD 956; deposited in PNM	GQ995547
Leptobrachium lumadorum	Mindanao Isl., South Cotobato Province, Municipality of Kiamba, Mt. Busa	PNM/CMNH-H 1702; deposited at CMNH	GQ995548
Leptobrachium gunungense	Borneo Isl.	AE 99-S41	DQ642118
Leptobrachium gunungense	East Malaysia, Borneo Isl., Sarawak, Mesilau, 2000m	ZRC 1.12444	GQ995546
Leptobrachium abbotti	Mulu National Park, northeast Sarawak	AH 196	GQ995543
Leptobrachium abbotti	East Malaysia, Borneo Isl., Northeast Sarawak	ZMH 10153	GQ995544
Leptobrachium montanum	Borneo Isl.	AE 98-S7	DQ642117
Leptobrachium montanum	East Malaysia, Borneo Isl., Sabah, Sipitang District,	FMNH 236702	GQ995545

sternal and humeral glands), interdigital webbing of feet, and size and shape of subarticular tubercles.

Acoustic Analyses

Advertisement calls were recorded with a Sony$^{\mathrm{TM}}$ WM D6C Professional Walkman with a Sony ECM-Z200 microphone or a Nagra ARES-BB+ solid-state recorder, and a Sennheiser$^{\mathrm{TM}}$ ME80 condenser microphone equipped with K3U power module. Calls were recorded at distances of approximately 1–3 m, ambient temperatures were taken during recordings, and frog cloacal temperature was taken immediately following recording. All calls were recorded within an ambient temperature range of 3 C, so no temperature corrections of the data were undertaken. Calls were digitized with Soundedit© (Macromedia, 1995) and analyzed with Canary© and Raven Pro v1.3© (Charif et al., 1996, 2008) software. We examined oscillograms (waveforms), audiospectrograms (sonograms), and results of the Fast Fourier Transformation (FFT; frequency spectrum) for a variety of temporal and spectral characters. Calling rate and note repetition rate was defined as ([total number of calls/notes − 1]/time from beginning of first call to beginning of last) and call element and structure terminology follows Brown and Gonzales (2007), and Brown and Richards (2008) and Brown et al. (2006*a*, 2006*b*).

Species Concept

We adopt the General Lineage Species Concept of de Queiroz (1998, 1999) as the natural extension of the Evolutionary Species Concept (Simpson, 1961; Frost and Hillis, 1990; Wiley, 1978). Application of lineage-based species concepts to recognizing Philippine biodiversity is unambiguous because of the ability to identify lineages with a history of isolation as island group endemics (Brown et al., 2000*b*, 2002, 2008, 2009; Brown and Guttman, 2002; Gaulke et al., 2007). Although sea level oscillations have allowed for intermittent dry land connection between some of the islands of today—and the formation of

TABLE 2.—Primers used to amplify the 16S ribosomal RNA mitochondrial gene and NADH Deydrogenase Subunit 1 protein coding gene regions included in the phylogenetic analysis (see text).

Genes and primers	Sequence (5′–3′)	Location on fragment	Source
Mitochondrial 16S			
16Sc-L	GTRGGCCTAAAAGCAGCCAC	External	Evans et al. (2003)
16Sd-H	CTCCGGTCTGAACTCAGATGACGTAG	External	Evans et al. (2003)
16S.intF1	YCGCCTGTTTACCAAAAACATCRCC	Internal	This study
Mitochondrial ND1			
16S	TTACCCTRGGGATAACAGCGCAA	External	Wiens et al. (2005)
tMet	TTGGGGTATGGGCCCAAAAGCT	External	Wiens et al. (2005)
LeptND1.NestF1	TACGTGATCTGAGTTCAGACCGG	Internal	This study
LeptND1.IntF1	HHTNCTYCARCCHDTDGCWGAYGG	Internal	This study
LeptND1.IntF2	NAARGGYCCNAAYATYRTHGGYCC	Internal	This study
LeptND1.NestR1	RTANCGRAADCGDGGRTANGAYGC	Internal	This study
LeptND1.IntR1	YCGDAGNGMNCCRATHARDGCRTA	Internal	This study
LeptND1.IntR2	DGANACDARYTCWGAYTCHCCYTC	Internal	This study

some Pleistocene Aggregate Island Complexes (PAICs; Hall, 1996, 1998; Voris, 2000) between islands separated by ocean channels less than 120 m depth—many of the islands of the archipelago arose as volcanoes from the sea floor and have never been connected to one another. Although it is clear that with enough time, frog dispersal over marine barriers does occur (Brown and Guttman, 2002; Evans et al., 2003), we assume that the strong constraint on dispersal imposed by marine barriers and the long history of isolation is the basis for exceptionally high PAIC-level endemism in the Philippines (Brown and Diesmos, 2002, 2009). In accordance with this history of isolation over geologic time, we consider as new species morphologically and genetically diagnosable, allopatric populations for which the hypothesis of conspecificity can be confidently rejected. In this paper we utilize a molecular estimate of phylogenetic relationships to guide species delimitation and diagnosis, and identify relevant comparisons for species diagnoses. Accordingly, we compare new species to the relevant congeneric taxa: those species that are phenotypically similar, geographically proximate, and phylogenetically related.

RESULTS

Phylogeny

Of the 2223 molecular characters, 941 were parsimony-informative. The maximum parsimony analysis inferred 10 equally most parsimonious trees (tree length = 4800). These 10 trees were highly consistent, differing only by the minor rearrangement of a few individuals within species (topology not shown; parsimony bootstraps summarized in Fig. 3). Results of the five initial, five-replicate GARLI searches produced highly consistent estimates of phylogeny; the best trees of each of the five sets of five replicates were only a few hundredths of a log likelihood value from one another and were topologically identical. We interpret this initial result as evidence that search parameters were appropriately set and that GARLI was finding the best trees. After confirming that unpartitioned GARLI (with final optimization performed in PAUP*) and unpartitioned RAxML analyses were finding identical topologies within a few hundredths of a log likelihood of each other, we proceeded with partitioned RAxML analyses.

The resulting 100 inferences from the partitioned RAxML maximum likelihood analysis produced a topology identical to those of the GARLI runs and showed an average likelihood score of $-\ln L$ 21549.825966, with a single inference having the highest likelihood score of $-\ln L$ 21549.823034. The trees recovered from ML and MP analyses had nearly identical topologies (Fig. 3), differing only by the position of short terminal branches within species. The results of the Bayesian analyses were, again, nearly identical to both the MP and ML analyses (topology not shown; posterior probabilities summarized in Fig. 3).

Frogs of the genus *Leptobrachium* cluster into two major clades (Clades A and B of

FIG. 3.—The preferred phylogenetic hypothesis of *Leptobrachium* species relationships, inferred from maximum likelihood analysis of mitochondrial ND1 and 16S genes. Bayesian and parsimony topologies were identical to the ML tree shown here; support values for those analyses are summarized with incrementally shaded circles at internodes (see key). Strong parsimony and likelihood support = nonparametric bootstraps, 75–100; strong Bayesian support = posterior probabilities, 0.95–1.0.

Fig. 3), each of which is strongly supported with parsimony and likelihood bootstrap support and Bayesian posterior probabilities of > 0.95. These clades contain 22 species, previously recognized on the basis of morphology, and demonstrated here to be additionally divergent in mitochondrial DNA (Fig 3; divergences between Clade B species presented in Table 3). Clade A contains 12 species, most of which were formerly referred to the genus *Vibrissaphora*. Clade B contains 10 species from northeastern Thailand, Peninsular Malaysia, the islands of the Sunda Shelf (predominantly Indonesia) and the Philippines. One subclade within Clade B contains *L. nigrops* from the peninsula and Borneo, sister to *L. hasseltii* and *L. hendricksoni* from the Peninsular Malaysia and Thailand. This group is sister to another subclade that contains Mindanao populations, hypothesized to be the sister taxon to a clade containing the remaining species from the Sunda Shelf (*L. montanum*, *L. abbotti*, and *L. gungungense*), plus Philippine populations from Palawan and Mindoro (Fig. 3). In the preferred tree, *L. gunungense* is the well supported (in Bayesian and likelihood analyses) closest relative of the Mindoro + Palawan species couplet, but the sister relationship of this three-species clade to the other Bornean taxa (*L. montanum* and *L. abbotti*) is weakly supported. All three new Philippine species are phylogenetically separate from *L. hasseltii*.

With a few exceptions, uncorrected pairwise sequence divergences are low within species and high between species (Table 3). Percent divergences were lower for 16S than ND1 but both gene fragments lead to the same conclusions, namely that the monophyletic lineages defined by our phylogenetic analyses (Mindoro, Palawan, and Mindanao island group lineages) are distinguished from congeners by levels of genetic divergence similar to those between previously defined species (Table 3; Fig. 3). Even the most closely related of putative new species (the Mindoro and Palawan lineages, separated by 4.3–6.5% sequence divergence in 16S are separated by divergences greater than those between *L. abbotti* and *L. montanum* (3.3–4.9%), two morphologically distinctive species that have never been confused. Divergences between Philippine and non-Philippine populations (including *L. hasseltii*) are likewise consistently high (Table 3). High levels of sequence divergence between allopatric populations of *L. nigrops* (Malaysian Peninsula versus Borneo populations), *L. abbotti* (two localities in Sarawak, Borneo; Table 1), and *L. hendricksoni* (Jerai, Kedah, in northern Peninsular Malaysia versus Kepong, near Kuala Lumpor, in southern Peninsular Malaysia), suggest that careful examination and possible reevaluation of the taxonomic status of these populations may be warranted in future studies.

Five species (a non-monophyletic group) occur on Borneo. These are *L. abbotti*, *L. gunungense*, *L. montanum*, *L. nigrops*, and *L. hendricksoni*; only *L. nigrops* and *L. hendricksoni* occupy the Peninsular Malaysia as far north as Thailand, where they may cooccur with *L. smithi*. The three new species identified here each occur allopatrically on isolated PAICs (Palawan, Mindoro, and Mindanao) in the Philippines and none are sympatic with any other taxa.

Morphology

Continuous variation in morphometric characters (Table 4), by itself, does not distinguish each of the four *Leptobrachium* lineages. However, univariate analyses of these characters do provide quantitative confirmation of the highly distinctive large body size of females of the Palawan lineage (and greater extent of sexual dimorphism in this species) when compared to the lineages from Mindoro, Mindanao, or Java (*L. hasseltii*). Head length, head width, and first finger length distinguishes females of Palawan Island from those of Mindoro Island and head width further distinguishes females of Palawan from those of Mindanao and Java (*L. hasseltii*). Upper arm length distinguishes females of Palawan from those of Mindoro and Java (*L. hasseltii*) whereas forearm length, femur length, and tibia length distinguishes the females of this species from all three remaining taxa (Table 4). Color pattern (in particular eye color, width of canthal stripe, tympanum coloration, dorsal and ventral body coloration, and transverse banding on limbs), and degree of interdigital webbing contribute qualitatively

Table 3.—Uncorrected pairwise sequences divergence (%) for 16S ribosomal RNA mitochondrial gene (above diagonal) and NADH Deydrogenase Subunit 1 protein coding gene (below diagonal) for Sunda Shelf and SE Asian island archipelagoes (Fig. 3, Clade B) species of the genus *Leptobrachium*. Entries on the diagonal depict ranges of intraspecific divergences for 16S/ND1 (bolded for emphasis; missing data indicated with —).

	nigrops	*hasseltii*	*hendricksoni*	*smithi*	*montanum*	*abbotti*	*gunungense*	*lumadorum*	*mangyanorum*	*tagbanorum*
nigrops	**8.6/—**	8.1–12.2	10.9–14.7	14.0–17.4	12.4–16.8	11.8–12.8	12.1–12.6	12.7–13.3	13.1–19.2	14.1–20.4
hasseltii	17.6–17.8	**0.6/0.4**	6.2–9.0	11.9–14.4	7.9–12.0	7.1–8.2	7.8–8.1	8.5–8.7	10.5–16.4	10.8–16.5
hendricksoni	19.5–20.5	14.1–16.4	**3.5/7.6**	13.0–14.7	9.5–13.6	8.8–9.0	10.4–10.9	10.6–11.4	12.1–17.8	11.4–17.8
smithi	21.5	18.0	19.8–22.3	**0.0/0.0**	11.2–13.5	10.4–11.4	12.1–12.5	12.2–12.4	11.8–15.5	12.1–16.2
montanum	20.7	15.4–15.8	18.3–20.8	18.5	**1.2/—**	3.3–4.9	5.4–5.9	6.2–6.7	7.7–14.4	7.1–14.4
abbotti	21.2–21.8	16.5–16.8	18.4–20.3	18.0–18.6	11.8–13.5	**1.5/6.7**	5.4–6.1	6.5–7.4	7.6–8.6	7.2–8.4
gunungense	19.3	15.8–16.0	17.0–19.2	19.6	10.6	12.7–12.9	**0.0/—**	6.3–6.5	5.5–6.3	5.0–6.3
lumadorum	19.3	14.0–14.1	16.4–18.0	18.0	10.8	12.1–13.2	11.2	**0.0–1.0/0.0**	7.6–8.4	8.2–9.5
mangyanorum	21.8–22.0	17.3–18.1	19.7–21.3	20.7–21.0	15.4–15.6	16.2–17.4	14.8–15.1	14.1–14.4	**0.1–2.2/0.3–2.5**	4.3–6.5
tagbanorum	20.6	16.1–16.7	18.5–20.6	18.9–19.5	14.3–14.6	15.4–15.9	13.0–13.5	12.3–12.8	10.6–10.9	**0.0–1.4/0.7–0.9**

to the diagnoses of the three new species described below (see species accounts, below).

Acoustic Analyses

Our analyses of recordings of the advertisement calls of Philippine and Javan *Leptobrachium* identify consistent structural and temporal differences between each Philippine population and *L. hasseltii* from Java Island, Indonesia (Figs. 4–7; Table 5). In the following section, we provide the first description of the advertisement call of true *L. hasseltii* from its type locality (Java Island). Full descriptions of the calls of the Philippine lineages are provided in the species accounts (see below); brief comparisons to Philippine populations are included below. To the best of our knowledge, all previous discussions of the advertisement call of *L. hasselti* (i.e., Dring, 1979) have been based on allopatric populations of congeners from outside the range of true *L. hasseltii* (Java and Bali Islands, Indonesia) and are thus referable to other species.

The advertisement call of Leptobrachium hasseltii *and comparison to calls from Philippine populations.*—Our description of the call of *L. hasseltii* is based on two recording segments. The first is from a male specimen (TNHC 67277; 47 mm snout–vent length 4.6g) collected on 1 August 2000 in Sukabumi, Gede Pangrango, Java, and kept in captivity for 48 h before preservation. The call was recorded at 2200 hr, in a darkened room on the campus of the University of Indonesia, Depok, Java (specimen not contained in plastic, and free to move about), at an ambient temperature of 23.9 C and cloacal temperature of 24.2 C, the night after it was collected. The second recording is from a male recorded in its natural habitat (a dry stream bank in secondary forest), at the same collection locality on 30 August 2000. The second male (TNHC 67279, 42.5 mm, 5.1g) was recorded at an ambient temperature of 22.6 C and a cloacal temperature of 24.1 C. TNHC 67277 called 38 times during recording and TNHC 67279 called 10 times.

The call of *L. hasseltii* (Fig. 4) is a series of medium range frequency barks, sounding to the human ear like laughter: “Wha-ha-ha-ha-

TABLE 4.—Univariate summaries of continuously varying mensural characters for *Leptobrachium mangyanorum* (Mindoro Isl.), *L. tagbanorum* (Palawan Isl.), *L. lumadorum* (Mindanao Isl.), and Java Island specimens of *L. hasseltii*. Entries include mean ± 1 SD, followed by range in parentheses; data are presented separately for males and females (m, f).

Species:	*L. mangyanorum* (33 m; 16 f)	*L. tagbanorum* (10 m; 12 f)	*L. lumadorum* (16 m; 12 f)	*L. hasseltii* (13 m; 15 f)
Snout–vent length (m)	44.0 ± 3.64 (35.5–49.0)	48.8 ± 4.6 (42.2–54.0)	45.3 ± 3.9 (39.1–50.4)	41.4 ± 2.1 (37.5.1–47.4)
Snout–vent length (f)	51.6 ± 3.8 (45.6–58.8)	72.6 ± 6.9 (65.1–80.0)	56.7 ± 6.0 (48.2–65.1)	58.4 ± 3.4 (53.9–62.0)
Head length (m)	18.9 ± 1.7 (15.1–22.4)	20.1 ± 1.6 (17.2–22.3)	19.2 ± 1.7 (16.4–21.0)	16.6 ± 0.7 (15.3–17.5)
Head length (f)	20.3 ± 2.2 (17.5–23.6)	28.3 ± 1.5 (26.1–30.0)	22.9 ± 2.2 (20.5–26.2)	23.2 ± 1.3 (20.6–24.8)
Head width (m)	9.0 ± 0.9 (15.2–22.0)	20.7 ± 2.6 (16.8–24.8)	20.8 ± 2.0 (17.4–24.0)	17.7 ± 0.8 (15.7–18.2)
Head width (f)	21.6 ± 2.1 (19.7–25.0)	30.3 ± 2.5 (26.2–32.1)	21.8 ± 2.3 (18.2–24.8)	24.0 ± 1.5 (20.9–26.0)
Snout length (m)	6.1 ± 1.1 (4.9–7.9)	7.3 ± 1.0 (5.8–8.0)	7.1 ± 1.5 (5.1–8.7)	7.2 ± 0.5 (6.6–8.2)
Snout length (f)	7.3 ± 1.2 (5.0–7.7)	11.2 ± 2.0 (8.3–13.1)	6.1 ± 0.5 (5.4–6.6)	9.5 ± 0.9 (7.8–10.7)
Interorbital distance (m)	6.3 ± 0.7 (5.1–7.3)	6.9 ± 1.1 (5.2–8.8)	6.4 ± 0.5 (5.2–7.0)	5.2 ± 0.5 (4.2–6.0)
Interorbital distance (f)	7.1 ± 0.7 (6.1–8.2)	9.1 ± 1.1 (7.1–10.6)	7.1 ± 0.5 (6.8–8.1)	6.8 ± 0.9 (5.2–7.8)
Eye diameter (m)	6.2 ± 0.6 (4.6–7.3)	6.5 ± 0.6 (5.5–7.4)	6.3 ± 0.8 (5.4–7.9)	5.4 ± 0.2 (5.2–5.6
Eye diameter (f)	6.6 ± 1.1 (5.6–8.5)	8.1 ± 0.8 (7.0–9.1)	6.3 ± 0.7 (5.3–7.6)	6.3 ± 0.7 (5.0–7.2)
Internarial distance (m)	3.9 ± 0.5 (3.0–4.9)	4.3 ± 0.4 (3.5–5.0)	4.3 ± 0.5 (3.4–4.9)	4.2 ± 0.4 (3.0–4.7)
Internarial distance (f)	4.5 ± 0.4 (4.1–5.0)	6.1 ± 0.6 (5.2–6.9)	5.1 ± 0.5 (4.5–5.7)	4.7 ± 0.6 (3.7–5.3)
Tympanum diameter (m)	2.9 ± 0.3 (2.2–3.5)	3.3 ± 0.3 (3.0–4.1)	3.1 ± 0.2 (2.9–3.5)	4.0 ± 0.2 (3.8–4.4)
Tympanum diameter (f)	3.0 ± 0.3 (2.5–3.6)	5.2 ± 0.4 (4.8–5.8)	4.0 ± 0.4 (3.6–4.5)	4.2 ± 0.5 (3.4–5.0)
Upper arm length (m)	8.9 ± 0.9 (6.8–10.9)	10.4 ± 0.8 (9.4–12.1)	9.6 ± 0.8 (7.8–11.4)	8.7 ± 0.8 (7.8–9.9)
Upper arm length (f)	10.2 ± 1.4 (8.2–12.7)	17.4 ± 2.0 (15.2–20.0)	18.0 ± 3.0 (14.9–21.9)	13.3 ± 1.3 (10.6–15.1)
Forearm length (m)	13.9 ± 1.4 (10.6–13.8)	15.0 ± 1.7 (12.5–17.2)	13.8 ± 1.4 (12.0–15.7)	12.7 ± 0.7 (11.3–13.7)
Forearm length (f)	15.1 ± 1.7 (12.5–17.3)	23.8 ± 1.1 (22.0–24.8)	21.1 ± 2.0 (15.0–20.1)	19.4 ± 1.2 (17.9–21.3)
Femur length (m)	19.2 ± 2.1 (15.0–23.4)	20.6 ± 2.1 (17.5–24.5)	19.4 ± 1.6 (16.5–22.0)	17.8 ± 0.9 (15.9–19.3)
Femur length (f)	20.0 ± 2.1 (17.4–24.5)	30.5 ± 2.5 (28.2–33.0)	21.1 ± 2.6 (17.2–24.5)	25.4 ± 2.0 (20.9–28.0)
Tibia length (m)	17.7 ± 1.813.7–20.8	17.9 ± 1.6 (16.1–21.3)	17.2 ± 1.4 (14.2–19.8)	15.3 ± 0.9 (13.5–16.3)
Tibia length (f)	20.1± 2.1 (16.0–23.2)	26.6 ± 1.5 (24.5–28.5)	21.8 ± 1.8 (19.0–23.5)	21.7 ± 1.6 (18.4–24.3)
Tarsus length (m)	10.7 ± 1.1 (8.3–12.5)	10.4 ± 1.1 (9.1–12.6)	10.2 ± 0.8 (8.5–11.5)	9.4 ± 0.8 (7.8–10.6)
Tarsus length (f)	10.4 ± 1.1 (9.1–12.6)	15.4 ± 1.2 (14.0–17.3)	12.1 ± 0.9 (11.0–13.5)	12.6 ± 1.1 (10.7–14.5)
Pes length (m)	16.7 ± 1.8 (13.0–20.0)	15.1 ± 1.3 (12.9–17.4)	16.2 ± 1.4 (14.4–18.7)	14.9 ± 0.7 (13.8–15.8)
Pes length (f)	15.1 ± 1.8 (13.2–18.4)	23.2 ± 2.8 (20.4–26.7)	20.7 ± 2.5 (17.0–24.0)	20.5 ± 1.4 (18.4–22.6)
Manus length (m)	10.6 ± 1.0 (8.2–12.5)	10.4 ± 1.1 (9.0–12.2)	10.6 ± 0.9 (9.4–12.0)	9.8 ± 0.8 (8.9–11.3)
Manus length (f)	10.4 ± 1.1 (8.6–12.2)	14.8 ± 1.5 (13.0–16.7)	15.2 ± 1.6 (13.7–17.8)	13.7 ± 1.1 (11.3–14.7)
Finger 1 length (m)	5.3 ± 0.6 (4.2–6.5)	5.3 ± 0.6 (4.1–6.0)	5.1 ± 0.4 (4.4–5.7)	5.1 ± 0.3 (4.8–5.3)
Finger 1 length (f)	5.3 ± 0.6 (4.0–6.1)	8.2 ± 0.9 (7.0–9.1)	6.7 ± 0.6 (5.9–7.4)	6.4 ± 0.9 (4.8–7.8)
Finger 3 length (m)	8.4 ± 0.7 (6.9–9.7)	7.1 ± 1.1 (6.2–9.4)	8.1 ± 0.8 (6.5–9.4)	6.9 ± 0.5 (6.3–7.8)
Finger 3 length (f)	7.9 ± 1.1 (6.2–9.4)	11.5 ± 0.8 (10.5–12.3)	10.0 ± 0.5 (9.5–10.8)	8.8 ± 1.1 (7.4–10.6)
Toe 4 length (m)	10.5 ± 1.2 (8.2–12.4)	10.1 ± 1.1 (8.9–13.0)	9.1 ± 1.1 (8.0–12.0)	8.9 ± 0.7 (7.9–10.2)
Toe 4 length (f)	10.1 ± 1.4 (8.6–13.0)	14.2 ± 1.8 (12.4–17.6)	12.8 ± 0.7 (12.1–13.8)	11.7 ± 1.6 (9.5–14.6)

ha-ha…." The call consists of 5–15 (but usually only 6 or 7) notes per call and note repetition rate is constant across the call. TNHC 67277 averaged of 6.9 notes per call (± 1.6 SD; range 5–15 notes/call; n = 38) and TNHC 67279 averaged 6.8 notes per call (± 0.6 SD; range 6–8 notes/call; n = 10). Although mean notes per call do not distinguish *L. hasseltii* from all the Philippine lineages, the Palawan and Mindoro populations exhibit considerably higher mean values for this character (Table 5).

Unlike the calls in Philippine populations (see species accounts) the first note is not spaced appreciably from the remainder of the call and no elongate internote interval separates the first and second notes. The call of *L. hasseltii* differs from those of *Leptobrachium* from Mindoro and Palawan by the absence of tonal prefixes and differs from those of Mindoro and Mindanao by the amplitude modulation or structured subpulses in the first notes of the call.

Intercall intervals range from 15–72 s ($\bar{x}$ = 34.8 ± 17.6 SD; n = 37) for TNHC 67277 and 12–42 ($\bar{x}$ = 27.9 ± 9.5 SD; n = 9) for TNHC 67279. This trait distinguishes *L. hasseltii* from all Philippine species, which have much shorter intercall intervals (Table 5). The call of TNHC 67277 has a rate of 0.029 calls/s; the recording of TNHC 67279 has 0.031 calls/s. These values are lower than those for calling rates of all Philippine species (Table 5).

Call length varies between 1.8–2.7 s ($\bar{x}$ = 2.2 ± 0.23 SD; n = 38) for TNHC 67277 and 1.8–2.3 s ($\bar{x}$=2.0 ± 0.16 SD; n = 10) for TNHC 67279. Note duration is 268.1–317.2 ms ($\bar{x}$ = 287.7 ± 17.1 SD; n = 258) for TNHC 67277 and 249.7–298.2 ms ($\bar{x}$ = 279.0 ± 13.1 SD; n = 68) for TNHC 67279. Although note duration in *L. hasseltii* does not distinguish this species from the calls of Mindanao population, mean note duration in the Mindoro and Palawan populations is much shorter (Table 5). Unlike the calls of Philippine species, there is no predictable pattern of internote interval variation across the call of *L. hasseltii* (Fig. 4C, D); internote interval is 112.2–163.4 ms ($\bar{x}$ = 138.1 ± 11.8 SD; n = 221) for TNHC 67277 and 118.2–149.6 ms ($\bar{x}$ = 133.0 ± 9.4 SD; n = 58) for TNHC 67279. Internote interval appears to only distinguish *L. hasseltii* from the Mindanao population (Table 5).

Within calls, note repetition rate ([total number of notes − 1]/time from beginning of first note to beginning of last) is 2.6–3.2 notes/s ($\bar{x}$ = 3.07 ± 0.13 SD; n = 22) for TNHC 67277 and 2.91–3.19 notes/s ($\bar{x}$ = 3.08 ± 0.07 SD; n = 15) for TNHC 67279. Note repitition rate only distinguishes *L. hasseltii* from the Palawan population (Table 5).

Relative amplitude across calls is nearly homogeneous, with only slightly lower relative amplitude in the first notes, an immediate rise to apparent peak amplitude achieved by the second or third note, and no appreciable decline in amplitude with subsequent notes, even toward the end of the call (Fig. 4E). Individual notes exhibit an immediate rise to peak amplitude, followed by a gradual trailing off of amplitude to ambient levels (Fig. 4B, D). Amplitude of the first note is approximately < 85–95% of the peak amplitude for the call (Fig. 4E). Individual notes are simple harsh barks, without tonal elements, prefixes, or variable, temporally structured notes of any kind (Fig. 4C). The shape of the note amplitude envelope and relative amplitude levels of notes across calls distinguishes *L. hasseltii* from all Philippine lineages (Figs. 4–7; Table 5).

Energy in the call consists of two frequency components (Fig. 4A, C): a lower frequency component of 1.37 kHz for TNHC 67277 and 1.4 kHz for TNHC 67279, and a higher, emphasized (fundamental) frequency component of 1.89 kHz for TNHC 67277 and 2.0 kHz for TNHC 67279. In a few audiospectrograms, faint harmonics are visible at one and two multiples of the fundamental (approximately 4 and 8 kHz, respectively). The dominant frequency of calls of *L. hasseltii* is substantially higher than those of Philippine populations (Figs. 4–7); this is consistent with the small body size of males of this species and the expectation of an inverse relationship between call frequency and body size (Duellman and Trueb, 1994; Wells, 2007).

In summary, although *Leptobrachium hasseltii* and *Leptobrachium* populations from the

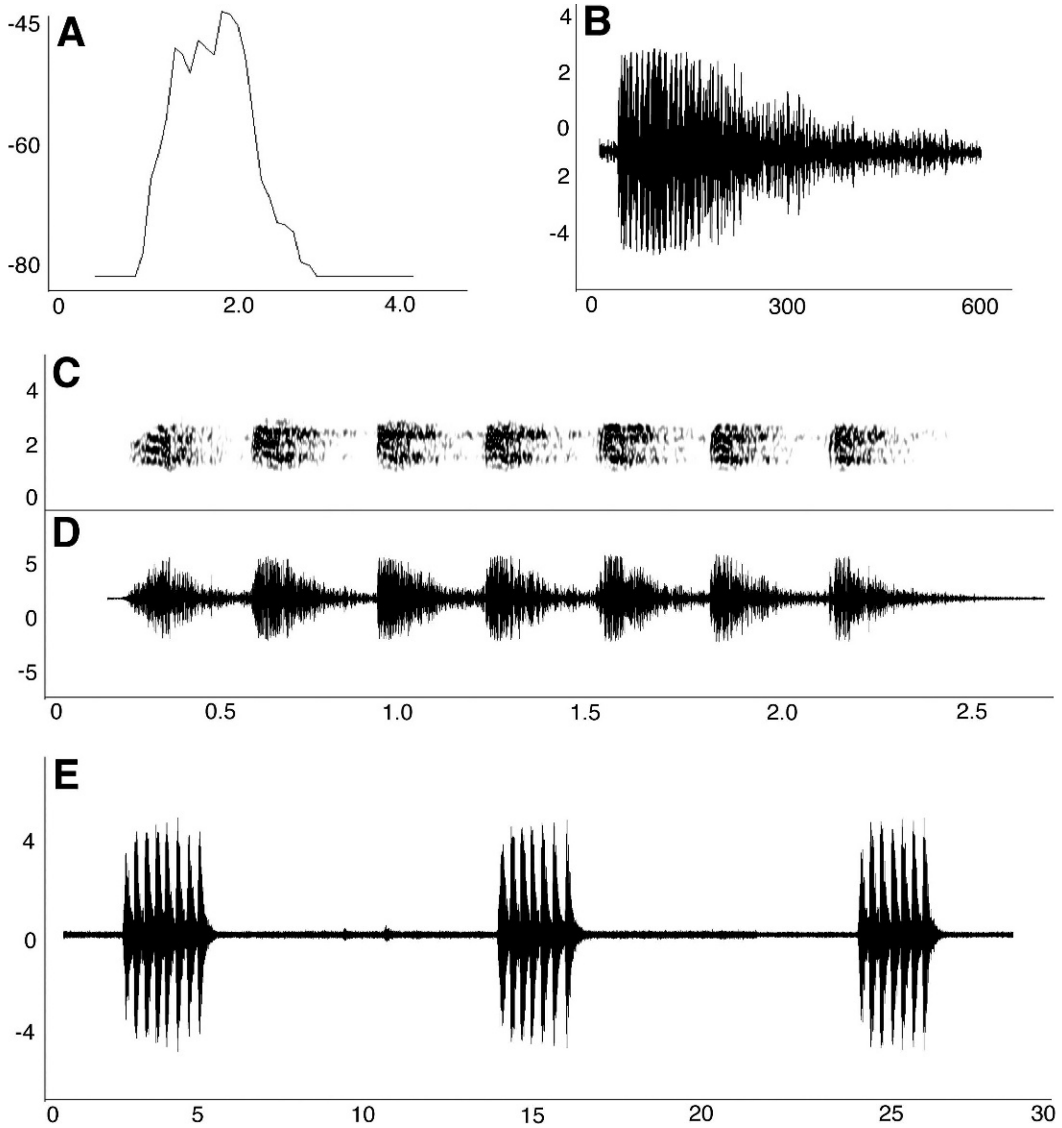

FIG. 4.—The advertisement call of *Leptobrachium hasseltii* (TNHC 27279) recorded at Gede Pangrango, Sukabumi, Java Isl., by RMB, 1 August 2000 (ambient temperature of 22.6°C (clocal temperature 24.1°C). Analyses include: a power spectrum (A: Fast Fourier Transformation; relative amplitude vs. frequency in kHz) calculated across notes 3–6 in C and D; a 600 ms expanded waveform (B: relative amplitude vs. time in ms) of a single note; a 2.5 s audiospectrogram (C: frequeny in kHz vs. time in s) and oscillogram (D: relative amplitude vs. time in s) of a typical call; and a 30 s oscillogram (E: relative amplitude vs. time in s) of four typical calls, illustrating typical rise and decline in note amplitude across the call.

Philippines have generally similar call structure (amplitude modulated, low frequency, rapidly pulsed "squawking" or "barking" calls), there exist subtle but diagnostic differences between each call type (Table 5; see individual call descriptions of new species, below). With the caveat that sampling is too limited to allow robust statistical comparisons, it is clear that the calls from these four populations (Java, Palawan, Mindoro, and Mindanao) are structurally and temporally distinct, with nonoverlapping ranges of acoustic variation. These distinctions lend support to the hypothesis that each call type corresponds to a distinct taxonomic entity. Thus, to the extent that calls are available for comparison, call data for Philippine and Indonesian *Leptobrachium* support our taxonomic conclusions (below).

Recognition of New Species

Our estimate of phylogeny (Fig. 3) and genetic distances between the taxa (Table 3) indicate the genetic distinctiveness of three new species, including one from Mindoro Island, one from the Palawan faunal region, and one from the Mindanao faunal region (Mindanao, Basilan, and possibly Dinagat Islands). Each new species is phenotypically, acoustically, and genetically distinct from the others and from close relatives, including the more distantly related *L. hasseltii*, with which these three new species were confused for so long. Additionally, each new species is endemic to one of three isolated PAICs (Brown and Diesmos, 2002, 2009; Hall, 1996, 1998; Voris, 2000), reinforcing our conviction that each represents a cohesive lineage with a unique evolutionary history and distinct evolutionary trajectory. Accordingly, we recognize the populations from Mindoro, Palawan, and Mindanao island groups each as new species.

The phylogeny suggests a close relationship of the three new species to other Southeast Asian species including *Leptobrachium montanum*, *L. gunungense* (Borneo), *L. abbotti* (Borneo and Sumatra), *L. nigrops* (Borneo, Subi Isl [Natunas], Singapore, and Peninsular Malaysia), *L. hasseltii* (Java and Bali), *L. hendricksoni* (Peninsular Malaysia, Thailand, Borneo, and Sumatra), and *L. smithi* (Peninsular Malaysia, Thailand, Laos, Myanmar). Accordingly, comparisons to these species are warranted and are included below. Unrelated Chinese and Indochinese taxa (*Leptobrachium mouhoti*, *L. chapaense*, *L. banae*, *L. hainanensis*, *L. xanthospilum*, *L. huashen*, and presumably *L. pullum* and *L. buchardi*) are omitted from comparisons for simplicity, as are comparisons to former members of the genus *Vibrissaphora* (*L. ngoclinhensis*, *L. promustache*, *L. leishanensis*, *L. liui*, *L. ailaonicum*, and *L. boringiae*). Additional available phylogenetic data (Brown et al., unpublished data; Fu et al., 2007; Rao and Wilkinson, 2008; Zheng et al., 2008) clearly indicate that none of these taxa from northern latitudes are closely related to the new species from the Philippines. As such, none are immediately relevant for the purposes of comparisons and recognition of the new taxa. With the phylogeny as our guide, we feel justified in providing detailed comparisons between the new species and their closest relatives, geographically proximate taxa, and phenotypically most similar congeners. These are the remaining species of *Leptobrachium* from the Thailand, Peninsular Malaysia, Sumatra, Java, Bali, Borneo, and the Philippines.

Leptobrachium **mangyanorum** *sp. nov.*
Figs. 2, 8, 9

Holotype.—PNM 9559 (formerly KU 301846, Field Number CDS 1249) adult male, from the Philippines, Mindoro Island, Mindoro Oriental Province, Municipality of Victoria, Barangay Loyal, Sitio Panguisan, Panguisan River (N 13.150104, E 121.200246, WGS 84), collected on 14 March 2005 by CDS, RMB, and ACD.

Paratypes.—Mindoro Island, Oriental Mindoro Province, ca. 30 km south of Calapan, Tarogin Barrio, SE Slope of Mt. Halcon (N: 13.199°, E: 121.13°), nine males and four females, collected by ACA and party: CAS-SUA 22241, 22275 (31 March 1963), 22178, 22277, 22278 (1 April 1963), 22276–78 (1 April 1963), 22279–80 (2 April 1963), 22294–95 (1 April 1963), 22296 (7 April 1963); male, collected by A. Tropisado: CAS SUA 22300 (30 March 1963); East slope of Mt. Halcon, Ilong Ridge (N: 13.266°; E: 121.039°), male, collected by ACA and party: CAS SUA 22579 (28 April 1963); East Side of Mt. Halcon, SE slope Barawanan Peak (N: 13.275°, E: 121.06°), male collected by ACA and party: CAS-SUA 16492 (April–May, 1954), male collected by B. Garger and party (N: 13.225°, E: 121.065°): CAS SUA 22283 (14 April 1963); male collected by ACA and party (N: 13.217°, E: 121.07°): CAS SUA 22297 (17 April 1963); Municipality of Baco, Baco Mountain Range, Barangay Aygatal, two males and two females, collected by R. Sison: PNM 1523, 1525–1527 (April 1991); Lake Naujan, male, collected by E. H. Taylor: MCZ

A-23163 (1–30 April 1922); Municipality of Baco, Mt. Baco, Aligatil and Alangsa Rivers, fourteen males, collected by R. Crombie and T. Ramos: USNM 508494–99 (3–6 June 1991), 508501–08 (7 June 1991); Mindoro Island, Occidental Mindoro Province, Municipality of Sablayan, Barangay Batong Buhay, Sitio Batulai, Mt. Siburan (N 13.796°, E 120.160°; WGS-84), an adult female and seven adult males collected by E. L. Rico: KU 303272–78, 305453 (16 February, 2006); Barangay Harrison, Sitio Ulasan, area known locally as "Matingaram" (N 13.463°, E 120.412°; WGS-84), seven adult females, 26 adult males, one juvenile of undetermined sex, collected by E. L. Rico: KU 308335–347, PNM 9655–62, (23 February 2007), PNM 9663–64 (26 February 2007), KU 308429 (juvenile; 2 March, 2007), KU 308542–43 (6 January 2007), KU 398570–77 (8 January 2007); Barangay Harrison, Sitio Ulasan (N 13.449°, E 120.424°; WGS-84), an adult female and nineteen adult males collected by E. L. Rico: KU 308504–17 (4 January 2007), KU 308529–33 (5 January 2007).

Referred specimens.—Mindoro Island, Oriental Mindoro Province, Municipality of Tarogin, Tarogin River, ca. 30 km S Calapan (N: 13.190°, E: 121.148°): CAS-SUA 22298; 30 km SW of Calapan, SE slope of Mt. Halcon, Tarogin Barrio (N: 13.195°, E: 121.138°): CAS-SUA 22274, (N: 13.188°; E: 121.135°) 22280, (N: 13.176°, E: 121.134°) 22282; Municipality of Baco, Mt. Halcon: PNM 1512; Municipality of Baco, Mt. Baco, Aligatil River: USNM 508500, PNM 1524, 1528; Municipality of Baco, Baco Mountain Range, Alangsa Creek: PNM uncatalogued male specimen, USNM 509066–69 (dry skeletons); Puerto Galera Municipality, Mt. Alinyalan, SW of Puerto Galera, National Museum of the Philippines Field Station: USNM 291536.

Diagnosis.—A species of *Leptobrachium* characterized by a combination of the following characters: (1) small body size, (2) absence or extreme reduction of dark tympanic coloration (Fig. 2), (3) narrow (or absent) canthal stripe, (4) predominantly brown dorsum with semicircular dark brown spots with black borders (Fig. 2), (5) gray venter with minute white spots on warts or white with distinct dark brown marbling, (6) entirely black eyes with a deep blue scleral arc under the eyelid (visible in corners of eye and when palpebrum is retracted), and (6) several characters related to its unique advertisement call (Table 5; Fig. 5). A summary of the distribution of character states distinguishing *L. mangyanorum* from the remaining Philippine species and *L. hasseltii* is presented in Table 6, and detailed comparisons to Philippine and Sunda Region species are provided in the Comparisons section, below.

Description of holotype.—A mature male, in excellent condition (Fig. 8), with only a small post-axial incision (small piece of liver removed before preservation). Habitus stocky, head length 101.8% of head width, head wider than body, neck indistinct; snout rounded to subacuminate in lateral aspect, and protruding slightly beyond lower jaw, nearly rounded in dorsal view; nostril much closer to tip of snout than to anterior corner of eye; eyes protruding slightly beyond silhouette of head in dorsal aspect (Fig. 8), well above dorsal surface of head in profile; lips not flared and only slightly swollen, not extending beyond most lateral edge of orbit when viewed in dorsal aspect; canthus rostralis sharply distinct, constricted behind nostrils in dorsal view; loreal region oblique, only slightly concave; eye diameter 84.1% of snout length; pupil vertically elliptical in preservative; iris dark gray-black; interorbital region 93.4% eye diameter; nostrils laterally protuberant, oriented posterolaterally; eye-narial distance 3.5 times distance from nostril to tip of snout; tympanum obliquely ovoid, longer axis oriented approximately 60° from the horizontal plane; tympanic annulus weakly distinct, 49.3% of eye diameter; dorsal edge of tympanic annulus concealed by supratympanic fold, the latter extending from posterior corner of eye to supra-axillary region; pineal ocellus absent.

Tongue moderate in size, ovoid (widest posteriorly), lacking posterior groove, notch, and papillae, with narrow anterior attachment; choanae situated at anterolateral edge of palate, slightly concealed by narrow palatal shelf of the maxillae, oval, separated by a distance five to six times greater than their diameters; dentigerous process of vomer indistinct, not protruding through buccal mucosa, vomerine teeth absent; vocal slits large, on lateral corners of the angle of jaws.

Forelimbs, digits, manus and pes well developed (Fig. 8), hindlimbs proportionally short, moderate to poorly developed; manus length 61.3% of pes length; pes length 92.0% of tibia length; femur 115.7% of tibia length; tibia length 41.2% of snout–vent length; digits of manus slender, long.

Tips of all fingers bluntly rounded, slightly swollen, relative finger lengths I = II = IV < III (Fig. 9); intradigital webbing absent; minute dermal flange bordering lateral edges of all fingers; subarticular tubercles indistinct, reduced to low, irregular, warty tubercular ridges that extend the length of Fingers I–IV; supernumerary tubercles absent (Fig. 9); inner thenar surface characterized by a long, velvety tubercular surface but no distinct tubercles; palmar tubercle divided into inner and outer metacarpal tubercles (two subtriangula palmar tubercles, barely in contact on medial surfaces); inner tubercle moderate, convex, lacking spade-like edge; outer metacarpal tubercle subequal to inner with convex ventral surface; nuptial pads absent, forearms moderate, musculature not hypertrophied (Fig. 8).

Tips of toes rounded, slightly to moderately expanded, relative lengths I < II < III = V < IV; lacking circummarginal grooves or supra-articular cutaneous flaps above phalangeal articulation; plantar surface of foot smooth, lacking distinct subarticular tubercles under digits (Fig. 9); supernumerary tubercles absent; interdigital webbing thick, acrenulate, homogeneous, modal webbing formula of toes (Savage and Heyer, 1969, 1997): **I** 1–1.5 **II** 0.5–3 **III** 2–4 **IV** 4–1 **V**. Inner metatarsal tubercle distinct, raised, ovoid, situated at base of Toe I, with a plantar spade-like edge; inner metatarsal tubercle less than half as long as Toe I; outer metatarsal tubercle absent; heels non-overlapping when legs are adpressed at right angles to the body; cloacal region glandular, with low tuberculate warts; supracloacal flap absent.

Skin on dorsum and dorsal surfaces of limbs smooth with limited scattering of fine, raised dermal ridges; skin of chin, throat, ventral surface of body, and ventral and posterior surfaces of thigh with dense aggregation of slight dermal asperities and minute warts; flanks highly tuberculate, with dense aggregation of moderate dermal warts; skin on ventral surfaces of forelimbs with low tuberculate ridges and skin on ventral surfaces of tibiotarsus smooth; circular axillary gland present ventrolaterally, immediate posterior to forelimb insertion; small, oval femoral gland present on posteroventral surface of each thigh; skin on surface of pectoral and femoral glands smooth.

Measurements of holotype.—Snout–vent length 49.0; head length 22.4; snout length 8.2; interorbital distance 6.5; internarial distance 4.3; eye diamater 6.9; tympanum diameter 3.4; head width 22.0; upper arm length 9.9; forearm length 14.3; femur length 23.4; tibia length 20.2; tarsus length 11.8; pes length 18.6; manus length 11.4; Toe 4 length 11.4; Finger 1 length 6.0; Finger 3 length 8.4.

Color of holotype in preservative.—(Fig. 8) Dorsum dark gray, with distinct brown-black spots with black borders on body and head; flanks varying shades of gray (lightest anteroventrally), with 10–15 large black spots, each with a white-tipped dermal wart; inner flash surface of groin marbled distinctly white and gray-brown; dorsal surfaces of forelimbs and upper arms gray with dark gray-black transverse bands (two on forearm, one on upper arm); dorsal surfaces of hindlimbs dark gray-brown with faint darker transverse bars (four on thigh, three on tibia, two on tarsus); anterior surface of thigh solid dark gray-black; posterior surfaces of thigh gray-black with distinct white spots; eye black with narrow light blue crescent on outer, dorsal margin of eyeball (below retracted palpebrum); less than 50% of tympanic annulus covered with brown spot extending ventrally from dark brown color ventrally bordering the supratympanic fold; dorsal surface of head with dark interorbital bar lateral surfaces slightly lighter than dorsal surfaces; canthus rostralis bordered ventrally by dark brown coloration extending anteroventrally from corner of eye; dorsal surface and tip of snout pale gray, contrasting with dark brown of lateral surfaces; labial bars absent, subocular blotch present; chin and throat dark brown with dense aggregation of creamy white warts; sternal region cream with indistinct brown blotches; sternal glands white; venter and groin marbled dark brown

TABLE 5.—Quantitative and qualitative characteristics of advertisement calls in three new species of Philippine *Leptobrachium*, and *L. hasseltii*. Quantitative entries include mean character values for two males per species (separated by comma, see species accounts and call descriptions).

Species:	*L. mangyanorum* Mindoro Isl.	*L. tagbanorum* Palawan & Dumaran Isls.	*L. lumadorum* Mindanao & Basilan Isls.	*L. hasseltii* Java & Bali Isls.
Mean notes per call	14.0, 14.6	8.3, 8.5	6.2, 7.5	6.8, 6.9
Mean note duration (ms)	179.7, 194.0	109.0, 114.7	257.0, 273.0	279.0, 287.7
Mean call length (s)	3.4, 3.7	1.5, 2.5	1.7, 3.5	2.0, 2.2
Call prefix	tonal	tonal	pulsed	—
Mean internote interval (ms)	130.3, 135.1	141.1, 151.7	203.0, 221.0	133.0, 138.0
Mean note repetition rate (notes/s)	3.51, 3.81	4.09, 4.2	1.9, 2.4	3.0, 3.1
Mean calling rate (calls/s)	0.104, 0.118	0.043, 0.047	0.065, 0.067	0.029, 0.031
Mean intercall interval (s)	4.5, 5.3	11.0, 12.7	11.7, 21.0	27.9, 34.8
Point of peak amplitude (as % of note duration)	60–70%	44–45%	5–10%	25–30%
First internote interval	> than remainder	> than remainder	= remainder	= remainder
Note amplitude envelope shape	symmetrically ovoid: gradual rise to peak, followed by gradual decline	symmetrically ovoid: gradual rise to peak, followed by gradual decline	symmetrically square: instantaneous rise to peak, constant for majority of note, instantaneous decline	asymetrical, triangular: instantaneous rise to peak, followed by steady decline

with white tuberculate warts and ridges; ventral surfaces of thighs dark gray-brown; ventral surfaces of tibiotarsus light gray with white irregularly blotched marbling on lateral edges; ventral surfaces of hands medium gray-brown, with light gray palmar tubercles and finger tips; ventral surfaces of feet dark gray-black with gray inner metatarsal tubercle and gray toe tips; femoral glands white.

Color in life.—Based on field notes by RMB and color images of holotype in life, before preservation (Fig. 2); color differences minimal between live and preserved specimen. In life, dorsal ground coloration brown, with distinct brown spots with black borders; lateral portions of head light brown with dark brown loreal region and suboccular coloration; dark supratympanic coloration extending ventrally to cover posterodorsal edge of tympanic annulus but majority of the tympanum lacks dark pigment; iris color dark brown-black, dorsal margin of the eyeball surrounded with deep, vibrant blue eye-ring under retracted palpebrum; blue eye ring only visible in corners of eyes in relaxed state; dorsal and lateral surfaces of limbs and feet dark brown with gray-black transverse limb bars and midline of white tipped asperities; ventral chin, throat, and body color light gray, with dark gray blotches; sternal region immaculate light cream-gray; flanks fading from dark brown above to nearly white below, with distinct round black spots, each with single white tubercle; ventral surfaces of fore- and hindlimbs light gray with dark gray lateral edges; thighs and tibia gray with dark gray bars on their anterior surface, and dark gray with tiny white spots on posterior surfaces; femoral and humeral glands white; finger and toe tips flat gray; palmar and plantar tubercles, and subarticular tuberculate ridges velvety gray on ventral surfaces.

Variation.—There is little color variation exhibited by the large series of available specimens, most of which have a brown or gray dorsum with variable markings across the dorsum. Some have several large, darker, irregular blotches and semicircular spots with black borders (KU 308574, 303274, 308576, 308512, 303278); in others, dorsal blotching is limited to the posterior portions of the head or the interorbital region (CAS-SUA 16494, 22294–96, 22300; MCZ A-508498; KU 308531, 308354, 308346, 308543). The vast majority of specimens have semicircular spots with black borders across the dorsum, mixed with distinct black spots, each with a single white tubercle, in the sacral and posterolateral regions of the trunk (PNM 1512, 1523, 1525; CAS-SUA 22229, 22579; USNM 508502, 508507). Some specimens have immaculate gray or brown dorsums (CAS-SUA 22241, 22274, 22277, 22280, 22282, 22580; KU 308337, 308351, 303273, 308511, 308343, 308341).

Most specimens have dark transverse bars on dorsal surfaces of most segments of the fore- and hindlimbs. The tibial segments of the hindlimbs have 0–5 dark bars ($\bar{x} = 3.2 \pm 0.96$ SD; $n = 47$). In nearly all specimens, transverse tibial bars are broken on the dorsal surface of the tibia (but present on anterior and posterior margins of tibia), resulting in the appearance of the absence of bars when the specimen is in the resting position. Exceptions include specimens with complete transverse bars across the tibia (KU 303275, 308513–14, 308518) and specimens in which bars are entirely absent (PNM 1525, KU 308542, 308336, 308341, 308384).

Some specimens have the posterodorsal portions of the tympanum partially covered by a small spot extending from the posterior edge of the supratympanic fold; the tympanic spot may be reduced to a tiny patch of pigment on the dorsal edge of the tympanum (CAS-SUA 16492, 22241, 22300, 22275–78, 22283; PNM 1524, 1528; KU 303273, 303276, 308506) or the center of the tympanum (PNM 1527). However in most remaining specimens, the tympanic melanic pigment consists of a narrow line along the posterior margin of the supratympanic fold.

The width of the canthal varies from 0.22 mm to 1.0 mm ($\bar{x} = 0.53 \pm 0.25$SD; $n = 47$). In most specimens, lateral portions of the head are traversed by three dark markings (see color description of holotype): a pair of vertical bars on the trip of the snout, a pair of vertical bars on either side of the snout in the in the narial region, and a pair of wide subocular bars. In some other specimens (CAS-SUA 16492, 22283, 22300, 22275–77, 22280; PNM 1526), these three vertical markings continue through the labial region, resulting in dark labial bars. In some specimens, these markings fade posteriorly and fail to contribute to dark labial bars (CAS–SUA 22241, 22578–80, 22178, 22277–79; PNM 1253, 1525).

Our sample exhibits two general ventral color patterns. The first, exhibited by the vast majority of specimens, is uniform dark gray with minute white spots on the warts of the throat, groin, and ventrolateral trunk. These specimens have a slightly paler pectoral region and a slightly darker throat. The other main pattern is white or cream ventral coloration, with distinctive dark gray marbling (CAS-SUA 22229, 22294–95, 22275–80; KU 308532, 308343, 308535, 308570, 308336, 308575, 308355, 308530, 308356, 308384, 303275). A few specimens (PNM 1523, 1525; KU 308340, 308571, 308577) have a solid gray venter.

We observed no variation in skin texture, subdigital tuberculation, or extent of interphalangeal webbing. Pectoral glands are predominantly invariant in size, color, and shape, with one exception: one female (PNM 1525) has minute pectoral glands. Femoral glands are tiny and barely perceptible (KU 308340, 308542), to small, and horizontally elongate (KU 308351, 308358, 308509), to moderate and round (remaining specimens).

Aside from sexual size dimorphism (Tables 3, 4) no subsamples or subpopulations of the available specimens exhibited detectable differences in size or body proportions. Mean female-biased sexual size dimorphism in the new species is 1.20 (female:male snout–vent length; min–max size disparity = 1.17–1.36). Morphometric data exhibited in the type series of *L. mangyanorum* are summarized in Table 4.

Advertisement call.—The following description of the call of *L. mangyanorum* is based on two recording segments. The first is an unvouchered, low-quality segment, recorded by RMB, 28 May 1992, near the Dulangan River drainage, Municipality of Baco, Oriental Mindoro, Mt. Halcon, 1200 m (26 calls, recorded at 19.8 C). The second is a high-quality recording of the holotype (PNM 9559; see type locality, above), recorded by CDS, 16 March 2005 (4 calls, recorded at 22.6 C). Despite the different quality of the two recordings, they are strikingly similar in all measurable characteristics and differ only slightly in rate-related call parameters.

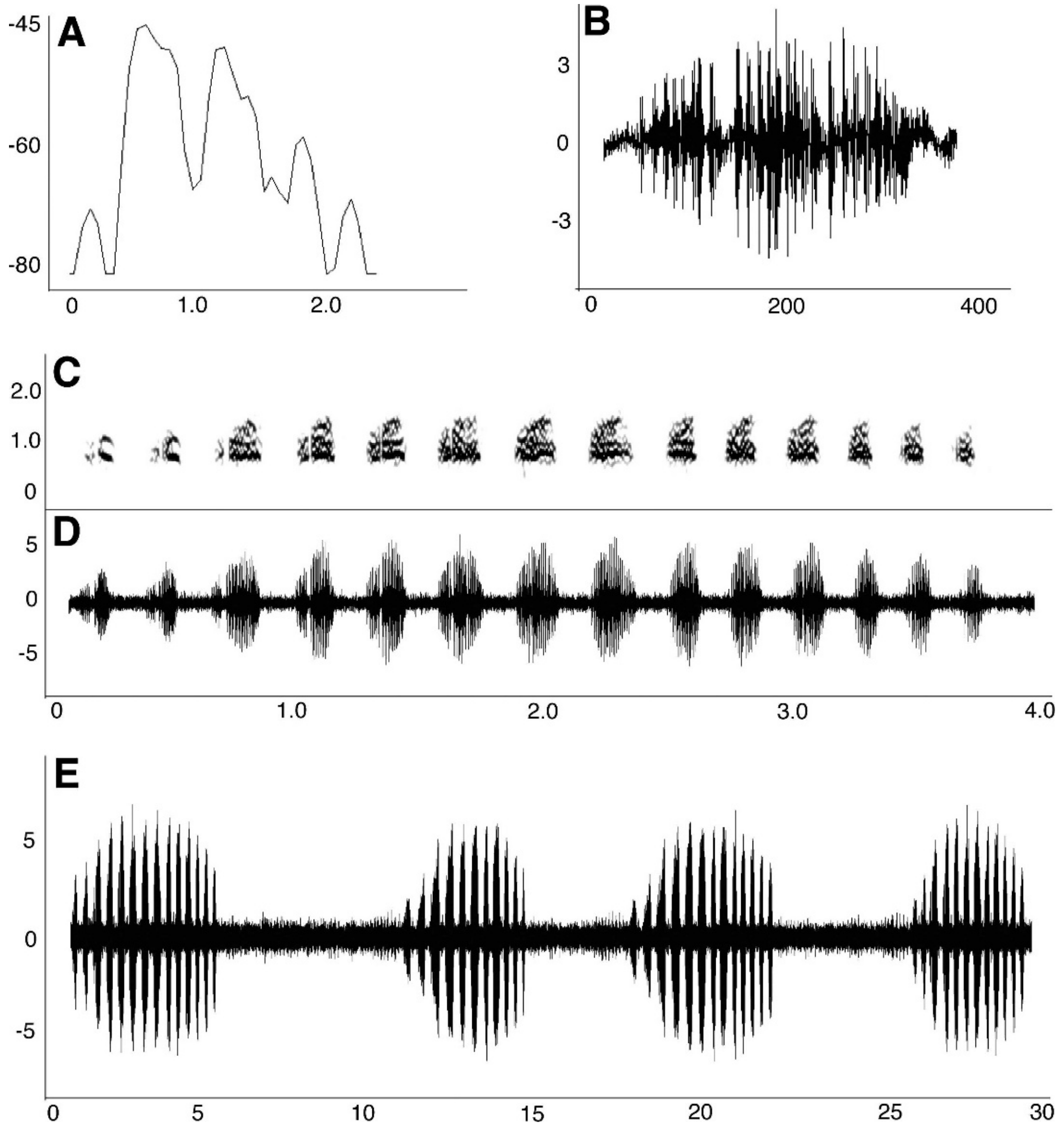

FIG. 5.—The advertisement call of *Leptobrachium mangyanorum* (holotype, PNM 9559, recorded at the type locality by CDS, 16 March 2005 (ambient temperature 22.6°C). Analyses include: a power spectrum (A: Fast Fourier Transformation; relative amplitude vs. frequency in kHz) calculated across notes 4–8 in C and D; a 400 ms expanded waveform (B: relative amplitude vs. time in ms) of a single note; a 4.0 s audiospectrogram (C: frequeny in kHz vs. time in s) and oscillogram (D: relative amplitude vs. time in s) of a typical call; and a 30 s oscillogram (E: relative amplitude vs. time in s) of four typical calls, illustrating typical rise and decline in note amplitude across the call.

The call of *L. mangyanorum* (Fig. 5) is an elongate series of low frequency paired grunts, giving the impression to the human ear of slow gurgling: "wher-err, wher-err, wher-err…." The call consists of 13–16 (but usually 13 or 14) major notes per call and note repetition rate is near constant across the call (unlike other Philippine species; see species accounts). The notes consist of two subpulses that fuse to form a single note by the middle or final two thirds of the call (Fig. 5D). The call's first few notes are spaced slightly farther apart from the remainder of the call and are separated by slightly longer internote intervals (Fig. 5C, D).

TABLE 6.—Summary of the distribution of selected qualitative (+ present, − absent) and quantitative diagnostic characters and ranges of morphometric ratios (from male specimens) in three new species of Philippine *Leptobrachium*, and *L. hasseltii* (number of male and female specimens measured included in parentheses). Summaries of body size and geographical range are included for reference. See Table 4 for full univariate summaries of mensural characters.

Species:	*L. mangyanorum* Mindoro Isl.	*L. tagbanorum* Palawan & Dumaran Isls.	*L. lumadorum* Mindanao & Basilan Isls.	*L. hasseltii* Java & Bali Isls.
Male Snout–vent (mm)	35.5–49.0	42.2–54.0	39.1–50.4	37.5.1–47.4
Female Snout–vent (mm)	45.6–58.8	65.1–80.0	48.2–65.1	53.9–62.0
Range	Mindoro Isl.	Palawan & Dumaran Isls.	Mindanao & Basilan Isls.	Java & Bali Isls.
Dark coloration covers most of tympanum	−	+	+	+, −
Canthal stripe	Narrow or absent (0.2–1.0 mm)	Broad (1.3–2.9)	Broad (1.2–2.6)	Narrow or absent (0.2–0.8)
Tibial bars	0–5 (3.2 ± 1.0)	2–4 (2.7 ± 0.8)	4–6 (4.7 ± 0.8)	3–4 (3.3 ± 0.6)
Predominant dorsal coloration and dorsal markings	Semicircular round dark spots with black borders	Immaculate tan or with faint irregular brown blotches	Immaculate gray with brown blotches anteriorly	Tan with distinct dark brown spots and blotches
Head/Snout–vent length	0.38–0.46	0.39–0.44	0.39–0.44	0.38–0.43
Tibia/Snout–vent length	0.39–0.45	0.36–0.40	0.33–0.40	0.33–0.38
Fprearm/Snout–vent length	0.28–0.35	0.28–0.34	0.26–0.33	0.27–0.33
Pes/Snout–vent length	0.32–0.47	0.31–0.38	0.28–0.36	0.35–0.38
Sexual dimorphism (mean female:male SVL)	1.20	1.50	1.25	1.34

Intercall intervals ranges from 3.3–9.1 s ($\bar{x}$ = 5.3 ± 1.3 SD; n = 25) for the unvouchered recording and 4.3–4.6 s ($\bar{x}$ = 4.5 ± 0.8 SD; n = 3) for PNM 9559. The unvouchered male called at a rate of 0.104 calls/s and PNM 9559 called at 0.118 calls/s. The unvouchered male had an average of 14 notes per call (± 0.9 SD; range 13–15 notes/call; n = 4) and PNM 9559 had an average of 14.8 notes per call (± 1.6 SD; range 13–16 notes/call; n = 26). Call length varies from 3.0–3.6 s ($\bar{x}$ = 3.4 ± 2.0 SD; n = 26) for the unvouchered recording and from 3.5–3.9 s ($\bar{x}$ = 3.7 ± 0.16 SD; n = 4) for PNM 9559. Note duration is 161.1–195.2 ms ($\bar{x}$ = 179.7 ± 13.9 SD; n = 360) for the unvouchered male and 181.4–200.7 ms ($\bar{x}$ = 194.0 ± 9.6 SD; n = 56) for PNM 9559. Internote interval is 122.6–146.6 ms ($\bar{x}$ = 135.1 ± 7.1 SD; n = 345) for the unvouchered recording and 124.2–148.9 ms ($\bar{x}$ = 130.3 ± 5.2 SD; n = 51) for PNM 9559.

Within calls, note repetition rate was 3.51–3.81 notes/s ($\bar{x}$ = 3.64 ± 2.3 SD; n = 25) for the unvouchered specimen and 3.56–3.77 notes/s ($\bar{x}$ = 3.66 ± 0.2 SD; n = 3) in PNM 9559.

Relative amplitude across calls varied symmetrically from start to finish, with a gradual rise to peak amplitude across the first half of the call, followed by a gradual decline across the second half of the call (Fig. 5D, E). Amplitude of the first and last notes was approximately 50–60% of the peak amplitude at the call's midpoint. Calls from Mt. Halcon lacked tonal elements or prefixes, but tonal prefixes are apparent in the recording from the type locality (Fig. 5C). Individual notes varied temporally, with two-pulsed notes (pulses separated by 10–15 ms gap) for the first half of the call, followed by a gradual fusing of the two pulses by the middle or final third of the call length, to form a single barking note (Fig. 5D).

Energy in the call consisted of three or four distinct frequency components (Fig. 5A, C): a fundamental (= dominant) frequency component of 0.8–0.9 kHz, a frequency band between 1.0 and 1.1 kHz, and a third component between 1.2 and 1.3 kHz. In some audiospectrograms, faint harmonics were visible at one multiple of the fundamental (approximately 3.7–3.8 kHz).

Comparisons.—Our phylogenetic estimate (Fig. 3) indicates that *L. mangyanorum* and *L. tagbanorum* share a most recent common ancestor, to the exclusion of all other known SE Asian species. Additionally genetic data indicate substantial levels of genetic divergence between *L. mangyanorum* and other Philippine, Bornean, and Indonesian species (Table 3). *Leptobrachium mangyanorum* differs from its sister species *L. tagbanorum* by a slightly smaller body size in males, a significantly smaller, non-overlapping body size in females (Table 1), the complete absence or extreme reduction of dark supratympanic fold coloration protusion onto the tympanum (vs. dark supratympanic fold coloration protruding extensively onto the tympanum in the form of a large tympanic spot), absence or reduction in thickness of the dark canthal stripe (vs. variable presence of a thicker and bolder canthal stripe), dorsum characterized by semicircular brown spots with black borders (vs. solid tan or brown with diffuse, irregular brown blotches), less extensive interdigital webbing and more pronounced inner metatarsal tubercle (Fig. 9), and its unique advertisement call (Fig. 5; Table 5). The new species differs from *L. lumadorum* by a tendency towards a smaller maximum body size (Tables 4, 6), the complete absence or extreme reduction in protrusion of dark supratympanic fold coloration onto the tympanum (vs. dark supratympanic fold coloration protruding extensively onto the tympanum in the form of a large tympanic spot), absence or reduction in thickness of the dark canthal stripe (vs. variable presence of a thicker and bolder canthal stripe), dorsum characterized by semicircular brown spots with black borders (vs. solid gray-black with brown and tan blotches on head and interorbital region), and its unique advertisement call (Fig. 5; Table 5). *Leptobrachium mangyanorum* differs from *L. hasseltii* by darker dorsal coloration in life (Fig. 2), absence or reduction in thickness of the dark canthal stripe (vs. variable presence of a thicker and bolder canthal stripe), and its unique advertisement call (Fig. 5). From *L. nigrops*, the new species differs by the presence of a deep blue scleral arc under the eyelid (vs. absent), absence or extreme reduction in melanic pigmentation of the tympanum (vs. tympanic spot present), a narrow (vs. thick) canthal stripe, absence of circular flank spots (vs. distinct black flank spots present). Additionally, unlike *L. mangyanorum*, *L. nigrops* has sharp, posteriorly recurved terminal phalanges (Inger and Stuebing, 1997). *Leptobrachium mangyanorum* differs from *L. abbotti* by the absence or extreme reduction in melanic pigmentation of the tympanum (vs. tympanic spot present), a narrow canthal stripe (vs. broad when present), and venter gray with white spots on warts, or white and brown marbled venter (vs. venter boldly patterned black and white). From *L. montanum* and *L. gunungense*, the new species differs by the presence of a deep blue scleral arc under the eyelid (vs. a bold white arc across the top of the eye), many narrow transverse bars of the limbs (vs. fewer broad bars), the absence or extreme reduction in melanic pigmentation of the tympanum (vs. tympanic spot present), and a narrow canthal stripe (vs. thick). From *L. hendricksoni* and *L. smithi* the new species differs by the presence of solid black eyes (vs. eyes with bright orange or orange-red upper half of iris), by absence of circular flank and posterior thigh spots (vs. distinct black flank and posterior thigh spots present). The new species differs further from *L. hendricksoni* by the presence of a gray venter with white spots on warts or a white venter with brown marbling (vs. venter gray with distinct black spots) and the presence of a brown or gray dorsum with dark brown spots with black borders (vs. lavender-brown with blotches on anterior portions of body).

Ecology and natural history.—This species has been collected in a wide variety of ecological conditions, from pristine higher elevation forests (1000–1200 m) on Mt. Halcon and Mt. Baco, north Mindoro Island, to highly disturbed, near coastal regions near the Municipality of Sablayan. The new species does not form tight choruses, but instead forms loose aggregations on the forest floor where males may be loosely grouped over a 50–100 m stretch of forest, with males separated by as few as 2–5 meters (RMB, personal observation, 1075 m, Mt. Halcon) to as many as 20 m. Males of this species appear tolerant of exposure, and call from perches like stumps and rocks or on the open forest floor, exposed on leaf litter. Other anuran species observed in sympatry with *L. mangyanorum* include *Rana* (*Hylarana*) *mangyanum*, *Limnonectes acanthi*, *Occidozyga laevis*, *Rhinella marina* (introduced), *Hoplobatrachus rugulosus* (introduced), *Fejervarya vittigera*, *Polypedates leucomystax*, *Philautus schmackeri*, *Kaloula picta*, *K. conjuncta conjuncta*, and *Platymantis* cf. *corrugatus*.

Distribution.—The new species is known only from the Mindoro PAIC (Fig. 1): Mindoro Island, including the provinces of both Oriental and Occidental Mindoro. It is conceivable that this species may inhabit the small land-bridge island of Semirara to the south of Mindoro.

Etymology.—The specific epithet is chosen from the term *Mangyan*, collectively referring to the eight ethnolinguistic tribal groups (The Alangan, Bangon, Buhid, Hanunoo, Iraya, Tadyawan, Tau-buid, and Ratagnon) of the Island of Mindoro. The tribal groups of Mindoro possess a rich and diverse societal, linguistic, and cultural history that is seldom understood and appreciated by outsiders, including many other Filipinos. Peace-loving and unwilling to fight, Mangyans have been displaced by the Spanish, coastal area pirates, and Tagalogs (Filipinos from south-central Luzon), and moved into the interior, mountainous, forested regions of central Mindoro. Many groups still live a semi-nomadic existence and practice belief systems that attribute spirits to animals, plants, and natural geographic features of forested regions of central Mindoro.

Leptobrachium **tagbanorum** *sp. nov.*

Figs. 2, 8, 9

Holotype.—PNM 9560 (formerly KU 309458, Field number RMB 7620), adult male, from the Philippines, Palawan Island, Palawan Province, Municipality of Puerto Princesa City, Barangay Irawan, Irawan Watershed (N: 9.833°, E 118.650°; WGS84) collected on 20 March 2007, by RMB and J. Fernandez.

Paratypes.—Palawan Island, Palawan Province, Municipality of Puerto Princesa, Barangay Iwahig, 7 km SW of Montible (Subcolony of Iwahig Penal Colony), Pulang Lupa, tributary of Montible River (N: 9.686°, E: 116.616°), male, collected by M. Piñero: CAS 145826 (22 April 1961); S slope of Thumb Peak, Malatgaw River (N: 9.763°, E: 118.603°), male, collected by Q. Alcala and S. Magusara: CAS 140535 (23 March, 1961); S slope of Thumb Peak, tributary of Malatgaw River (N: 9.773°, E: 118.614°), two males, collected by Q. Alcala and party: CAS 140538, CAS-SUA 24298 (27 March 1961); 6–9 km W of Malabo, NE slope of Malabo Mountain (Central Peak; N: 9.631°, E: 118.575°), male, collected by ACA and party: CAS 140542 (30 April 1961); S slope of Thumb Peak, Malatgaw River (N: 9.762°, E: 118.605°), female, collected by Q. Alcala and party: CAS 140536 (31 March 1961); Municipality of Nara, Taritien Barrio, Estrella Falls, a male and a female, collected by C. A. Ross: USNM 122491, 122492 (4 April 1987); Municipality of Taytay, ca. 9 km S. of Lake Danao, female, collected by C. A. Ross: USNM 120263 (no date); Thumb peak, near Iwahig Penal Colony, two females collected by E. H. Taylor: MCZ A-14526–27 (14 June 1923); Municipality of Puerto Princesa, Barangay Cabayugan, Sugod 1, female, collected by R. Sison: PNM 6339 (19 January 1998); Municipality of Puerto Princesa, Barangay Tagabinet, Lamod, Keyasan, male, collected by Roger Sison: PNM 6381 (22 February 1998); Mt. Mantalingayan Range, S. slope Mt. Balabag, two male specimens, collected by F. Werner: FMNH 51027–28 (4 May 1947); Municipality of Puerto Princesa City, Barangay Irawan, Irawan watershed (N 9.8368°, E 118.6413°; WGS 84), seven males and seven females, collected by RMB and J. Fernandez: PNM 9665–9672; KU 308983, 309071–75 (14–15 March 2007; N: 9.837°, E: 118.643°; WGS 84), eight males, collected by RMB and J. Fernandez: KU 309096–97, 309166, 309172 (16 March 2007), KU 309177–78, 309180, 309248 (17 March 2007; N: 9.837°, E: 118.642°; WGS 84), three males, collected by RMB and J. Fernandez: KU 309457–58 (18 March 2007); Municipality of Brookes Point, Barangay Mainit (N: 9.751°, E: 117.691°; WGS 84), male, collected by RMB: KU 309459 (20 March 2007); Municipality of

Brooke's Point, Boundary of Barangay Samariñana and Barangay Saulog, Mt. Mantalingahan, area known locally as "Pitang," (N: 9.750°, E: 117.690°; WGS 84), three males and a female, collected by RMB and J. Fernandez: KU 309460–61 (29 March 2008), 309462–63 (31 March 2008).

Referred specimens.—Palawan Island, Palawan Province, Municipality of Iwahi, Puerto Princesa, Barangay Iwahig, ca. 3.5 km WNW of Iwahig, tributary of Malatgaw River (N: 9.745°, E: 118.63°): CAS 145811; S slope of Thumb Peak, Malatgaw River (N: 9.761°, E: 118.605°): CAS 145809; ca. 10 km S of Iwahig along Tagbuni creek: CAS 145825; 4 km W of Montible (Subcolony of Iwahig Penal Colony), small tributary of Montible River (N: 9.729°, E: 118.605°): CAS 145824; tributary of Malatgaw River (N: 9.741°, E: 118.636°): CAS 140537; 13 km SW Iwahig, Malabo (N: 9.66°, E: 118.585°): CAS 140539–41; Municipality of Puerto Princesa, Barangay Cabayugan, Sitio Sugod 1: PNM 6304, 6335, 6359; Palawan Island: FMNH 51025–26; Municipality of Brooke's Point, Barangay Borangbato, Mainit falls: PNM uncatalogued female specimen; Palawan Island, Palawan Province, Taytay, ca. 9 km S of, Lake Danao (= Lake Manguao), Taytay District: USNM 229509; 73 km N of Puerto Princesa City: USNM 158219; Municipality of Narra, Taritien Barrio, "Australia Falls" (= Estrella Falls): USNM 287329–30.

Diagnosis.—A species of *Leptobrachium* characterized by a combination of the following characters: (1) moderate body size in males, large body size in females (Tables 4,6); (2) protrusion of dark supratympanic fold coloration posteriorly to form a dark tympanic spot that covers, or nearly covers, the tympanum (Fig. 2); (3) a broad canthal stripe (Table 1); (4) a homogenous tan, light gray, or light brown dorsum with or without diffuse, irregular brown blotches (Fig. 8); (5) venter gray with minute white spots on warts, cream, or with dark blotches on throat and groin; (6) entirely black eyes with a deep blue scleral arc under the eyelid (visible in corners of eye and when palpebrum is retracted); and (7) several characters related to its unique advertisement call (Table 5; Fig. 6). A summary of the distribution of character states distinguishing *L. tagbanorum* from the remaining Philippine species and *L. hasseltii* is presented in Table 6 and detailed comparisons to Philippine and Sunda Region species are provided in the Comparisons section, below.

Description of holotype.—A mature male, in excellent condition (Fig. 8), with only a small post-axiallary incision (small piece of liver removed before preservation). Habitus stocky, head length 89.1% head width, head wider than body, neck indistinct; snout rounded to subacuminate in lateral aspect, and protruding slightly beyond lower jaw, nearly rounded in dorsal view; nostril much closer to tip of snout than to anterior corner of eye; eyes protruding well beyond silhouette of head in dorsal aspect (Fig. 8), well above dorsal surface of head in profile; lips not flared and only very slightly swollen, not extending beyond most lateral edge of orbits when viewed in dorsal aspect; canthus rostralis sharply distinct, constricted behind nostrils in dorsal view; loreal region oblique, only slightly concave; eye 73.6% of snout length; pupil vertically elliptical in preservative; iris dark gray; interorbital region 120.8% eye diameter; nostrils laterally protuberant, oriented laterally; eye–narial distance 3.5 times distance from nostril to tip of snout; tympanum obliquely ovoid, longer axis oriented dorsoanteriorly and posteroventrally; tympanic annulus weakly distinct, 55.9% of eye diameter; dorsal edge of tympanic annulus sightly concealed by supratympanic fold, the latter extending from posterior corner of eye to supra-axillary region; pineal ocellus absent.

Tongue narrow, ovoid (widest posteriorly), with shallow posterior groove, tiny posterior papillae, and narrow anterior attachment; choanae situated at anterolateral edge of palate, not concealed by narrow palatal shelf of the maxillae, irregularly ovoid, moderate, separated by a distance four to five times greater than their diameters; dentigerous process of vomer indistinct, not protruding through buccal mucoasa, vomerine teeth absent; openings to vocal sacs large slits on the floor of the buccal cavity, on lateral corners of the angle of jaws.

Forelimbs, digits, manus, and pes well developed (Fig. 9), hindlimbs proportionally short, moderate to poorly developed; manus length 66.3% of pes length; pes length 86.3% of tibia length; femur 114.9% of tibia length; tibia length 41.2% of snout–vent length; digits of manus slender, long.

Tips of all fingers bluntly rounded, not swollen or appreciably expanded, relative finger lengths I = II = IV < III (Fig. 9); intradigital webbing absent; broad dermal flange bordering lateral edges of all fingers; subarticular tubercles indistinct, reduced to low, irregular, warty tubercular ridges that extend the length of Fingers I–IV; supernumerary tubercles absent; inner thenar surface characterized by a long, velvety tubercular surface but no distinct tubercles; palmar tubercle divided into inner and outer metacarpal tubercles (two oval subequal palmar tubercles, not in contact on medial surfaces); inner tubercle moderate, oblong, convex, with slight anteroventrally protrusion; outer metacarpal tubercle equal in size, low, convex ventral surface; nuptial pads absent, forearms moderate, musculature not hypertrophied (Fig. 8).

Tips of toes rounded, not expanded, relative lengths I < II = IV < III < IV (Fig. 9); lacking circummarginal grooves or supraarticular cutaneous flaps above phalangeal articulation; plantar surface of foot smooth, lacking distinct subarticular tubercles under digits; supernumerary tubercles absent; interdigital webbing thick, acrenulate, homogeneous, modal webbing formula of toes (Savage and Heyer, 1969, 1997): **I** 0.5–1 **II** 0–2.5 **III** 2–3.5 **IV** 3.5–1 **V**. Inner metatarsal tubercle distinct, raised, irregularly ovoid to subtriangular, situated at base of Toe I, with a moderate plantar spade-like edge; inner metatarsal tubercle less than half as long as long as Toe I; outer metatarsal tubercle absent; heels nonoverlapping when legs are held at right angles to the body; cloacal region glandular, with low tuberculate warts; supracloacal flap absent.

Skin on dorsum and dorsal surfaces of limbs with fine scattering of fine, raised dermal ridges and a slightly glandular texture; skin of chin, throat, ventral surface of body, and ventral and posterior surfaces of thigh with dense aggregation of slight dermal asperities and minute warts; flanks highly tuberculate, with dense aggregation of moderate dermal warts; skin on ventral surfaces of forelimbs with low tuberculate ridges and skin on ventral surfaces of tibiotarsus smooth; circular axillary gland present ventrolaterally, immediate posterior to forelimb insertion; a pair of small, oval femoral glands present on posteroventral surface of left thigh (right femoral gland not differentiated from remaining low warts on surface of thigh); skin on surface of pectoral and femoral glands smooth.

Measurements of holotype.—Snout–vent length 48.8; head length 20.1; snout length 7.3; interorbital distance 6.9; internarial distance 4.3; eye diameter 6.6; tympanum diameter 3.3; head width 20.7; upper arm length 10.4; forearm length 15.0; femur length 20.6; tibial length 18.0; tarsus length 10.5; pes length 15.2; manus length 10.5; Toe 4 length 9.1; Finger 1 length 5.3; Finger 3 length 7.9.

Color of holotype in preservative.—Dorsum medium gray (Fig. 8), with indistinct blotches on snout, posterior portions of head, suprascapular region, and dorsal trunk; other than a large dark brown spot on the left eyelid, the dorsum is devoid of enlarged round spots; flanks gray-brown with black and white flecks (more so ventrally) and enlarged, white dermal warts surrounded by black oscelli; dorsal surfaces of forelimbs and upper arms gray with dark spots on inner edges and indistinct dark blotches on outer edges; dorsal surfaces of hindlimbs dark gray-brown with faint darker transverse bars (most evident on lateral surfaces of limbs where ground coloration is lighter); transverse bars dark brown with black borders on anterior surfaces of thigh; anterior and posterior surfaces of thigh solid dark gray-black, with minute white spots; eye black with narrow light blue crescent on outer, dorsal margin of eyeball (below retracted palpebrum); upper 80% of tympanic annulus covered with large brown spot with black border; lateral surfaces of head same color as dorsal surfaces; canthus rostralis bordered ventrally by a narrow dark brown line, bordered with black; dorsal surface and tip of snout light gray, contrasting with dark brown of lateral surfaces; labial bars and suboccular blotches absent; chin and throat creamy with medium brown blotches; sternal region creamy gray-white; sternal glands yellowish; venter creamy white with brown blotches; groin brown between white warts;

ventral surfaces of thighs creamy white with brown blotches on outer margins; ventral surfaces of tibiotarsus dark gray-black with white irregularly blotched marbling; ventral surfaces of hands medium gray with light gray palmar tubercles and finger tips; ventral surfaces of feet medium dark gray-black with gray inner metatarsal tubercle and gray toe tips; femoral glands cream-white.

Color in life.—Based on field notes by RMB and color images of holotype in life, before preservation (Fig. 2); color differences minimal between live and preserved specimen. In life, dorsal ground coloration tan-gray, with indistinct brown blotches throughout dorsal surfaces, concentrated most in interorbital and middorsal regions; mid-dorsal dark brown coloration broken posteriorly into large round dark brown blotches; lateral portions of the head light brown; labial bars and suboccular blotches absent; canthal stripe moderately wide, brown; posterior border of the supratympanic flap black; large dark brown spot with a black border covered the dorsoposterior edge of the tympanic annulus; iris color dark brown-black, dorsal margin of the eyeball surrounded with deep, vibrant blue eye-ring under retracted palpebrum; only visible in corners of eyes in relaxed state; dorsal and lateral surfaces of the limbs and feet light tan-brown, crossed by thick, indistinct, light brown transverse limb bars; ventral chin, throat, and body color was light gray, with dark gray blotches; the sternal region immaculate light cream-gray; flanks gray with white tubercles; ventral surfaces of fore- and hindlimbs light gray with dark gray lateral edges; thighs and tibia gray with dark gray blotches on their anterior surface, and dark gray with tiny white spots on posterior surfaces; femoral and humeral glands white; finger and toe tips flat gray; palmar and plantar tubercles and subarticular tuberculate ridges velvety gray on ventral surfaces.

Variation.—There is little color variation in the type series. Two basic color patterns are represented in specimens available to us. The first includes specimens with a homogenous tan, medium brown, or pale gray dorsum, lacking dark blotches or spots or with dark markings limited to the posterior portion of the head and interorbital region (PNM 6304, 6335, 6339, 6359, 6381; CAS-SUA 24298; FMNH 51027; USNM 120263, 122491; CAS 140535–42, 145809, 145811, 145824–26; MCZ A-14525–26; KU 308983, 309035, 309053, 309058, 309060–61, 309071, 309073, 309075, 309096–97, 309166, 309172–73, 309177–78, 309180, 309248, 309457, 309459–61, 309463); others have faint dark gray blotches with black borders on posterior portions of the dorsum (KU 309052, 309062, 309074, 309045, 309059, 309072, 309075, 309035, 309166).

All specimens have dark transverse bars on dorsal surfaces of most segments of the fore- and hindlimbs; the tibial segment of the hind limb has 2–4 transverse bars ($\bar{x} = 2.73 \pm 0.75$ SD; $n = 58$). In nearly all specimens, transverse tibial bars are broken on the dorsal surface of the tibia (but present on anterior and posterior margins of tibia), resulting in the appearance of the absence of bars when if specimen is in the resting position. Exceptions include specimens with complete transverse bars across the tibia (KU 309045, 309052, 309059–60, 309073, 309096).

Canthal stripe width varied from 1.0 to 2.9 mm ($\bar{x} = 1.63 \pm 2.58$ SD; $n = 62$). All specimens have the tympanum covered or nearly covered by a large spot extending from the posterior edge of the supratympanic fold. In most specimens, lateral portions of the head are traversed by three dark markings (see holotype color description) that terminate posteriorly in the labial region, resulting in three distinct bars on the lips. In some specimens these markings fade posteriorly and fail to terminate in lip bars (CAS-SUA 14298; CAS 140538, 140542; PNM 6339).

Three ventral color patterns are evident. The first is nearly solid gray with minute white spots on warts of the throat and posterior portions of venter (USNM 122491–92, 120263; PNM 6339, 6381; FMNH 51025–26; KU 309059, 309072, 309061–62, 309074, 309461). Some specimens have homogenous gray venters (CAS 145809, 145811, 145824–26, 145536–38; CAS-SUA 24298). Finally, most specimens have a gray venter, white to light cream sternal region, and dark brown marbling (KU 309172, 309097, 309073, 309180, 309035, 309075, 309096) or blotches on the throat and venter (CAS 140535; PNM 6359, 6381; KU 308983, 309463, 309178, 309058, 309060).

We observed no variation in skin texture, subdigital tuberculation, or extent of interphalangeal webbing. Pectoral glands are circular and white when present but absent in a few specimens (CAS 145811, 145809, 140535). The majority of specimens had moderate, circular femoral glands. A few specimens had femoral glands that varied from tiny and barely perceptible (KU 309074, 308983, 309061), to small, and horizontally elongate (KU 309072, 309166, 309073), to irregular and fragmented (KU 309060).

Aside from sexual size dimorphism (Table 4, 6) no subsamples or subpopulations exhibited detectable differences in size or body proportions. Mean female-biased sexual size dimorphism in the new species is 1.50 (female:male snout–vent length; min–max size disparity = 1.34–1.59), markedly more than that detected in *L. mangyanorum* or *L. lumadorum*. Morphometric data exhibited in the type series of *L. tagbanorum* are summarized in Table 6.

Advertisement call.—The following description is based on two recording segments, all recorded in the Irawan watershed, near Puerto Princesa City, Palawan Island. One unvouchered recording was collected by ACD in April 2003 (22 calls over 486 s at 24.3 C) and the other by RMB on 15 March 2007 (paratype KU 309052; 15 calls over 310 s at 22.9 C). These recording segments vary only slightly in rate-related call parameters and are otherwise invariant.

The call of *L. tagbanorum* (Fig. 6) is a series of deep squawks, sounding to the human ear like a rapid "Wok…wok, wok, wok, wok, wok, wok…" and is delivered at a near constant rate over an approximately 2.0 s period, with 7–12 squawks (notes) per call. Intercall intervals ranges from 6–33 s ($\bar{x}$ = 12.7 ± 6.7 SD; *n* = 21) for the unvouchered male to 7–23 s ($\bar{x}$ = 11.0 ± 4.3 SD; *n* = 14) for KU 309052. The unvouchered male had a calling rate of 0.043 calls/s and KU 309052 called at 0.047 calls/s. The unvouchered male averaged 8.3 notes per call (± 1.4 SD; range 7–12 notes/call; *n* = 22) and KU 309052 averaged 8.5 notes per call (± 0.8 SD; range 7–10 notes/call; *n* = 15). Call length varies from 1.4–1.6 s ($\bar{x}$ = 1.5 ± 0.07 SD; *n* = 5) for six note calls to 2.4–2.6 s ($\bar{x}$ = 2.5 ± 0.13 SD; *n* = 6) for 11 and 12 note calls in the unvouchered recording. Call length varies from 1.6–1.8 s ($\bar{x}$ = 1.7 ± 0.19 SD; *n* = 4) for seven note calls to 2.7–2.9 s ($\bar{x}$ = 2.8 ± 0.18 SD; *n* = 5) for 13 note calls in KU 309052. Note duration is 101.2–133.4 ms ($\bar{x}$ = 114.7 ± 9.4 SD; *n* = 180) for the unvouchered recording and 98.6–117.1 ($\bar{x}$ = 109.0 ± 5.8 SD; *n* = 127) for KU 309052. Internote interval (excluding intervals between first four notes) is largely invariant, and ranges from 122–165 ms ($\bar{x}$ = 141.1 ± 7.1 SD; *n* = 180) for all calls recorded from the unvouchered recording and 131–179 ms ($\bar{x}$ = 151.7 ± 12.1 SD; *n* = 127) for KU 309052. The slight exception to the invariant internote interval of *L. tagbanorum* is the slightly longer intervals between notes 1–4, resulting in barely perceptible decreased note repetition rate at the beginning of calls (Fig. 6C, D). In both recordings, the first internote interval is longest (i.e., > 2.0 ms) and then the next two intervals steadily decline in duration until a constant repetition rate is achieved and internote intervals become apparently stereotyped or fixed. Within calls, note repetition rate is 3.9–4.2 notes/s ($\bar{x}$ = 4.09 ± 0.09 SD; *n* = 22) for the unvouchered recording and 4.1–4.4 notes/s ($\bar{x}$ = 4.2 ± 0.1 SD; *n* = 15) for KU 309052.

Relative amplitude across calls is heterogeneous and patterned, with low relative amplitude in the first notes, a steady rise in amplitude with each note thereafter (notes 2–4), an apparent peak amplitude achieved by notes 5–7, and then a steady decline in amplitude with each note thereafter (Fig. 6E). Amplitude of the first note is approximately 30–50% of the peak amplitude for the call. Individual notes begin with three or four distinct stridulating pulses (the first 35–50 ms of the note), followed by a single extended (60–75 ms) tonal element (Fig. 6C).

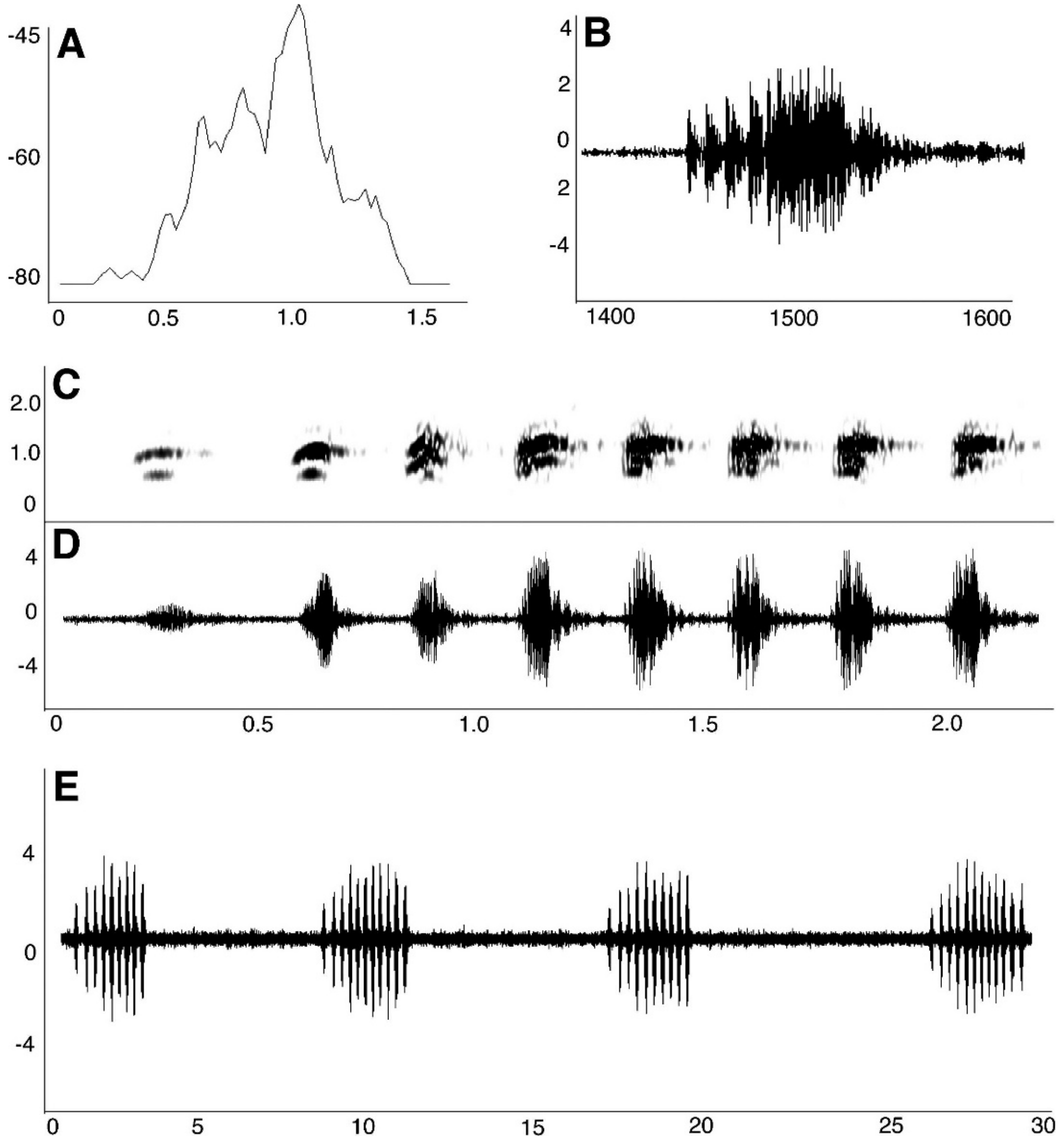

FIG. 6.—The advertisement call of *Leptobrachium tagbanorum* (male paratype KU 309052, recorded 15 March, 2007; 22.9°C ambient temperature). Analyses include: a power spectrum (A: Fast Fourier Transformation; relative amplitude vs. frequency in kHz) calculated across notes 3–5 in C and D; a 200 ms expanded waveform (B: relative amplitude vs. time in ms) of a single note; a 2.0 s audiospectrogram (C: frequeny in kHz vs. time in s) and oscillogram (D: relative amplitude vs. time in s) of a typical call; and an 30 s oscillogram (E: relative amplitude vs. time in s) of four typical calls from a recording segment of 15 calls, illustrating typical rise and decline in note amplitude across the call.

Energy in the call consists of two distinct frequency components, with a lower frequency component between 0.6 and 0.7 kHz and a higher, emphasized (fundamental) frequency component between 1.0 and 1.1 kHz in the unvouchered recording (Fig. 6A). In KU 309052, the dominant frequency is slightly lower (0.9–1.0 kHz). In many calls of both males, the lower frequency component is not visible in audiospectrograms, and all call energy is confined to the emphasized frequency component that peaks at approximately 1.0 kHz. In a few audiospectrograms, faint harmonics are visible at 1.2–1.4 kHz.

Comparisons.—As indicated in the *L. mangyanorum* diagnosis (above), our phylogeny (Fig. 3) indicates that *L. tagbanorum* and *L. mangyanorum* are more closely related to each another than either is to any other species. Additionally, genetic data indicate substantial levels of genetic divergence (Table 3) between *L. tagbanorum* and other Philippine, Bornean, and Indonesian species. *Leptobrachium tagbanorum* differs from *L. mangyanorum* by having a slightly larger body size in males and a significantly larger body size of females (Tables 4, 6), a dark supratympanic fold coloration protruding extensively onto the tympanum in the form of a large tympanic spot (vs. the complete absence or extreme reduction size of the tympanic spot), a thicker and bolder canthal stripe (vs. canthal stripe absent or reduced), a less variable, predominantly tan dorsal color pattern (vs. dorsum with many semicircular brown spots with black borders), more extensive interdigital webbing and much less pronounced inner metatarsal tubercle (Fig. 9), and its unique advertisement call (Fig. 6; Table 5). *Leptobrachium tagbanorum* differs from *L. lumadorum* by having a larger female body size (Tables 4, 6), a dorsum tan to brown with indistinct darker blotches (vs. solid gray-black with brown and tan blotches on anterior portions of body, head, and interorbital region), more extensive interdigital webbing and much less pronounced inner metatarsal tubercle (Fig. 9), and its unique advertisement call (Fig. 6; Table 5). The new species differs from *L. hasseltii* by a larger body size in females (Tables 4, 6), a more uniform tan dorsal coloration (vs. dark spots and blotches on tan or pale brown; Fig. 8), and its unique advertisement call (Fig. 6). From *L. abbotti*, the new species differs by having a gray venter with white spots on warts, a white sternal region, and dark marbling on throat (vs. venter boldly patterned black and white). From *L. montanum* and *L. gunungense*, the new species differs by the presence of a deep blue scleral arc under the eyelid (vs. a bold white arc across the top of the eye), having many narrow transverse bars of the limbs (vs. one or two broad bars), and a nearly uniform tan dorsum (vs. dorsum boldly patterned with dark blotches). From *L. nigrops*, the new species differs by having a larger body size (Table 6, vs. *L. nigrops*; males 30–45 mm; females 39–50 mm), the presence of a deep blue scleral arc under the eyelid (vs. absent), and the absence of circular flank spots (vs. distinct black flank spots present). Additionally *L. nigrops* appears unique in the possession of sharp, posteriorly recurved terminal phalanges (Inger and Stuebing, 1997). From *L. hendricksoni* and *L. smithi*, the new species differs by the presence of solid black eyes (vs. eyes with bright orange or orange-red upper half of iris, above pupil), and absence of circular flank and posterior thigh spots (vs. distinct black flank and posterior thigh spots present).

Ecology and natural history.—We have observed specimens of the new species at a variety of sites, all characterized by the presence of some forest cover. The new species seems to be most common in swampy areas adjacent to rivers or along secondary stream banks when water levels are low and ambient noise is minimal. *Leptobrachium tagbanorum* does not form choruses but instead loosely aggregates in groups of 3–10 calling males spread over 20–50 m, with individual males separated by approximately 2–10 m. All individuals (including calling males) observed were exposed on forest floor soil, on rocks in dry stream-beds, or on exposed soil at the base of overhanging stream banks.

Other anuran species observed in sympatry with *L. tagbanorum* on Palawan Island include *Megophrys ligayae*, *Barbourula busuangensis*, *Rana* (*Hylarana*) *moellendorffi*, *Rana* (*Sanguirana*) *sanguinea*, *Occidozyga laevis*, *Starois natator*, *Limnonectes acanthi*, *L. palavanensis*, *Rhinella marina* (introduced), *Ingerophrynus philippinicus*, *Pelophryne albotaeniata*, *Hoplobatrachus rugulosus* (introduced), *Fejervarya vittigera*, *Polypedates leucomystax*, *P. macrotis*, *Rhacophorus everetti*, *Nictixalus pictus*, *Philautus longicrus*, *Chaperina fusca*, *Kaloula picta*, *K. baleata*, *K. pulchra* (introduced), and *Ingerana mariae*.

Distribution.—The new species is known only from the Palawan PAIC (Fig. 1): Palawan Island including the municipalities of Irawan, Aborlan, Quezon, Nara, Puerta Princesa, and Brookes Point. Surveys of Dumaran, Balabac, Culion, Coron, and Busuanga have produced no specimens of this species.

Etymology.—The specific epithet is chosen from the term collectively referring to the indegenous peoples of northern and central Palawan Island, the *Tagbanua*. From the municipalities of Quezon, Aborlan, and Puerto Princesa, the *Tagbanua* are known for their religious system that incorporates beliefs in animal spirits and deities found in the natural environment, mountainous regions, and forests. Although the entirety of Palawan Island is a protected area, the forested ancestral tribal domains of the *Tagbanua* are now under increasing threat of destruction due to logging and, more recently, widespread mining in virtually all municipalities on the island.

Leptobrachium **lumadorum** *sp. nov.*

Figs. 2, 8, 9

Holotype.—PNM 9561 (formerly KU 314133, Field number RMB 10182), adult male, from the Philippines, Mindanao Island, Zamboanga Del Sur Province, Zamboanga City, Barangay Baluno, Pasonanca Natural Park, Sitio km 24 (N 07.108°, E 122.0289° WGS 84), collected 14 July 2008 by RMB, CDS, L. Welton, and J. W. Phenix.

Paratopotypes.—Philippines, Mindanao Island, Zamboanga City Province, Barangay Baluno, Pasonanca Natural Park, Sitio km 24, six adult males and two adult females, collected by RMB, CDS, L. Welton, and J. W. Phenix: KU 314134, 314138–314140 (15 July 2008), 314135–314137 (14 July 2008), 314141 (16 July 2008); seven metamorphic tadpoles: KU 314142–314144 (12 July 2008), 314145–314148 (16 July 2008); Upper Cauit, female, collected by R. Sison: PNM 3324 (May 1993).

Other paratypes.—Mindanao Island, Misamis Oriental Province, Municipality of Gingoag City, Barangay Limotan, Sitio San Isidro, Mt. Balatucan Range National Park (N: 08.732°, E: 125.004°), 1435 m, three males and one female, colleted by ACD: KU 319773–319776 (8–19 November, 2008); Misamis Occidental Province, 3 km NW of Masawan, S bank of Dapitan River (N: 8.348°, E: 123.587°), female, collected by Q. Alcala and party: CAS-SUA 19971 (24 April 1959); Masawan area (N. 8.304°, E: 123.604°), female, collected by Q. Alcala and R. Empeso: CAS-SUA 19953 (15 April 1959); CAS-SUA 20153; 6 km SE of Buena Suerte, Gumay Barrio (N: 8.309°, E: 123.517°), female, collected by B. Lusoc, T. Serate and M. Pinero: CAS-SUA 19984 (28 April 1959); Cuyot Creek (N: 8.318°, E: 123.519°), two males, collected by ACA and party: CAS-SUA 20163–64 (8 April 1959); Davao City Province, Mt. Apo, a male and a female, collected by E. Mearns: USNM 34786–87 (no date); Bukidnon Province, Municipality of Libona, Barangay Silipan, Mt. Tubukan South Mahayahay, male, collected by ACD: PNM 6616 (19 September 1996); Bukidnon Province, Municipality of Sumilao, Barangay Lupiagan, a male and a female, collected by N. Ingle: FMNH 260363, 260365 (19–21 February 1999); Cotobato Province, Municipality of Upi, Barangay Burungkot, three males, collected by P. Anonuevo: FMNH 50921–23 (2 January 1947); Davao Del Norte Province, 60 km S Bislig, an adult male and two adult females, collected by B. Smith: LSU 41886–41888 (27 April, 30 June, and 15 August 1982); Davao Oriental Province, 35 km S, 10 km W Bislig, two juveniles of undetermined sex, collected by S. Babao: LSU 41889, 41890 (4 September 1982); Davao City Province, Mt. Apo, Minit, male, collected by H. Hoogstral: FMNH 50919 (20 November 1946); Davao Del Sur Province, Municipality of Toril, Barangay Upper Baracatan, Sitio San Roque, male, collected by RMB: TNHC 59872 (19 July 1996); Zamboanga del Norte Province, Municipality of Pinan, 6 km SE of Buena Suerte, Gumay Barrio (N: 8.304°, E: 123.517°), a male, collected by ACA and party, 8 May 1959: Zamboanga City Province, Barangay La Paz, Sitio Nancy, Pasonanca Natural Park (N: 07.085°, E: 122.0127°), 1130m, 20 metamorphs and juveniles of undetermined sex, four adult males and two adult females, collected by RMB, ACD, and C. R. Infante: PNM 9642–9647, KU 319669–319688 (31 March–5 April 2009); Barangay Tulosa, Sitio Santa Clara, Cabo Negro Outpost, Pasonanca Natural park (N: 07.108°, E: 122.119°), 620 m, six metamorphs, four juveniles, six adult males and four adult females, collected by RMB, ACD, and C. R. Infante: PNM 9648–54, KU 319692–708.

Referred specimens.—Mindanao Island, Misamis Occidental Province, 8 km SE of Masawan, headwaters of Dapitan River (N: 8.326°, E: 123.611°): CAS-SUA 19735, 19836; New Pinan, 14 km SE of Buena Suerte, Masawan (N: 8.304°, E: 123.588°): CAS-SUA 19698, 19701, CAS 138429, 180294–300; Zamboanga Del Sur Province, Municipality of Baluno, Upper Cauit: PNM 3339; Municipality of Katipunan, 30 km up Dicayo River: FMNH 69057; Cotobato Province Upi, Burungkot: FMNH 50920; Bukidnon Province, Municipality of Sumilao, Barangay Lupiagan: FMNH 260364; Mindanao Island, no specific locality: FMNH 50924–28, 63205, 50916–17; Mindnao Island "San Ramon:" FMNH 14893; "Cotabato Coast" (= South Cotobato or Sultan Kudarat Province), Municipality of Tatayan: MCZ A-23164–65; Basilan Island, Basilan Province, Municipality of Abung-abung: MCZ A-23162; Dinagat Island, Dinagat Province: PNM 2252.

Diagnosis.—A species of *Leptobrachium* characterized by a combination of the following characters: (1) moderate body size (Table 1), (2) protrusion of dark supratympanic fold coloration posteriorly to form a dark tympanic spot that covers, or nearly covers, the tympanic annulus (Fig. 2), (3) a broad canthal stripe (Table 6), (4) predominant dorsal color pattern with a nearly homogenous dark gray-black dorsum with brown blotches limited to anterior portions of body, head, and interorbital region (Figs. 2,8), (5) venter gray with minute white spots on warts, solid light gray, or with dark throat, (6) entirely black eyes with a deep blue scleral arc under the eyelid (visible in corners of eye and when palpebrum is retracted), and (7) several characters related to its unique advertisement call (Table 5; Fig. 7). A summary of the distribution of character states distinguishing *L. lumadorum* from the remaining Philippine species and *L. hasseltii* is presented in Table 6 and detailed comparisons to Philippine and Sunda Region species are provided in the Comparisons section, below.

Description of holotype.—A mature male, in excellent condition (Fig. 8), with only a small post-axiallary incision (small piece of liver removed before preservation). Habitus stocky, head length 90.4% of head width, head as wide as body neck indistinct; snout rounded to subacuminate in lateral aspect, and protruding slightly beyond lower jaw, nearly rounded in dorsal view; nostril much closer to tip of snout than to anterior corner of eye; eyes protruding well beyond silhouette of head in dorsal aspect (Fig. 8), well above dorsal surface of head in profile; lips not flared and only very slightly swollen, not extending beyond most lateral edge of orbits when viewed in dorsal aspect; canthus rostralis sharply distinct, constricted behind nostrils in dorsal view; loreal region oblique, only slightly concave; eye diameter 73.6% of snout length; pupil vertically elliptical in preservative; iris dark gray; interorbital region 106.2% of eye diameter; nostrils laterally protuberant, oriented posterolaterally; eye–narial distance 3.6 times longer than distance from nostril to tip of snout; tympanum obliquely ovoid, longer axis oriented dorsoanteriorly and posteroventrally; tympanic annulus weakly distinct, 48.4% of eye diameter; dorsal edge of tympanic annulus slightly concealed by supratympanic fold, the latter extending from posterior corner of eye to supra-axillary region; pineal ocellus absent.

Tongue very large, nearly circular (widest posteriorly), with deep posterior groove, enlarged posterior papillae, and narrow anterior attachment; choanae situated at anterolateral edge of palate, not concealed by narrow palatal shelf of the maxillae, round, small, widely separated by a distance six to seven times greater than their diameters; dentigerous process of vomer indistinct, not protruding through buccal mucosa, vomerine teeth absent; vocal sacs openings large slits on the floor of the buccal cavity, on lateral corners of the angle of jaws.

Forelimbs, digits, manus and pes well developed (Fig. 8) hindlimbs proportionally short, moderate to poorly developed; manus length 59.9% of pes length; pes length 103.8% of tibia length; femur 113.8% of tibia length; tibia length 37.5% of snout–vent length; digits of manus slender, long.

Tips of all fingers bluntly rounded, not swollen or appreciably expanded, relative finger lengths I = II = IV < III (Fig. 9); intradigital webbing absent; broad dermal flange bordering lateral edges of all fingers; subarticular tubercles indistinct, reduced to low, irregular, warty tubercular ridges that extend the length of fingers I–IV; supernumerary tubercles absent; inner thenar surface characterized by a long, velvety tubercular surface but no distinct tubercles; palmar tubercle divided into inner and outer metacarpal tubercles (two oval subequal palmar tubercles in contact on medial surfaces); inner tubercle large, oblong, convex, with sharp anteroventrally protrusion to a spade-like surface; outer metacarpal tubercle narrower, elongate, just over than half the size of inner metacarpal tubercle; nuptial pads absent, forearms moderate, musculature not hypertrophied.

Tips of toes rounded, not expanded, relative lengths I < II = IV < III < IV (Fig. 9); lacking circummarginal grooves or supraarticular cutaneous flaps above phalangeal articulation; plantar surface of foot smooth, lacking distinct subarticular tubercles under digits; supernumerary tubercles absent; interdigital webbing thick, acrenulate, homogeneous, modal webbing formula of toes (Savage and Heyer, 1969, 1997): **I** 1–1.5 **II** 1–2.5 **III** 2–3.5 **IV** 3.5–1 **V**.

Inner metatarsal tubercle distinct, raised, irregularly ovoid to subtriangular, situated at base of Toe I, with sharp plantar spade-like edge; metatarsal tubercle half as long as Toe I; outer metatarsal tubercle absent; heels nonoverlapping when legs are held at right angles to the body; cloacal region glandular, with low tuberculate warts; supracloacal flap absent.

Skin on dorsum and dorsal surfaces of limbs with fine scattering of fine, raised dermal ridges and a slightly glandular texture; skin of flanks, chin, throat, ventral surface of body, and ventral and posterior surfaces of thigh with dense aggregation of slight dermal asperities and minute warts; skin on ventral surfaces of forelimbs and tibiotarsus smooth; enlarged, round circular axillary gland present ventrolaterally, immediate posterior to forelimb; moderate, subcircular femoral glands present on posterior surface of each thigh; skin on surface of pectoral and femoral glands smooth.

Measurements of holotype.—Snout–vent length 48.0; head length 19.2; snout length 7.1; interorbital distance 6.5; internarial distance 4.5; eye diameter 6.4; tympanum diameter 3.1; head width 20.8; upper arm length 9.6; forearm length 13.8; femur length 19.4; tibia length 17.2; tarsus length 10.5; pes length 16.2; manus length 11.2; Toe 4 length 9.9; Finger 1 length 5.1; Finger 3 length 8.1.

Color of holotype in preservative.—(Fig. 8) Dorsal coloration of the holotype is nearly uniform dark gray-black, with darker interorbital bar, slightly darker blotching on posterior portions of the head, a faintly darker series of mid-vertebral blotches stretching to the sacral region, and snout slightly lighter than rest of body; flanks fade from very dark gray (dorsally), fading to light gray (ventrally), with small, distinct, scattered black and cream spots and dirty white tipped dermal tubercles surrounded by black oscelli; dorsal surfaces of forelimbs and hindlimbs dark gray-black with darker transverse bars (most evident on lateral surfaces of limbs where ground coloration is lighter), transverse bars reddish brown on anterior surfaces of thigh; posterior surfaces of thigh with brown transverse bands dorsally, solid dark gray ventrally, with minute white spots; eye black with narrow light blue crescent on outer, dorsal margin of eyeball (below retracted palpebrum); upper 80% of tympanic annulus covered with black spot; lateral surfaces of head slightly lighter than dorsal surfaces; canthus rostralis bordered ventrally by a narrow dark brown line; a pair of narrow black lines travel from each nostril to the tip of the snout; a thicker dark gray-black line from the nostril, through loreal region, terminating in a widened blotch in the labial region; a wide dark gray-black blotch bisects the suboccular region; chin and throat heterogeneous medium dark gray, owing to gray gular coloration and a fine speckling of tiny white spots; sternal region nearly white, with two dark brown clusters of pigment immediately anterior to forelimb insertions; venter medium gray, darker laterally towards flanks; ventral surfaces of thighs uniform solid dark gray, with minute white spots on posterior margins; ventral surfaces of tibiotarsus medium gray with white irregularly blotched marbling; ventral surfaces of hands medium gray with white palmar tubercles and finger tips; ventral surfaces of feet medium gray with light gray inner metatarsal tubercle and light gray toe tips; femoral glands immaculate white.

Color in life.—Based on field notes by RMB and color images of holotype in life, before preservation (Fig. 2); color differences are extreme between live and preserved specimen. In life, holotype ground coloration variable, with dark gray dorsum, fading to light gray laterally; distinct dark chocolate-brown mid-dorsal blotches, concentrated most intensely on posterior portions of head and scapular region; dark brown head coloration strongest in the interorbital region and dorsal surfaces of the snout; these areas bordered anteriorly with light tan interorbital and anterior snout coloration; mid-dorsum dark brown posteriorly, fading and broken into large round dark brown spots, surrounded with fine black borders; lateral portions of the head gray except for three darker markings, transversing the side of the snout dorsoventrally, and terminating in the labial region as dark lip bars; these darker markings include chocolate brown spots under the snout's tip, a large blotch beneath beneath nostrils, and a wide suboccular blotch below orbit; canthal stripe thick, brown; supratympanic fold bordered posteriorly with narrow black line; large dark brown spot covers dorso-posterior edge of the tympanic annulus and most of the tympanum; iris color was dark lavender brown, dorsal margin of the eyeball surrounded with deep, vibrant blue eye-ring under retracted palpebrum; only visible in corners of eyes in relaxed state; dorsal surfaces of limbs, hands and feet light orange-brown, crossed by medium brown transverse limb bars; lateral surfaces of limbs were light gray (similar to dorsal body coloration) and traversed with same dark brown bars of anterior surface of the limbs; ventral chin, throat, and body color medium gray, owing to infusion of tiny cream spots, usually associated with dermal warts, on dark gray ground coloration; sternal region nearly immaculate light cream-gray; flanks and ventral surfaces of fore- and hindlimbs marbled dark and light gray; thighs and tibia medium gray on posterior surfaces, gray with black bars on anterior surface, dark gray with tiny cream-white spots on posterior surfaces; femoral and humeral glands were creamy pale yellow. Finger and toe tips were flat gray; palmar and plantar tubercles, and subarticular tuberculate ridges velvety gray on their ventral surfaces.

Variation.—There is little color variation in the type series. A few specimens exhibit a markedly lighter gray dorsum and a reduction in number and intensity of darker dorsal blotches (KU 314138; CAS-SUA 19953, 20158), several specimens have a black dorsum with blotches absent (KU 314134–314141; PNM 3324, PNM 6616; FMNH 50922; CAS 60190), several exhibit widespread dorsal blotches (CAS-SUA 19984, 19971) and many others have a dark dorsum with pale brown blotches limited to the posterior portions of the head, or the interorbital region (CAS-SUA 20163–64; FMNH 50919, 50921, 50923, 50957, 260363–65; PNM 9561 [holotype]; Figs. 2, 8). Most specimens have dark transverse bars on dorsal surfaces of many segments of the fore- and hindlimbs. The tibial segments of the hindlimbs have 4–6 bars ($\bar{x} = 4.7 \pm 0.75$ SD; $n = 42$). Exceptions include a few specimens that lack dark forearm bars (KU 314134, 314140) and several that lack dark bars on the dorsal surface of the tibia (CAS 60190; USNM 34786–87; MCZ A-23162–63; KU 314134, 314135, 314137, 314138, 314140). Western Mindanao populations (as represented by Zambonga specimens at KU, MCZ, and CAS) appear to lack dark transverse bands on the dorsal surface of the tibia. Nearly all specimens have the tympanum covered by a large spot extending from the posterior edge of the supratympanic fold; in a few specimens (e.g., CAS-SUA 20158, 19984; KU 314138, PNM 9561 [holotype]) this character is slightly reduced.

Canthal stripe width varied from 1.1–2.6 mm ($\bar{x} = 2.1 \pm 0.45$ SD; $n = 37$). In most specimens, lateral portions of the head are traversed by three dark markings (see holotype color description) that terminate posteriorly in the labial region, resulting in three distinct bars on the lips. In specimens with extremely dark dorsal coloration, these markings are partially obscured by dark ground coloration but can be faintly ascertained. The predominant ventral color pattern is nearly solid gray with minute white spots on warts; spotting may be absent in sternal region (immaculate white or cream) and most intense in groin. Exceptions include specimens with pure white venters (CAS-SUA 19984, 19953, 20163–64), light gray venters (CAS 60190; PNM 2252), or gray with dark scattered flecks (FMNH 260363, 50919–23). Some males have dark gray to black throats (PNM 6616; FMNH 260365), as do some juveniles and metamorphs (PNM 2252; FMNH 260364).

We observed no variation in skin texture, subdigital tuberculation, or extent of interphalangeal webbing. Pectoral glands are largely invariant in size, color, and shape, but femoral glands vary from tiny and barely perceptible (KU 314139), to small, and horizontally elongate (KU 314134, 314137, 314140), to moderate and round (KU 314135, 314138), or irregularly-shaped and even fragmented (KU 314136, 314141).

Aside from sexual size dimorphism (Table 6), no subsamples or subpopulations exhibit detectable differences in size or body proportions. Mean female-biased sexual size dimorphism in the new species is 1.25 (female:male snout–vent length; min–max size disparity = 1.23–1.29). Seven paratypes are metamorphic tadpoles. KU 314143 and 314144 have well developed hindlimbs, forearms covered by the non-ruptured operculum, and tail reabsorption had just begun at the time of preservation. KU 314142, 314145–314148 exhibit fully formed forelimbs and substantial tail reabsorption.

Morphometric data exhibited in the type series of *L. lumadorum* are summarized in Table 4.

Advertisement call.—The following description is based on two recording segments from Mindanao Island. One unvouchered recording was collected by ACD in March 2004 (5 calls over 103 s at 25.1 C) on Mt. Hamiguitan, extreme eastern Mindanao, and the other by RMB on 14 July 2008 (paratype KU 314139; 17 calls over 310 s at 22.4 C) at Barangay Baluno, Pasonanca Natural Park, Zamboanga City, western Mindanao. These recordings vary only in numbers of notes per call.

The call of *L. lumadorum* (Fig. 7) is a series of low frequency grunts, starting with 1–3 slow chuckling notes, with successive notes becoming increasingly brief, grunt-like, and terminating in a final rapid laughing bout: “Wherrrr… wherrr…wher, wher, wer-wer-werwerwer!” The call consists of 5–10 (but usually seven) notes per call. The call’s first two or three notes are elongate and differentiated from the remainder of the call (Fig. 7C, D).

Intercall intervals range from 16–30 s ($\bar{x}$ = 21 ± 6.2 SD; *n* = 4) for the unvouchered recording and 6–20 s ($\bar{x}$ = 11.7 ± 4.7 SD; *n* = 16) for KU 314139. Calling rate for the unvouchered specimen is 0.067 calls/s; the calling rate for KU 314139 is 0.065 calls/s. The unvouchered specimen averaged 7.5 notes per call (± 1.2 SD; range 7–10 notes/call; *n* = 6) and KU 314139 averaged 6.2 notes per call (± 1.1 SD; range 5–8 notes/call; *n* = 10). Call length varies from 2.6–4.2 s ($\bar{x}$ = 3.5 ± 0.6 SD; *n* = 6) for the unvouchered specimen and 1.0–2.6 s ($\bar{x}$ = 1.7 ± 0.52 SD; *n* = 16) for KU 314139.

Note duration is heterogeneous, and steadily declines over the call. Most calls begin with 1–3 drawn out, elongate vibrational notes with multiple subpulses (Fig. 7B–D), lasting approximately 400–600 ms in the unvouchered specimen and 200–250 ms for KU 314139. During the course of the call, note duration steadily declines until the final notes which last only 225–250 ms in the unvouchered specimen and 70–90 ms for KU 314139. Normal internote intervals are largely invariant, and range from 210–230 ms ($\bar{x}$ = 221 ± 2.1 SD; *n* = 39) for the unvouchered specimen and 195–215 ms ($\bar{x}$ = 203 ± 3.2 SD; *n* = 89) for KU 314139. Within calls, note repetition rate is 1.8–2.1 notes/s ($\bar{x}$ = 1.9 ± 0.1 SD; *n* = 4) for the unvouchered specimen and 2.0–3.1 notes/s ($\bar{x}$ = 2.4 ± 0.3 SD; *n* = 16) for KU 314139.

Amplitude across individual notes is relatively homogeneous, with the only variable pattern being a slow rise in amplitude at the first note of the call. In all other notes, call energy is characterized by an immediate rise to peak amplitude which is held steady for the duration of the note, followed by a sharp

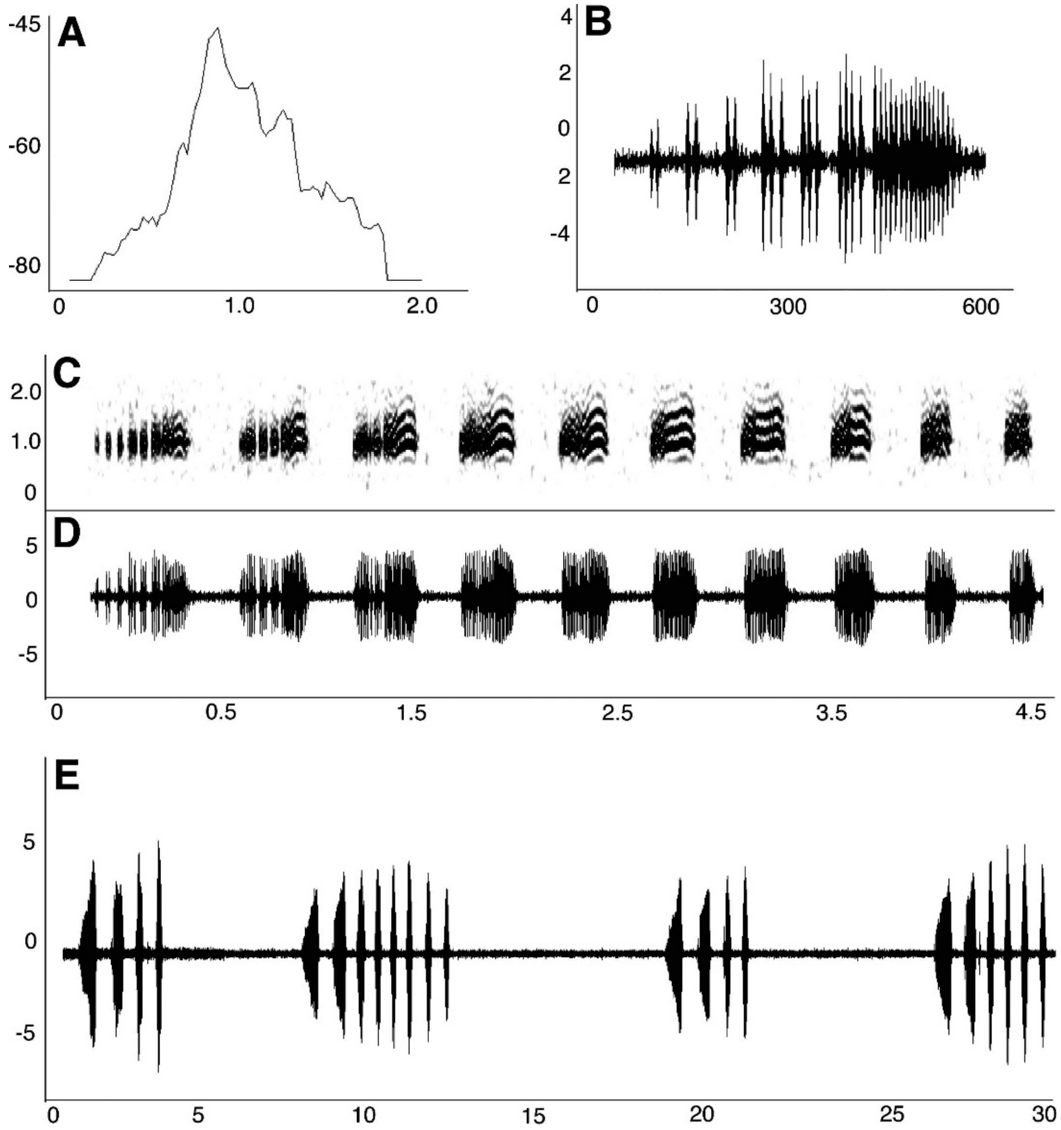

FIG. 7.—The advertisement call of *Leptobrachium lumadorum* (holotype, PNM 9561) recorded 7 March, 2008; 26.9°C ambient temperature). Analyses include: a power spectrum (A: Fast Fourier Transformation; relative amplitude vs. frequency in kHz) calculated notes 4–5 in C; a 200 ms expanded waveform (B: relative amplitude vs. time in ms) of the first note in C; a 4.5 s audiospectrogram (C: frequeny in kHz vs. time in s) and oscillogram (D: relative amplitude vs. time in s) of a typical call; and a 30 s oscillogram (E: relative amplitude vs. time in s) of four tightly spaced calls.

decline to ambient levels, resulting in a square amplitude envelope for each note (Fig. 7D). Across calls, a gradual rise to peak amplitude is achieved by the fifth or sixth note, after which amplitude usually declines gradually per note to the end of the call (Fig. 7E). Amplitude of the first note is approximately 80–95% of the peak amplitude for the call. Individual notes have two components: an initial prefix of harsh tightly-spaced individual pulses (Fig. 7C, D), followed by a transition to a low frequency tonal suffix (Fig. 7C).

Energy in the call consists of a single low, dominant frequency band spanning approximately 0.5–1.5 kHz for both specimens (peak frequency 0.86 kHz for the unvouchered specimen and 0.91 kHz for KU 314139). In a few audiospectrograms, faint harmonics are visible at one and two multiples of the fundamental (approximately 2 and 4 kHz, respectively).

Comparisons.—Our estimate of phylogeny indicates that *L. lumadorum* is a divergent lineage, sister to the clade consisting of Bornean and Sumatran species *L. abbotti*, Bornean species *L. montanum* and *L. gunungense*, and Philippine species *L. mangyanorum* and *L. tagbanorum*. Additionally, genetic data (Table 3) indicate significant genetic divergence between *L. lumadorum* and other Philippine, Bornean, and Indonesian species. From *L. montanum* and *L. gunungense*, *L. lumadorum* differs by the presence of a deep blue scleral arc under the eyelid (vs. a bold white arc across the top of the eye), many narrow transverse bars of the limbs (vs. fewer, broader bars), a predominant ventral color pattern of gray with white spots on warts, and darker throats in some males (versus uniform dirty gray). The new species differs from *L. abbotti* by having a smaller maximum body size (Table 6; vs. *L. abbotti* males 45–75 mm; females 60–95 mm), a gray ventral coloration with white spots on warts and a dark throat (vs. venter boldly patterned black and white), and a smaller maximum body size (Table 6; vs. *L. abbotti* males 45–75 mm; females 60–95 mm). *Leptobrachium lumadorum* differs from *L. mangyanorum* by a tendency towards a larger maximum body size (Table 6), by dark supratympanic fold coloration protruding extensively onto the tympanum (vs. absence or extreme reduction in protrusion of dark supratympanic fold coloration onto the tympanum), presence of a broader and bolder canthal stripe (vs. absent or highly reduced), having a nearly uniform gray-black dorsum with brown and tan blotches on anterior portions of body, head, and interorbital region (vs. more variable dorsal color pattern with semicircular brown spots with black borders), and its unique advertisement call (Fig. 6; Table 5). From *Leptobrachium tagbanorum*, the new species differs by having a slightly larger body size in males and a significantly larger body size in females (Tables 4, 6), a nearly uniform gray-black dorsum with brown and tan blotches on anterior portions of body, head, and interorbital region (vs. solid tan or brown with diffuse, irregular brown blotches), and its unique advertisement call (Fig. 6; Table 5). *Leptobrachium lumadorum* differs from the distantly allopatric *L. hasseltii* by having a darker, more uniform dorsal coloration in life (Fig. 2), and its unique advertisement call (Fig. 7; Table 5). From *L. nigrops*, the new species differs by the presence of a deep blue scleral arc under the eyelid (vs. absent), and absence of circular flank spots (vs. distinct black flank spots present). Additionally, *L. nigrops* has sharp, posteriorly recurved terminal phalanges (Inger and Stuebing, 1997). From *Leptobrachium hendricksoni* and *L. smithi*, *L. lumadorum* differs by the presence of solid black eyes (vs. eyes with bright orange or orange-red upper half of iris, above pupil), and the absence of circular flank and posterior thigh spots (vs. distinct black flank and posterior thigh spots present).

Ecology and natural history.—We have collected or observed specimens of the new species in low-lying swampy areas in saddles between ridges in the foothills of Mt. Apo (Davao City Province, eastern Mindanao), along small forested, densely vegetated stream banks at mid-elevations (800–900 m) on the southern end of the mountains of the Zamboanga Peninsula, and in the foothills of Mt. Busa, South Cotobato Province, southern Mindanao. At the beginning of the rainy season (July–September) the new species does not form choruses but instead loosely aggregates in groups of calling males spread over 50–100 m of forest, with individual males separated by approximately 5–20 m. All individuals we observed were in leaf litter or exposed soil on the forest floor, usually associated with exposed tree roots, cavities beneath boulders, over-hanging stream banks, or other cover.

Other anuran species observed in sympatry with *L. lumadorum* include *Megophrys stejnegeri*, *Rana* (*Hylarana*) *grandocula*, *R.* (*Hylarana*) *everetti*, *R.* (*Hylarana*) *albotuberculata*, *Occidozyga laevis*, *O. dimunitiva*, *Starois natator*, *Limnonectes magnus*, *L. diuatus*, *L. ferneri* (Siler et al., 2009), *L. leytensis*, *L. parvus*, *Rhinella marina* (introduced), *Ansonia muelleri*,

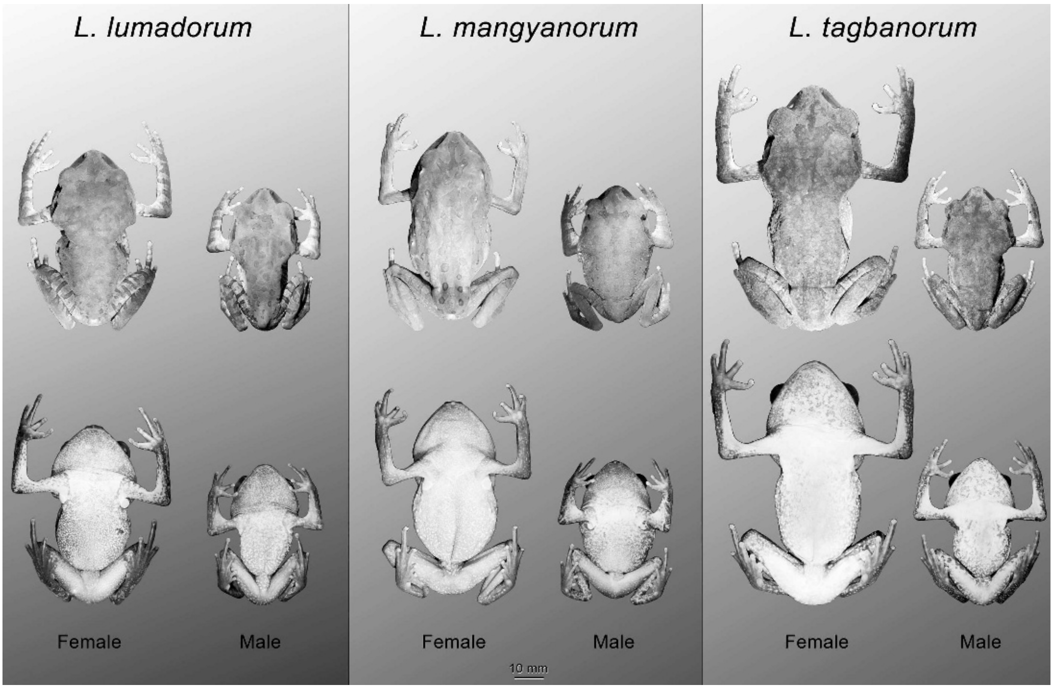

FIG. 8.—Dorsal (above) and ventral (below) views of female (larger, on left) and male (smaller, on right) specimens of each species. Specimen pairs, from left to right, include: *Leptobrachium lumadorum* female paratype (KU 314141) and male holotype (PNM 9561); *Leptobrachium mangyanorum* female paratype (KU 303272) and male holotype (PNM 9559); and *Leptobrachium tagbanorum* female paratype (KU 309075) and male holotype (PNM 9560).

A. mcgregori, *Pelophryne brevipes*, *Hoplobatrachus rugulosus* (introduced), *Fejervarya vittigera*, *Polypedates leucomystax*, *Rhacophorus pardalis*, *R. appendiculatus*, *R. bimaculatus*, *Nictixalus spinosus*, *Philautus leitensis*, *P. worcesteri*, *P. acutirostris*, *P. surrufus*, *P. poecilius*, *Kaloula picta*, *K. conjuncta meridionalis*, *Kalophrynus pleurostigma*, *Chaperina fusca*, *Oreophryne annulata*, *Platymantis* cf. *corrugatus*, *P.* cf. *dorsalis*, *P. guentheri*, and *P. rabori*.

Distribution.—The new species is known only from southern portions of the Mindanao PAIC (Fig. 1): Basilan and Mindanao islands, including the provinces of Basilan, Zamboanga del Sur, Zamboanga del Norte, Misamis Occidental, Davao City, Agusan del Sur, South Cotobato, Bukidon, and Sultan Kudarat. A single metamorph from Dinagat Island, apparently representing this species, is deposited at the National Museum of the Philippines (PNM 2252; no specific locality data) but earlier surveys failed to detect this species presence on Dinagat and and nearby Siargao islands (Ross and Lazell, 1990). Our own recent surveys (February and July, 2007) in Loreto, Dinagat Island, also failed to uncover this species, suggesting to us that the PNM record may be in error or, if this species does occur on Dinagat, it may occur at extremely low abundances or be patchily distributed.

The species is conspicuously absent from Samar, Leyte, Bohol, and smaller islands associated with these large landmasses. Brown and Alcala's (1970; duplicated in Dubois and Ohler, 1998) record of this species on Bohol may be in error; no specimens from Bohol were found in any collections canvassed by us and all recent fieldwork has failed to produce specimens of this species.

Etymology.—The specific epithet is chosen from the Cebuano term *Lumad*, meaning indigenous, and collectively referring to at least 22 tribal groups (e.g., the Ata, Badjao, Bagobo, Banwaon, B'laan, Bukidnon, Dibabawon, Higaunon, Kalagan, Mamanwa, Mandaya, Mangguwangan, Manobo, Mansaka, Sama, Subanen, Tagakaolo, Tausug, T'boli, Teduray, Ubo, and the Yakan) of Mindanao Island. Although the

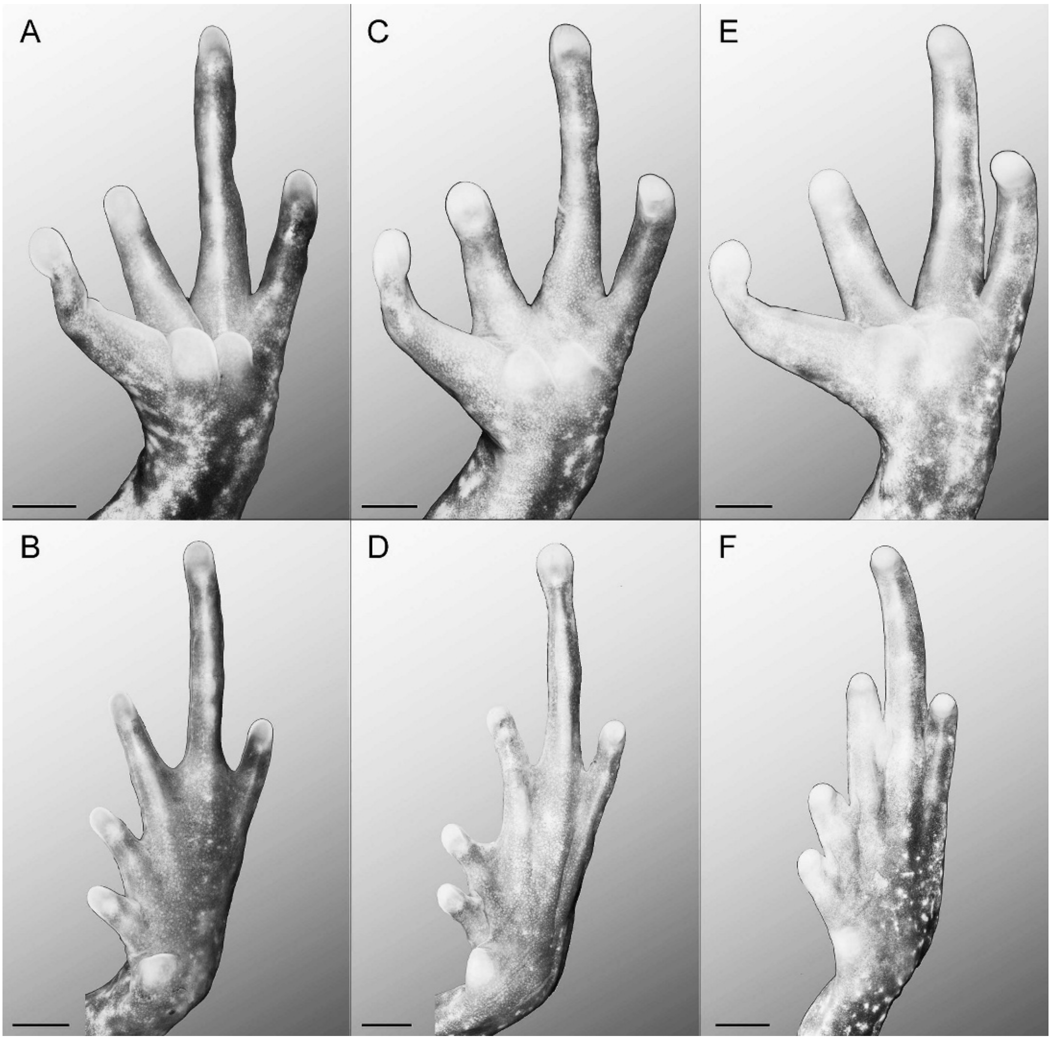

FIG. 9.—Palmar views of hands (upper) and plantar views of feet (lower) of the holotypes of *Leptobrachium lumadorum* (A, B; PNM 9561), *L. mangyanorum* (C, D; PNM 9559) and *L. tagbanorum* (E, F; PNM 9560). Scale bars = 2mm.

cultural, historical, and linguistic diversity of the tribes of Mindanao defy many generalizations, most groups share strong cultural value systems that include self-determination, rich cultural heritage and shared identity, and the desire to secure forested ancestral homelands from the environmental destruction brought about by mining and logging.

DISCUSSION

Our data reinforce the degree to which basic biodiversity surveys, natural history studies, and careful taxonomic reappraisals of polytypic taxonomy are still badly needed in the Philippines (Brown, 2007; Brown and Diesmos, 2002; Inger, 1954). Our results also underscore the need to consider non-traditional characters in taxonomic assessments, especially revisionary studies that involve analyses of "widespread species" in archipelagoes. Such groups have become increasingly appreciated for their tendency to harbor multiple cryptic but evolutionarily distinct lineages (Brown and Richards, 2008; Brown et al., 2006*a*, 2006*b*; Evans et al., 2003; Gaulke et al., 2007; Stuart et al., 2006).

Recognition of morphologically indistinct cryptic species has become an important part of the estimation of true Southeast Asian herpetological biodiversity (Bickford et al., 2007; Brown, 2004; Brown and Diesmos, 2009; Brown et al., 2009). In these studies, characters other than external morphology (e.g., advertisement calls, ecological differences, subtle differences in body size and proportions, and DNA sequence data) are invaluable for the recognition of diversity in amphibian systematics (Inger et al., 2009; Siler et al., 2007; Stuart et al., 2006).

Recognition of *Leptobrachium* from the Mindoro, Palawan, and Mindanao PAICs as distinct evolutionary species is nonproblematic because the history of isolation of each of these geological platforms is so well documented (Brown and Diesmos, 2002; Hall, 1996, 1998; Voris, 2000). Thus, recognition of each faunal region's endemic species is consistent with available information that precludes the possibility of a dry land connection for dispersal that might afford an opportunity for gene flow and reticulation between the species (Brown and Diesmos, 2002; Brown and Diesmos, 2009; Voris, 2000). Each species is phenotypically and genetically distinct, acoustically and morphologically diagnosable, and allopatric. As such, each is definable as a unique evolutionary lineage segment with a distinct history and evolutionary predictable fate (i.e., continuation as allopatric lineages). Thus, we reject the hypothesis of conspecificity of Philippine + Javan + Balinese populations and restrict *L. hasseltii* to populations from Java, Bali, and associated small islands. We also emphasize that the pattern of endemism in Philippine *Leptobrachium* is entirely consistent with recent phylogenetic and taxonomic studies of other amphibian and reptile species (e.g., Brown and Diesmos, 2002; Brown and Guttman, 2002; Evans et al., 2003; Gaulke et al, 2007; McGuire and Kiew, 2001), most of which have demonstrated patterns of faunal endemism that are often strikingly consistent with the isolation of the Philippine PAICs (Brown and Diesmos, 2002, 2009; Brown et al., 2002). Recognition of distinct and diagnosable species on these isolated PAIC landmasses is also in accordance with the basic tenants of all modern lineage-based species concepts (de Queiroz, 1998, 1999; Frost and Hillis, 1990; Simpson, 1961; Wiley, 1978). We are entirely confident in our taxonomic decisions and note that the only alterations to our new taxonomy that we could imagine would be the addition of more discoveries of species on small islands or isolated mountain ranges so far unsurveyed by herpetologists.

It comes as no surprise that the Mindoro, Palawan, and Mindanao faunal regions each harbor genetically, acoustically, and morphologically distinct lineages of frogs of the genus *Leptobrachium*. Rather, we find it surprising that amphibian taxonomists were content, for so long, to consider these populations conspecific with each other, and with *Leptobrachium hasseltii* from the distantly allopatric islands of Java and Bali, Indonesia (Brown, 2007). We acknowledge that several herpetologists before us have predicted the eventual recognition of Philippine "*L. hasseltii*" as full species (personal communication with W. C. Brown, and R. I. Crombie). Dubois and Ohler (1998) suggested that Philippine *L. "hasseltii"* may not be conspecific with Javan populations. Iskandar and Colijn (2000) suggested that Philippine populations might be referable to *L. abbotti*. Matsui et al. (1999) expressed doubts as to previous identification of Philippine populations as *L. hasseltii* and suggested that Philippine populations might be recognizable as distinct species.

The hesitancy of past workers to recognize Philippine *Leptobrachium* as distinct species is most likely due to a lack of recent collections and accompanying natural history data that would suggest ecological and/or acoustic differences between the species. Until recently, no molecular or acoustic data that would suggest distinctiveness or possible taxonomic affinities have been available. Ours are the first recordings of the advertisement calls of Philippine populations of *Leptobrachium*. Although the lack of sample sizes sufficient for statistical analyses of the acoustic data prevent quantitative comparisons, our descriptions of the advertisement calls of the new species support their taxonomic distinctiveness, to the extent that calls of congeners are available. Future comparative analyses of the calls of all Philippine and closely related Bornean congeners would be particularly desirable; to date, few recordings of the calls of Bornean species are available (but see Malkmus et al., 2002). A qualitative appraisal of the amplitude envelopes depicted in oscillograms of Bornean species' calls suggests that the advertisement call of *L. gunungense* may be very similar to that of *L. lumadorum* and that the calls of Bornean *L. montanum* appear quite similar to *L. mangyanorum*.

Our phylogenetic estimate is inferred from a gene tree based on 16S and ND1 mitochondrial genes. The topology inferred from Bayesian, maximum likelihood and parsimony analyses of these gene segments suggests that Philippine populations of *Leptobrachium* are derived from two faunal exchanges with the landmasses of the Sunda Shelf (Fig. 1), one giving rise to the sister species *L. mangyanorum* (Mindoro Isl.) and *L. tagbanorum* (Palawan faunal region), and the other giving rise to *L. lumadorum* (Mindanao faunal region). Reminiscent of the dual-invasion hypothesis of Brown and Guttman (2002), the pattern revealed by our data suggests that southern Philippine biodiversity is, in part, derived from two faunal exchanges with the landmasses of the Sunda Shelf (Brown and Guttman, 2002; Evans et al., 2003).

The sister relationship between *L. mangyanorum* and *L. tagbanorum* is not surprising despite the fact that this relationship postulates a recent common ancestry between two taxa on either side of Huxley's modification of Wallace's Line. Although the northern extension (Huxley, 1868) of Wallace's Line (Wallace, 1860, 1896) is recognized as part of one of the sharpest faunal demarcations on the planet (Mayr, 1944; Simpson, 1977; Whitmore, 1987), most available phylogenetic analyses of amphibians and reptiles that involve taxa from the Palawan faunal region and the oceanic portions of the Philippines have demonstrated a close relationship between these faunal regions, to the exclusion of Borneo and other islands of the Sunda Shelf (Brown et al., 2000*a*; Brown and Guttman, 2002; Evans et al., 2003; McGuire and Kiew, 2001). The relationships inferred from our analyses of molecular sequence data demonstrate yet another faunal group in which the simplistic view of Palawan as a simple faunal peninsula of northern Borneo is not supported by available evidence (Brown and Diesmos, 2009). In this case, populations east of Huxley's modification of Wallace's Line on Mindoro Island (*L. mangyanorum*) are most closely related to populations west of this faunal barrier on Palawan (*L. tagbanorum*). Despite the deep water that prevented a connection between northern Palawan and Mindoro, the intervening straits have most likely served as a filter barrier, across which some lineages have successfully dispersed (Brown and Guttman, 2002; Evans et al., 2003). Faunal exchange between Palawan and the oceanic islands of the Philippines clearly has proceeded in both directions (Brown and Guttman, 2002; Evans et al., 2003; McGuire and Kiew, 2001), leading us now to consider Palawan as a transitional region with a rich fauna representing an amalgamation of lineages from a variety of sources (Brown and Diesmos, 2009). Comparative, multi-lineage evaluation of the major hypothesized faunal dispersal routes into the oceanic islands of the Philippines provides compelling questions for future research (Brown and Guttman, 2002; Jones and Kennedy, 2008).

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APPENDIX

Additional Specimens Examined

Numbers in parentheses indicate the number of specimens examined.

Leptobrachium abbotti.—(24) MALAYSIA, BORNEO ISLAND, *Sabah*, Lahad Datu District: FMNH 234320, 241003, 244777, 244785; Sipitang District: FMNH 234318–19; Tawau District: FMNH 248323; Tenom District: FMNH 242611–12, 242616–17, 242620–21; Ranau District: 234324, 241003; *Sarawak*, 4th Division, Bintulu District, Labang Camp on Sungai Seran: KU 155571–75; Terengganu, Gunung Lawit, Sungai Kelebang Camp: KU 194709–11; INDONESIA, Sumatra Island, *Langkat*, E coast Sumatra: MCZ A-22500.

Leptobrachium banae.—(1) LAOS, *Xe Kong Province*: FMNH 258079.

Leptobrachium buchardi.—(11) LAOS, *Champasak Province*: FMNH 258080–90.

Leptobrachium chapaensis.—(19) VIETNAM, *Nghe An Province*: FMNH 255669–72, 255678; LAOS, *Bolikhamxay Province*: FMNH 258067–71; MYANMAR, Taunggyi State: CAS 230942, 230950–53, 235838–41.

Leptobrachium hainanensis.—(8) CHINA, *Guangxi Province*: KU 311576–83.

Leptobrachium hasseltii.—(58) INDONESIA, Java Island, *Jawa Barat Province*, Mt. Gede, Tijbodas: USNM 44054, 44056, 44058, MCZ A-14878–82, 19218; Pengalongan: MCZ A-2483; *Java Barat Province*, Kabupaten Sukabumi, Kecamatan Kadudampit, Desa Gede Pangrango: TNHC 67265–67282, 67323, JAM 2773, RMB 2691, 2692, 2695, 2417and 2913 (deposited at MZB), LSU 81928–81949; *Java Barat Province*, Taman Safari Park, near Cibodas: UTA A-53688.

Leptobrachium hendricksoni.—(30) MALAYSIA, Borneo Island, *Sarawak*, 4th Division, Bintulu District: FMNH 148271, 148273, 148276, 148280, 156562, 156568, 156575, 156577, 156582–83, 156590, 156595–97, 158216–17; WEST MALAYSIA, Selangor: FMNH 185821, 185827–28, 185834, 185840–41, 185847, 185853, 185859, 185860, 185866–67, 185873; Pahang: FMNH 178260 (paratype).

Leptobrachium leishanense.—(2) CHINA, *Guizhou Province*, Leishan: KU 206424–25.

Leptobrachium liui.—(2) CHINA, *Guangxi Province*, Yaoshan: KU 206426–27.

Leptobrachium montanum.—(14) MALAYSIA, Borneo Island, *Sarawak*, Batang Balui, tributary stream Jangan Umi flowing into Batang Besua: USNM 314123; *Sabah*, Kota Marudu, Karak-Parak, Tahobang: USNM 306196–97; Tenom, Purulon, Kipipio: USNM 306197; East Coast Residency, Sandakan District: FMNH 63493–94, 63541, 77220; East Coast Residency, Kinabatangan District: FMNH 63533–36, 63539–40.

Leptobrachium mouhoti.—(4) CAMBODIA, *Mondolkiri Province*: FMNH 261765, 262753–55 (paratypes).

Leptobrachium nigrops.—(49) MALAYSIA, Borneo Island, *Sarawak*, 4th Division, Bintulu, Sungei Nyambu Camp, Nyabu Forest Reserve: MCZ A-64810–11; 4th Div, Bintulu District: FMNH 148237–39, 148241–42, 148245–47, 148250–53, 148256, 148259, 148260–63, 148265, 148268, 148270, 148272, 148275, 148278–79, 148284–85, 151515–16, 151518–21, 156601, 156603–05, 158209–11, 158213–14; INDONESIA, Subi Island: TNHC 64305; Sumatra Island, *Jambi Province*, Road between Tapan and Sungaipenuh, 41 km W Sungaipenuh: UTA A-53689; "SINGAPORE:" CAS-SUA 3258; SINGAPORE, Nee Soon Rifle Range: KU 194713–14.

Leptobrachium pullum.—(4) THAILAND, *Phangnga Province*: FMNH 206820; *Loei Province*, Dansai District: FMNH 135984, 108524; VIETNAM, Annam: FMNH 196015 (syntype).

Leptobrachium smithi.—(13) THAILAND, Chiang Mai *Province*: FMNH 173973–75, DSM 910 (uncataloged specimen deposited at KU); LAOS, *Sanyaboury Province*: FMNH 258091–92, 258097, 258101–03, 258104–06.

Leptobrachium xanthospilum.—(10) VIETNAM, Buon Loy, ca. 20 km NW Kan Nack, An Khe District: MVZ 221341; VIETNAM, *Gai Lai Province*: FMNH 252902–03, 252908, 252912–14, 252918–20.