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Systematics and biogeography of the *Hylarana* frog (Anura: Ranidae) radiation across tropical Australasia, Southeast Asia, and Africa ☆

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A B S T R A C T

We present an inclusive molecular phylogeny for *Hylarana* across its global distribution, utilizing two mitochondrial and four nuclear gene regions for 69 of the 97 currently described species. We use phylogenetic methods to test monophyly of *Hylarana*, determine relationships among ten putative subgenera, identify major clades, reconstruct biogeographic history, and estimate continental dispersal dates. Results support *Hylarana* as a monophyletic group originating approximately 26.9 MYA and comprising eight clades that partly correspond to currently described subgenera plus two new groups. The African and Australasian species each form clades embedded within a paraphyletic Southeast Asian group. We estimate that Africa and Australasia were colonized by *Hylarana s.l.* from SE Asia approximately 18.7 and 10.8 MYA, respectively. Biogeographic reconstructions also support three separate colonization events in India from Southeast Asia. Examination of museum specimens identified morphological characters useful for delineating subgenera and species. We herein elevate all supported subgenera to genus rank and formally describe two new genera to produce a revised taxonomy congruent with our new phylogenetic and biogeographic findings.

1. Introduction

Hylarana is a diverse genus of ranid frogs of great systematic and biogeographic interest due to its broad distribution across Africa, Southeast Asia, and Australasia. However, its phylogeny is still poorly known, rendering global biogeographic studies problematic. Crossing multiple biogeographic barriers, *Hylarana* is one of a few amphibian genera that extends from Southeast Asia past Wallace's Line to Sulawesi and the Philippines, and further, past Lydekker's Line to Australasia (Fig. 1); and it is one of only two southeast Asian ranoid genera that has reached Africa, the other being *Chiromantis* Peters, 1854 (Rhacophoridae). *Hylarana* is the only amphibian genus to inhabit all three of these biogeographic regions, providing a unique opportunity to calculate timing of continental colonization events. Other terrestrial vertebrate families have a similar distribution across Australasia, Asia, and Africa, such as Varanidae (monitor lizards), Pteropodidae (megabats), and Pythonidae (pythons).

There are currently 97 described species of *Hylarana s.l.*, with 11 in Africa, 73 in Southeast Asia, and 13 in Australasia (primarily New Guinea, with only *H. daemeli* reaching the northern portion of Australia) (Frost, 2014). The species diversity in *Hylarana* is undoubtedly underestimated; multiple molecular studies reveal that when widespread species are examined at the population level, these "species" actually contain multiple deeply divergent and independently evolving lineages, some of which are not monophyletic, e.g., *H. arfaki*, *H. aurantiaca*, *H. chalconota*, *H. flavescens*, *H. signata*, and *H. temporalis* (Biju et al., 2014; Brown and Guttman, 2002; Brown and Siler, 2014; Donnellan et al., 2010; Inger et al., 2009; Stuart et al., 2006; Zainudin and Sazali, 2012). An increasing number of described species in *Hylarana*, combined with its large geographic range, has led to regional studies of limited and inconsistent sampling for both molecular and morphological data. The content of the genus has also been revised, based on comparative studies that include other closely related ranid genera such as *Amolops*, *Babina*, *Glandirana*, *Huia*, *Meristogenys*, *Odorrana*, and

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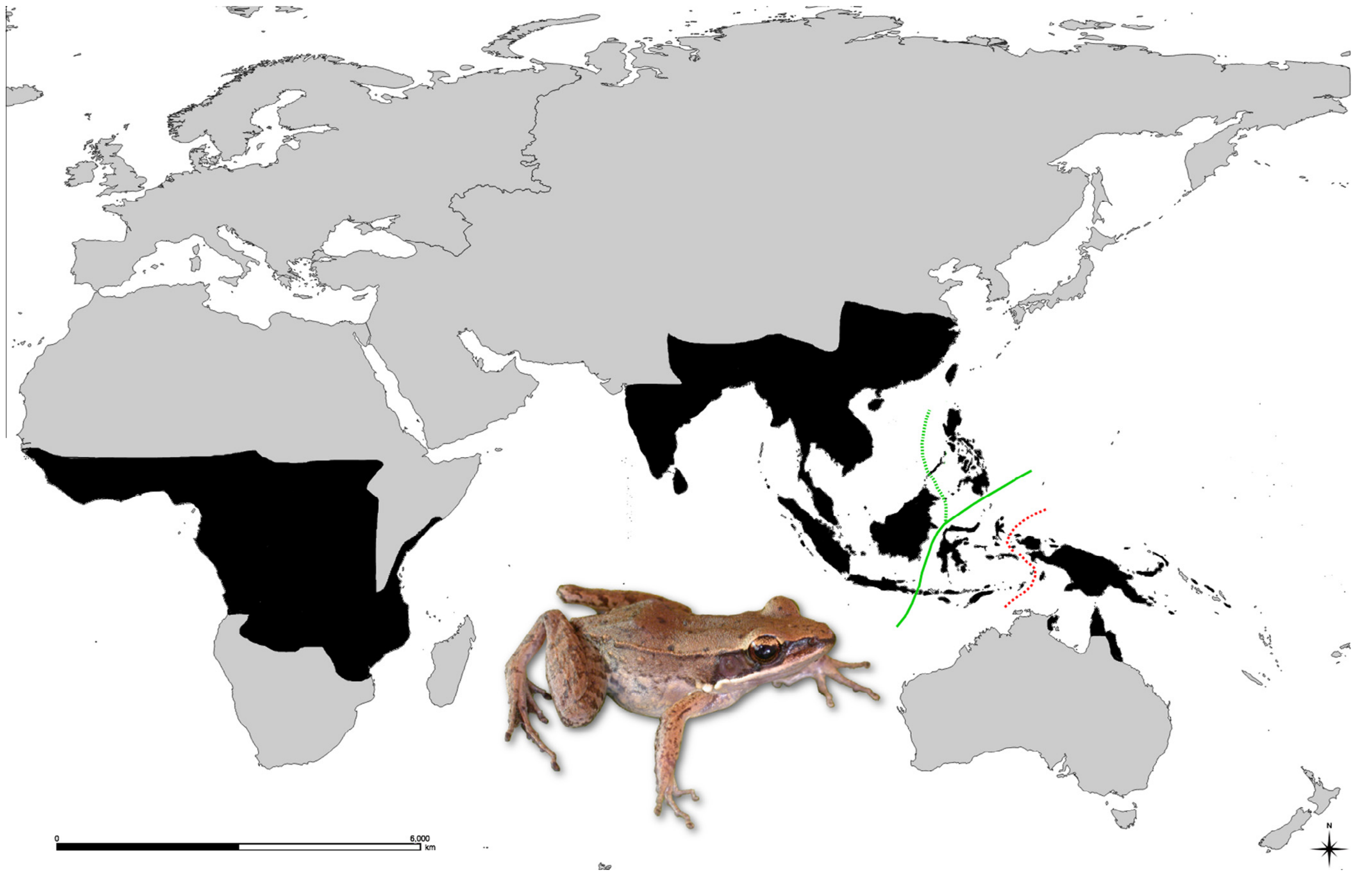

Fig. 1. Distribution of *Hylarana s.l.* in Africa, Asia, and Australasia. Range based on occurrence records by islands and/or countries in Frost (2014). The dotted red line between Southeast Asia and Australasia denotes Lydekker's Line. The green line denotes Wallace's Line, following Mayr (solid) and Huxley (stippled). Photo of *Papurana papua* by F. Kraus (BPBM 16325).

Sanguirana; *Glandirana* and/or *Sanguinrana* form the sister taxon to *Hylarana s.l.* (Bossuyt et al., 2006; Che et al., 2007; Dubois, 1992; Fei et al., 1990, 2010; Frost et al., 2006; Fuiten et al., 2011; Kurabayashi et al., 2010; Pyron and Wiens, 2011; Stuart, 2008; Wiens et al., 2009).

On the basis of phenetic similarity, Dubois (1992) erected eight subgenera within *Hylarana* (detailed in Table 1), which he explicitly stated were preliminary hypotheses. These are *Amnirana* (Africa); *Chalcorana*, *Humerana*, *Pulchrana*, *Sanguirana*, and *Sylvirana* (Southeast Asia); and *Papurana* and *Tylerana* (Australasia). Based on the species originally assigned to these subgenera, some (e.g., *Sylvirana*) have been found to be paraphyletic by molecular analyses having moderately complete taxonomic sampling (Che et al., 2007; Frost et al., 2006). A further three generic names are currently synonymized within *Hylarana*: *Hydrophylax* (Fitzinger, 1843), *Tenuirana* (Fei et al., 1990), and *Boulengerana* (Fei et al., 2010). The need to partition *Hylarana* into multiple genera has been previously suggested based on phylogeny, morphology and geography (Biju et al., 2014; Brown and Guttman, 2002; Donnellan et al., 2010; Dubois, 1992). However, such taxonomic revision has not yet been undertaken, most likely because previous studies were geographically restricted, employed uneven taxonomic sampling, or contained non-overlapping sets of taxa. There are also numerous problems with incorrect species

Table 1
Summary of current taxonomy for each subgenus with original author, type species, whether the type species was included in this analysis, and whether the subgenus is being elevated to generic status (G) or synonymized (S).

Subgenus	Description	Type species	Included in analysis	Clade in phylogeny	Taxonomic status
Abavorana	This study	*Limnodytes luctuosus* Peters, 1871	Yes	A	G
Amnirana	Dubois (1992)	*Hylarana amnicola* Perret, 1977	Yes	D	G
Boulengerana	Fei et al. (2010)	*Rana guentheri* Boulenger, 1882	Yes	H2	S
Chalcorana	Dubois (1992)	*Hyla chalconotus* Schlegel, 1837	Yes	C	G
Humerana	Dubois (1992)	*Rana humeralis* Boulenger, 1887	Yes	E	G
Hydrophylax	Fitzinger (1843)	*Rana malabarica* Tschudi, 1838	GenBank	I	G
Hylarana	Tschudi (1838)	*Hyla erythraea* Schlegel, 1837	Yes	F	G
Indosylvirana	This study	*Rana flavescens* Jerdon, 1853	GenBank	G	G
Papurana	Dubois (1992)	*Rana papua* Lesson, 1826	Yes	J	G
Pulchrana	Dubois (1992)	*Polypedates signatus* Günther, 1872	Yes	B	G
Sylvirana	Dubois (1992)	*Lymnodytes nigrovittatus* Blyth, 1856	Yes	H	G
Tenuirana	Fei et al. (1990)	*Rana taipehensis* Van Denburgh, 1909	Yes	F2	S
Tylerana	Dubois (1992)	*Rana jimiensis* Tyler, 1963	Yes	J2	S

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determinations for tissues in museum collections, and "widespread" taxa that are probably not conspecific across their entire range. The lack of a complete and robust identification key to the genus, combined with a large number of species and taxonomic uncertainty, makes a large-scale genetic approach with dense taxonomic sampling appropriate to identify clades within *Hylarana*.

Here, we present the most comprehensive molecular phylogeny to date for *Hylarana* so as to test the monophyly of the genus, investigate validity and relationships of subgenera, and assign previously unstudied species to clades. We also present biogeographic reconstructions to examine the history of dispersal of *Hylarana* across major biogeographic regions that other amphibians have failed to cross. Lastly, we present a time-calibrated phylogeny to test the timing of major dispersal events across continents.

2. Materials and methods

2.1. Tissue and voucher sampling

We obtained tissue samples from existing museum collections of the American Museum of Natural History, New York (AMNH); Bernice Pauahi Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); Museum of Vertebrate Zoology, Berkeley (MVZ); National Museum of Natural History (USNM), Washington, D.C.; Port Elizabeth Museum, Port Elizabeth (PEM); Royal Ontario Museum, Toronto (ROM); Museum für Naturkunde, Berlin (RG/ZMB); as well as some tissues from private collections (Appendix A). The dataset also includes GenBank sequences from studies providing initial species descriptions or that experts identified on *Hylarana* from that geographic region. Final analyses included a total of 160 individuals (Appendix A): we sequenced 97 during this study and obtained 63 from GenBank (Biju et al., 2014; Bossuyt et al., 2006; Brown and Siler, 2014; Che et al., 2007; Hasan et al., 2012; Jeong et al., 2013; Matsui and Hamidy, 2012; Stuart, 2008; Stuart et al., 2006; van der Meijden et al., 2005). A total of 69 of 97 described species of *Hylarana s.l.* are included, with 53 of 73 species from Southeast Asia, 5 of 11 from Africa, and 11 of 13 from Australasia. Outgroup taxa include species from the closely related genera *Babina*, *Glandirana*, *Odorrana*, and *Sanguirana*. We used *Rana japonica* as the outgroup for all phylogenetic analyses.

The type species for each subgenus (Table 1 and Appendix A) is included in our dataset, as described by Fitzinger (1843), Fei et al. (1990), Dubois (1992), and Fei et al. (2010). For *Humerana* (*H. humeralis*) we used a sample from Biju et al. (2014), which they labeled as "*Hylarana cf. humeralis.*" Frost et al. (2006) did not include any species allocated to *Humerana* in their phylogenetic analysis, and they kept this subgenus separate from *Hylarana s.l.* because they could not assess its status. Multiple studies since then have suggested that *Humerana* should be subsumed under *Hylarana* (Bortamuli et al., 2010; Hasan et al., 2012; Matsui et al., 2005; Pyron and Wiens, 2011), and we here treat all these subgeneric names as hypotheses to be tested.

We excluded all museum tissue samples of "*Hylarana*" when preliminary analyses did not group the sample within *Hylarana* or any of the above-mentioned closely related outgroup genera and when voucher examination confirmed the misidentification. We resolved identity of vouchers of non-monophyletic terminals bearing the same taxon designation from various institutions by: (a) checking available voucher specimens against taxon descriptions, and renaming as "sp." any that did not match that description nor could be identified to another species; (b) examining locality data to determine whether the individual was within the species' known range, and using proximity to the type locality as a factor; (c) expertise of the person determining the sample at the tissue's depository. In many cases, an expert who had recently published on a particular species group had identified some of the samples used here, and we favored that identification over anonymous ones. In most cases, misidentified material had been assigned to widespread taxa with older names, e.g., *H. albolabris*, *H. maosonensis*, *H. nigrovittata*, *H. signata*, *H. taipehensis*. In the case of *H. nigrovittata* in particular, previous studies have noted extreme geographic variation, suggesting cryptic diversity and the possibility that there may be at least five species in the "*nigrovittata*" complex (Gawor et al., 2009; Matsui et al., 2001; Ohler et al., 2002). We thus consider the stated identity of our "*H. nigrovittata*" samples to be preliminary. We retained all sequence data for these unidentified but vouchered samples and included them in the analysis, listed as "*Hylarana* (subgenus) sp." (in Appendix A), for future taxonomic study.

We used voucher specimens with molecular sequence data, supplemented with additional vouchers from the AMNH collection, to identify shared morphological characteristics of clades identified in the molecular phylogeny.

2.2. DNA isolation, amplification, and sequencing

We extracted whole genomic DNA from liver or muscle tissue using the Qiagen DNeasy Blood and Tissue Kit (Valencia, California, USA). We sequenced two partial mitochondrial gene regions (16S rRNA, *Cytochrome b*) and four partial nuclear gene regions – C-X-C chemokine receptor type 4 (CXCR4), recombination-activating gene 1 (RAG1), nuclear proto-oncogene cellular myelocytomatosis exon 2 (C-myc 2), and Tyrosinase exon 1(Tyr) – for all samples. We used published primers for *Hylarana* or closely related genera (Bossuyt and Milinkovitch, 2000; Pauly et al., 2004; Shimada et al., 2011; Wiens et al., 2005). Gene regions, primer pairs, annealing temperatures, and basepair lengths are listed in Table 2. We amplified target gene regions using standard PCR protocols and cleaned amplicons using Agencourt AMPure XP on a Beckman Coulter Biomek FX robot. We cycle sequenced purified amplicons in both directions with a BigDye v. 3.1 Terminator Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and sequenced on an Applied Biosystems Inc. Prism™ 3730xl automated sequencer. We assembled and edited complementary strands using Geneious v. 6.1 (Biomatters Inc.; www.geneious.com) and aligned in MAFFT v. 7.0 (Katoh and Standley, 2013). We deposited all sequences in GenBank and accession numbers are: KR264033–KR264511.

2.3. Phylogenetic analysis

We used maximum likelihood (ML) and Bayesian inference on the concatenated dataset for all six loci as well as for individual gene trees. For both analyses, we tested a variety of models and partitioning strategies in jModelTest v. 2 (Posada, 2008) and PartitionFinder v. 1.1 (Lanfear et al., 2012), respectively, using the Bayesian Information Criterion (BIC; Table 2) to determine the best model. Partitioning strategies included by locus and by codon position for the five protein coding genes (*Cyt b*, C-myc 2, CXCR4, RAG1, and Tyr). We implemented maximum likelihood analysis in RAxML v. 7.0 (Stamatakis, 2006) under default parameters and assessed branch support with 1000 thorough bootstrap replicates. We also generated individual gene trees for each locus in RAxML using the same parameters. We implemented Bayesian analyses in MrBayes v. 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) on CIPRES Science Gateway (www.phylo.org/sub_sections/portal/) for two independent runs, each with four chains, and run for 25 million generations with sampling every

Table 2
List of loci sequenced, PCR primers, length, and best-fit model. Partitioning scheme was recovered as divided by gene region.

Gene region	Primer	Sequence (5′–3′)	Length (bp)	Annealing temp	Citation	Best fit model
16S	12sm	GGCAAGTCGTAACATGGTAAG	1512	51	Pauley et al. (2004)	GTR + I + G
	16sd	CTCCGGTCTGAACTCAGATCACGTAG				
Cyt b	cytb-c	CTACTGGTTGTCCTCCGATTCATGT	567	51	Bossuyt and Milinkovich (2000)	GTR + I + G
	CB-J-10933	TATGTTCTACCATGAGGACAAATATC				
C-myc exon 2	cmyc1U	GAGGACATCTGGAARAARTT	422	49	Wiens (2005)	HKY + I + G
	cmyc-ex2dR	TCATTCAATGGGTAAGGGAAGACC				
CXCR exon 4	CXCR4-B	ATCATTGGCAATGGAYTRGT	650	50	Biju and Bossuyt (2003)	HKY + I + G
	CXCR4-G	AGGCAACAGTGGAARAANGC				
Rag exon 1	Rag1_1F	GCMTTGCTSCCRGGGTATCA	750	50	Shimada et al. (2011)	HKY + I + G
	Rag1_2R	TCAATGGACGGAAGGGTTTCAATAA				
Tyrosinase exon 1	Tyr1A	AGGTCCTCTTRAGCAAGGAATG	597	57	Bossuyt and Milinkovich (2000)	GTR + I + G
	Tyr 1G	TGCTGGGCRTCTCTC-CARTCCCA				

1000 generations. We unlinked substitution models, relative rates of substitution, transition/transversion ratio, and stationary nucleotide frequency parameters for all partitions, and set rate priors to variable to allow differing substitution rates among partitions. We left all other parameters at default settings. We assessed convergence by examining (1) the potential scale-reduction factors in MrBayes and (2) the traces of all parameters and the effective sample sizes in Tracer v. 1.6 (Rambaut et al., 2014). We discarded the first 25% of samples as burn-in.

We also created a reduced matrix of 95 terminals for both ML and Bayesian analyses with one individual per species (based on the sample with the most loci successfully sequenced), including "species" left unidentified ("sp.") after we examined voucher specimens (Appendix A). We used this reduced matrix in both the biogeographic and time-calibrated analyses. This approach limited the amount of missing data in the phylogenetic analyses.

We also attempted to account for the differences between gene trees and species trees using coalescent analysis (Degnan and Rosenberg, 2009, 2006; Edwards, 2009; Edwards et al., 2007; Maddison, 1997). However, due to the large number of terminals, combined with the amount of missing data for some taxa (e.g., the GenBank samples), species tree analyses would not converge or produce bifurcating trees (in the case of maximum likelihood species tree analyses).

2.4. Biogeographic reconstructions

To examine the biogeographic history of *Hylarana s.l.*, we implemented (1) maximum likelihood ancestral reconstruction (MLSAR) in Mesquite v. 2.74 (Maddison and Maddison, 2010), (2) Statistical Dispersal-Vicariance Analysis (S-DIVA) in RASP v. 3.0 (Yu et al., 2010, 2014), and (3) Dispersal-Extinction Cladogenesis (DEC) (Ree et al., 2005), also in RASP, to determine ancestral ranges for each node. We defined geographic areas of occurrence as: A = sub-Saharan and central Africa; B = India, Nepal, and Sri Lanka; C = Southeast Asia, (Myanmar, Thailand, Cambodia, Vietnam, Laos, China, Malaysia, Java, Sumatra); D = Sulawesi; E = Phillipines; F = Australasia. We defined regions based on well-established biogeographic and continental boundaries (e.g., Lydekker's Line, Wallace's Line, Africa, Sunda Shelf, etc.). For all biogeographic analyses, we used the MrBayes reduced concatenated tree.

2.5. Time-calibration

Fossil taxa that can be unambiguously assigned to Ranidae are sparse, and there are currently no known fossils of *Hylarana s.l.* However, we calibrated the tree with two calibration points: (1) one fossil calibration based on the earliest fossil remains of European water frogs, *Pelophylax* (Rage and Roček, 2003), and (2) one published divergence date between *Limnonectes kochangae* and the remaining ranids (Roelants et al., 2007). Therefore, for this analysis, we included GenBank sequence data for *Meristogenys kinabaluensis* and *Rana temporaria* to calibrate the phylogeny with the water frog fossil, as in Roelants et al. (2007). Both mitochondrial gene regions and three of the four nuclear loci (with the exception of C-myc 2) used in this study were available for *M. kinabaluensis* and *R. temporaria*. Additionally, we sequenced *Limnonectes kochangae* for the root and used the published divergence date from Roelants et al. (2007) for calibration. We used BEAST v. 1.8 (Drummond et al., 2012; Heled and Drummond, 2010) to calculate divergence dates. We constrained monophyly for (1) *Hylarana*, and (2) all taxa but *Limnonectes*. Otherwise, we used BEAST to estimate the topology independently so as not to interfere with dating estimates.

We estimated divergence times using an uncorrelated lognormal clock with a CTMC Rate Reference prior separately for each gene partition and a birth–death incomplete-sampling tree prior (Gernhard, 2008) for 100 million generations, with the first 30% of samples being discarded as burn-in. We evaluated root dates using a lognormal prior from 60 to 81 MY before present to calibrate the phylogeny based on the same previously published dataset (Roelants et al., 2007). We set the tmrca (time of most recent common ancestor) for *M. kinabaluensis* and *R. temporaria* using a lognormal prior between 28.6 and 40.5 MY before present (Rage and Roček, 2003; Roelants et al., 2007). For more recent colonization events (e.g. before 15 MYA), we calculated genetic distance values for *cytochrome b* within and between clades in Mega 5.0 (Tamura et al., 2011) to corroborate divergence time estimates assuming a rate of ~1% divergence per lineage per million years. We divided a sequence distance value by the inferred age of the corresponding node; therefore, we used a value of approximately 2 as an indicator of a more robust time estimate.

3. Results

3.1. Phylogenetic analyses and taxonomy

The final aligned length of the combined mitochondrial and nuclear dataset was 4498 bp. The partitioning scheme and best-fit models for nucleotide substitution are provided in Table 2. Once we examined voucher specimens and re-identified or removed misidentified individuals from the dataset, the concatenated analyses (Fig. 2) recovered a monophyletic *Hylarana s.l.* (64 ML bootstrap, 0.93 BPP). We found strong support (100 ML bootstrap, 1.00 BPP) for the monophyly of the Australasian group of species and the African group (94 ML bootstrap, 1.00 BPP). However, both are embedded within a paraphyletic Asian group. Relationships among *Amnirana*, *Chalcorana*, and *Pulchrana* are incongruent between the maximum likelihood and Bayesian

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Fig. 2. Concatenated tree of *Hylarana s.l.* based on maximum likelihood and Bayesian inference of two mitochondrial and four nuclear gene regions. The tree is the consensus topology from the reduced matrix Bayesian analysis and is rooted with *Rana japonica*. Outgroup taxa are in gray and ingroup taxa (*Hylarana s.l.*) in black. Names on terminals correspond to the generic level taxonomy proposed in this paper. Node-support values are maximum likelihood bootstraps (above) and Bayesian posterior probabilities (below), respectively. Black circles on nodes indicate ML bootstrap ⩾75 and BPP ⩾0.95. White circles indicate BPP ⩾0.95. Black squares indicate ML bootstrap ⩾50 and BPP ⩾0.75. White squares indicate ML bootstrap ⩾75. Nodes that have a BPP <0.75 and ML bootstrap <50 are not listed. Bold terminals with an asterisk (∗) are the type species for genera proposed in this paper. Letters A–J represent clades corresponding to the putative (and newly recognized) genera recovered in both maximum likelihood and Bayesian analyses. (A) *Abavorana*, gen. nov. (B) *Pulchrana*, (C) *Chalcorana*, (D) *Amnirana*, (E) *Humerana* (F) *Hylarana s.s.*, (F2), *Tenuirana*, (G) *Indosylvirana*, gen. nov. (H) *Sylvirana*, (H2) *Boulengerana*, (I) *Hydrophylax*, (J) *Papurana*, (J2) *Tylerana*. Clade B is split into two clades (BA and BB) based on morphological differences.

analyses, with the ML analysis having very low support (i.e., 19 ML bootstrap) and the Bayesian analysis good or strong support. Additionally, although some species-level relationships are incongruent, the species composition of major clades are consistent across analyses. *Hylarana luctuosa* is recovered as the sister taxon to all other *Hylarana s.l.* In both analyses, *Glandirana* + *Sanguirana* are recovered as the sister group to *Hylarana s.l.*, although our analysis did not support their reciprocal monophyly. However, the support for this topological arrangement is low and based on limited GenBank sample data.

Our analyses retrieved each of *Chalcorana* and *Humerana* (as described by Dubois, 1992) as monophyletic (Appendix A). The other phenetically based subgenera described by Fei et al. (1990), Dubois (1992), and Fei et al. (2010) are all paraphyletic, as originally suspected by these authors. However, it is possible to redefine most of these taxa to be monophyletic around their respective type species (Appendix A). *Pulchrana* contained the same species as Dubois (1992) originally assigned to it, with the exception of *H. luctuosa*, which was consistent with Pyron and Wiens (2011). Furthermore, we found *Pulchrana* to consist of two morphologically diagnosable subclades (BA and BB). African species grouped into a single clade around *H. amnicola*, the type species of *Amnirana*. We recovered *Hylarana nicobariensis*, a Southeast Asian species previously assigned to *Sylvirana* by Dubois (1992), as the sister taxon to all African species, and we transfer it to *Amnirana*. *Hylarana malabarica*, the type species of *Hydrophylax* (Fitzinger, 1843), groups with *H. leptoglossa* and *H. gracilis* (both assigned to *Sylvirana* by Dubois (1992)) in both analyses (98 ML bootstrap, 1.00 BPP). The analyses also recovered monophyly of *Tylerana*, but this clade was embedded within *Papurana*. Dubois (1992) described both *Tylerana* and *Papurana*, and subsequently gave priority to *Papurana* (Dubois, 1999: Table 2). We retrieved *Tenuirana* (*H. macrodactyla* and *H. taipehensis*) as paraphyletic and embedded within the subgenus *Hylarana*, which has precedence. Phylogenetic analyses did not support *Sylvirana* as described by Dubois (1992). Rather, the species that Dubois (1992) placed in *Sylvirana* grouped primarily into two clades that are not sister taxa. The nominate clade (formed around the type species, *H. nigrovittata*) is the sister taxon to (*Hydrophylax* + *Papurana*). The monotypic *Boulengerana* (*H. guentheri*) was embedded within the nominate clade of *Sylvirana*, and *Sylvirana* takes precedence over that name. Remaining species originally assigned to *Sylvirana* by Dubois (1992) grouped into an unnamed clade comprising the *H. aurantiaca* group, *H. flavescens* group, *H. intermedia*, *H. milleti*, *H. montana*, and *H. temporalis* group, which is sister to (*Sylvirana* (*Hydrophylax* + *Papurana*)). We therefore synonymize the names *Boulengerana*, *Tylerana* and *Tenuirana* based on our phylogenetic results, raise remaining redefined subgenera to generic rank (see Section 4.3), and describe two new clades to accommodate the unnamed taxa.

3.2. Morphology of voucher specimens

We provide a summary of morphological character states that serve to distinguish among clades (Table 3). Clade names correspond to those depicted in Fig. 2. We also include additional diagnostic characters of described subgenera as provided by Dubois (1992).

3.3. Biogeographic reconstructions and time calibration

MLSAR, S-DIVA, and DEC all support a Southeast Asian origin for *Hylarana s.l.* (Fig. 3, Table 4). The analyses also support single colonization events into Africa and into Australasia from Southeast Asia. There is strong support for three separate dispersal events from Southeast Asia to India/Nepal/Sri Lanka by the *Hydrophylax*, *Hylarana s.s.*, and *Indosylvirana* gen. nov. clades. Colonization of Sulawesi and Philippines is more ambiguous, with historic range estimations unable to distinguish between Southeast Asia and Sulawesi, or between Southeast Asia and the Philippines.

The topology from the BEAST time-calibrated tree (Fig. 4) mostly agrees with the MrBayes and RAxML phylogenies except for some species relationships within genera (e.g., within *Chalcorana*, *Papurana* and *Pulchrana*). *Babina* is recovered as within the sister taxon to the ingroup in the BEAST analysis, but the support is very low. The relationship between clades of *Hylarana s.l.* is congruent with the MrBayes concatenated phylogeny and is well-supported. *Papurana* colonized Australasia approximately 10.8 MYA and *Amnirana* colonized Africa approximately 18.7 MYA. The mean group genetic distance for *cytochrome b* within *Papurana* is 20.5%; when divided by the age of the node (in millions of years) this gives a value of 1.9. India was colonized at least three times, approximately 16 MYA by *Indosylvirana* gen. nov. and 8.8 MYA by *Hydrophylax*. The mean group genetic distance for *cytochrome b* within Indian *Hydrophylax* was 18.9%; when divided by the age of the node this gives a value 2.1. *Hylarana tytleri* also reaches India, but we did not have accurately identified species from India to test colonization time. We found the root age of *Hylarana s.l.* to be 26.9 MYA.

4. Discussion

4.1. Continental colonization and diversification

The relationships among deep nodes of the tree for *Hylarana s.l.* were poorly supported in the ML analyses, but the Bayesian results provided much stronger support. Previous studies with reasonable taxonomic sampling have also had trouble resolving relationships among deeply divergent clades in *Hylarana s.l.*, retrieving low support or no support at all (Pyron and Wiens, 2011; Stuart, 2008; Wiens et al., 2009). There could be multiple reasons why this incongruence is replicated across multiple studies. A combination of the age of the nodes and an early, rapid diversification as *Hylarana s.l.* dispersed and colonized multiple continents would make it difficult to resolve relationships (Fishbein et al., 2001; Fishbein and Soltis, 2004; Rokas et al., 2005). Regardless, our analyses strongly support monophyletic African (*Amnirana*) and Australasian (*Papurana*) groups, indicating single colonizations of both biogeographic regions.

Australasian species had been hypothesized by Dubois (1992) to comprise two separate groups (*Papurana* and *Tylerana*), possibly due to the morphological disparity of *H. jimiensis* from most other species. New Guinean species can be extremely large for *Hylarana s.l.* (e.g., *H. supragrisea* and *H. arfaki*) and stand in some contrast to other species in the clade. This is possibly due to the availability of unoccupied niches (large, semi-aquatic, terrestrial frogs were previously absent from New Guinea) in the newly colonized region. Previous molecular studies did not sample sufficient species diversity to test the monophyly of *Papurana* or *Tylerana*. The colonization age estimate of New Guinea (Australasia) around 10–11 MYA corresponds with the docking of the Vogelkop Peninsula onto New Guinea from the west, which occurred approximately 10 MYA (Baldwin et al., 2012; Davies et al., 1997; Polhemus, 2007). There has also been subsequent overwater dispersal of a single species to the Solomon and Bismarck Islands (Fig. 3, Table 4).

Amnirana colonized Africa approximately 18–19 MYA. The sister taxon of the African species was found to be *H. nicobariensis* from Southeast Asia (Nicobar Islands, Peninsular Thailand, Java, Sumatra, Borneo, and Philippines). This disjunct relationship suggests the possibility of a direct Indian Ocean dispersal event to sub-Saharan Africa. It is also possible that the current distribution is relictual due to extinction from the dry intervening regions.

We have estimated times of dispersal for two migrations into India (e.g., *Indosylvirana* gen. nov. at 16 MYA and *Hydrophylax* at 6–9 MYA). However, *Humerana* (e.g., *H. humeralis*), *Hylarana s.s.* (e.g., *H. tytleri*), and *Sylvirana* (*H. nigrovittata*) also occur in India, suggesting at least three more instances of colonization in India.

Table 3
Summary of morphological diagnoses for each genus. Clade names correspond to Figs. 2–4 and descriptions in Section 4.3.

	Clade A *Abavorana*	Clade B *Pulchrana*	Clade C *Chalcorana*	Clade D *Amnirana*	Clade E *Humerana*	Clade F *Hylarana*	Clade G *Indosylvirana*	Clade H *Sylvirana*	Clade I *Hydrophylax*	Clade J *Papurana*
Posterior part of abdominal skin	Granular	BA is smooth and BB is granular	Granular	Smooth or granular	Smooth or slightly wrinkled	Smooth or slightly wrinkled	Granular or wrinkled	Smooth or granular	Smooth or granular	Smooth
Length of 1st versus 2nd finger	1st > 2nd	1st ⩾ 2nd	1st ⩽ 2nd	1st ⩾ 2nd	1st > 2nd	1 = 2	1 > 2	1 ⩾ 2	1 > 2	1 > 2
(Width of disc on Finger 3)/(Width of Finger 3)	1–1.5	1.2–1.7	2–3.5	1–1.8	1–1.2	1.2–1.7	1.4–2	1.2–1.9	1–1.5	1.5–2
(Width of disc on Toe 4)/(Width of Toe 4)	1–1.5	1–1.7	1.5–2	1–1.8	1–1.2	1–1.7	1.5–2	1–1.9	1–1.5	1.3–2
Dorsolateral folds: texture	Indistinct	Fine or warty and poorly developed	Thin or made up of a line of warts	Absent to extremely well-developed (*A. galamensis*)	Complete and thin to well-developed	Well-developed	Thin and well-defined	Medium and well-developed	Thick and well-developed	Fine and granular with asperities to absent
Dorsolateral folds: color	May be white or yellow	Pale or bright coloration, or as dorsum	Generally colored as dorsum	Variable	Pale coloration	Pale	Differential coloration to dorsum	Pale or same coloration as dorsum	Differential coloration to dorsum and often with dark stripe underneath	Variable
Humeral gland (1) raised or flat, (2) size, and (3) position	(1) Prominent and raised, (2) 2/3 length of arm, and (3) centrally positioned on the ventral surface of the humerus	(1) Prominent and raised, (2) 2/3 length of arm, and (3) centrally positioned on the anteroventral surface of the humerus	(1) Raised, (2) 1/3 to 1/2 length of humerus, and (3) centrally positioned on the anteroventral surface of the humerus	(1) Prominent and raised, (2) 2/3 to 3/4 length of humerus (3) positioned on the anteroventral surface of the humerus. May be variable in size and position	Dubois (1992) states suprabrachial glands are present and large (not seen during This study)	Variable	(1) Prominent and raised, (2) 3/4 length of humerus, and (3) on anteroventral surface	(1) Prominent and raised with dark pigment, (2) 2/3 length of the humerus, and (3) on anteroventral surface	(1) Less prominent than *Sylvirana* and with dark pigment, (2) 2/3 length of humerus, and (3) on anteroventral surface	(1) Less prominent than *Sylvirana* and with dark pigment (2) 2/3 length of humerus, and (3) on anteroventral surface
Rictal ridge	Weak or absent	Medium to well-developed	Medium to well-developed	Very large and well-developed	Relatively large and broken	Large and well-developed and white or cream	Medium and white	Medium to well-developed and white or cream	Very large and well-developed and white or cream	Thin and distinct or linear series of warts and variable color
Upper lip coloration	Gray or as rest of face	May be mottled, spotted, or uniform	Usually white	Usually white; dark in *A. lepus*	White	White and relatively thicker than in other clades	White	Gray, off-white, or occasionally mottled	White glandular ridge on upper part and dark mottles on lower part of jaw	May be gray, white, vermiculated or dark
Outer metatarsal tubercle	Absent	Present and large	Present or absent	Present or absent	Absent or small	Present and medium	Present and large	Present and medium	Present and large	Present and medium to large
Dorsum	Shagreened and may have a vivid red or reddish-brown coloration	Mottled to spotted	Shagreened, fine mottles, and may have small, round glands which may be tipped with spicules	Smooth to shagreened and uniform to mottled	Shagreened to slightly warty and with a pale or dark mid-dorsal line	Striped, mottled or uniform, and shagreened, smooth, white spicules	Shagreened, with spicules and uniform with speckles or faint spots	Shagreened with spicules or may be warty	Finely to coarsely shagreened, sometimes with white spicules, and usually mottled or spotted, but may have stripes	Evenly shagreened to warty, with or without spicules

(*continued on next page*)

Table 3 (*continued*)

	Clade A *Abavorana*	Clade B *Pulchrana*	Clade C *Chalcorana*	Clade D *Amnirana*	Clade E *Humerana*	Clade F *Hylarana*	Clade G *Indosylvirana*	Clade H *Sylvirana*	Clade I *Hydrophylax*	Clade J *Papurana*
Pattern on dorsal surface of hind limbs	Fine pale speckles or mottled	Bars with wavy edges, spotted, or vermiculated	General lack of bars, but may be faint	Mottled or blotched, occasionally striped	Faint bars to mottled and shanks may have faint lines	Generally not barred, except for the gracile 'grass' adapted species. Calves may have faint lines	Barred on the calf and femur. Calves may have ridges or lines of spicules	Finely or coarsely barred to mottled. Calves may have linearly arranged spicules	Thin, irregular bars on dorsal surface of thigh only. White spicules on dorsal surface of legs in breeding males	Strong glandular bars to no bars. May be uniformly warty
Posterior surface of thigh	Faintly stippled or mottled	Generally mottled, spotted, or reticulated	Same as dorsum	Speckled to strongly vermiculated	Vermiculated to mottled	Mottled to striped	Lightly stippled to vermiculated	Mottled or vermiculated	Strongly vermiculated	Vermiculated to finely mottled, but variable among species
Body size and shape	Medium and robust	Small and gracile in BA and large and robust in BB	Small to medium-sized with a long head and bullet-shaped body, limbs and body gracile	Robust and medium to very large	Variable in size and gracile to robust	Gracile to medium and robust	Medium and robust	Generally medium and robust	Robust, small to medium-sized	Robust, medium to extremely large
Flank coloration	Dark brown or black below dorsal fold grading to pale on ventrum	Mottled or spotted, if pattern present, or as dorsum (ground color may be paler)	Coloration as dorsum	Variable, but usually mottled	As dorsum or dark and mottled	Uniform to bicolor to mottled	As dorsum	Dark coloration underneath lateral ridges fading to pale with well-defined dark spots	Strongly mottled and usually with darker background	Mostly as dorsum, but may have dark patches or be mottled
Flank texture and glands	Smooth	Clade BB is strongly warty, clade BA is weakly warty	Accessory glandular ridges often present and often arranged linearly	Glandular or warty	Smooth	Smooth	Shagreened or few, scattered warts	Smooth or with small warts	Flanks may be strongly warty and glandular, but not arrayed in lines	May have warts
Tympanum	No faint pale coloration on margins	No faint pale coloration on margins	No faint pale coloration on margins	May have faint pale coloration anteriorly and posteriorly	Faint pale coloration around margins	Faint pale coloration on margins	No faint pale coloration on margins	Sometimes with faint pale coloration on margins	Large; no faint pale coloration on margins	Very small in *P. jimiensis* to large; no faint pale coloration on margins
Notes	Brown or black throat and sometimes with small, pale spots (Boulenger, 1920). Was grouped with *Pulchrana* in Dubois (1992)	See Brown and Guttman (2002) for species-level characters	May have many, species-specific accessory body glands	Morphologically a highly variable clade. May be highly glandular on ventrum and have other accessory body glands	Pointed snout		See Biju et al. (2014) for species-level characters	Similar postocular masks as in *Papurana*	Femoral granules are 3/4 the length of the thigh or more	Postocular mask present in many species
Dubois (1992) additional putative characters	Males without vocal sacs (Inger, 1966)	Males with or without paired internal vocal sacs	Males with or without paired vocal sacs, which do not protrude externally	Males with paired vocal sacs, which may be internal, or protrude externally, as reported by Channing (2001)	Males reported to have paired vocal sacs, which protrude externally	Dubois stated outer metatarsal tubercle present or absent and males lack vocal sacs	Included in Sylvirana by Dubois (1992)	Disc with circum-marginal groove is sometimes absent on finger 1, and paired vocal sacs may be internal or external	Paired external vocal sacs	Paired external vocal sacs

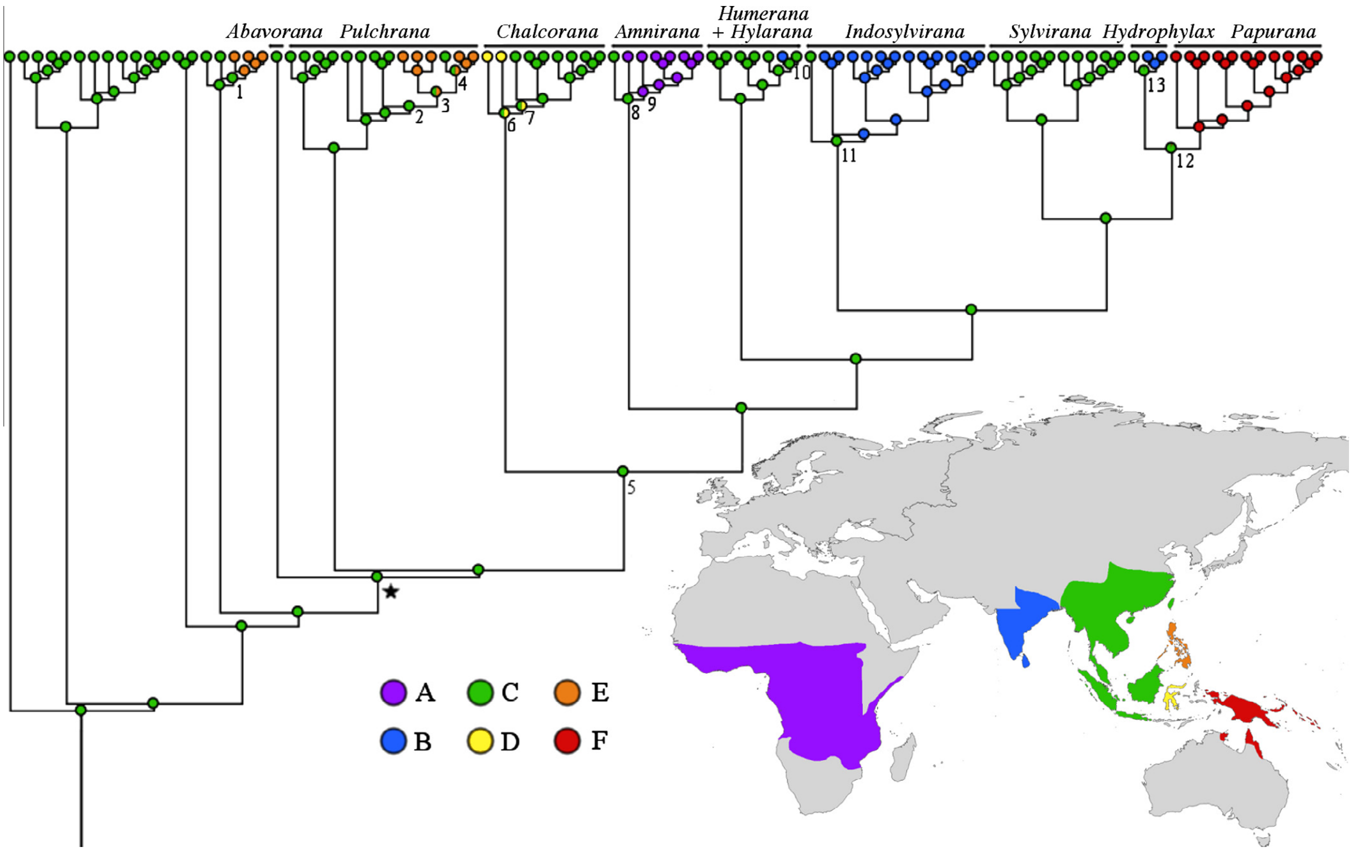

Fig. 3. Biogeographic reconstruction for *Hylarana s.l.* Ball-and-stick model exported from Mesquite MLSAR analysis. The black star denotes the ancestral node for the ingroup *Hylarana s.l.* Biogeographic regions: A – Africa; B – South Asia (India, Nepal, Sri Lanka); C – Southeast Asia (Myanmar, Thailand, Cambodia, Vietnam, Laos, China, Malaysia, Java, Sumatra); D – Sulawesi; E – Philippines; F – Australasia. Numbers on nodes correspond to values in Table 4. Unnumbered nodes designate a probability of 1.00 for all three analyses for that biogeographic region. Island groups that are not colored, but fit within the known range, are excluded because of lack of samples from that locality/region. Assigned biogeographic regions are based on range of species and collection locality when range has slight overlap across biogeographic regions.

Although there is ambiguity in the number of colonization events for the Philippines in our biogeographic reconstruction, Brown and Siler (2014) conducted a more detailed biogeographic analysis of Philippine dispersal of *Hylarana s.l.* and found a 'dual-invasion' for the eastern and western arcs.

Hylarana luctuosa is the sister taxon to all other *Hylarana s.l.* species and has a disjunct distribution in small areas of peninsular Thailand and Malaysia, Borneo, and Sumatra. As noted earlier, African and Australasian clades render Southeast Asian *Hylarana s.l.* paraphyletic, indicating the need for nomenclatural revision. A paraphyletic Southeast Asian group is unsurprising inasmuch as it lies between the other biogeographic regions inhabited by the clade.

Hylarana s.l. as a taxonomic unit is uninformative as to the evolutionary diversification and biogeography of this large and broadly distributed group. In the Systematic Account, we propose to recognize ten genera, provide notes on taxonomy, and diagnose external morphological characters for each genus. We expect this approach to stimulate further detailed morphological and taxonomic study on these newly defined genera.

4.2. Morphology of genera

Examination of voucher specimens and a review of the literature highlighted several important morphological characters that are potentially taxonomically informative at both the genus and species levels (Table 3). Here, we briefly list these characters, primarily to aid future studies examining widespread species or attempting to resolve relationships among species within each genus. We stress that these observations are based solely on the literature and our examination of a limited set of voucher specimens from our molecular study or the AMNH collection. We grouped vouchers into demonstrably monophyletic groups retrieved in our molecular phylogeny and then attempted to make phylogenetically informed generalizations regarding the morphology of the entire clade. These observations are presented as hypotheses to be tested, and diagnoses may change with additional work and more extensive examination of material. This approach was used previously for scorpions in the study of Vaejovidae (Scorpiones) and represents a useful start for approaching large, morphologically difficult taxa (González-Santillán and Prendini, 2014).

Dubois (1992) considered humeral glands in males to be distinct (for "*Rana* subsection *Hydrophylax*") in subgenera *Amnirana*, *Humerana*, *Hydrophylax*, *Papurana*, *Pulchrana* and *Sylvirana*) and indistinct or absent (for "Rana subsection *Hylarana*") for subgenera *Chalcorana*, *Hylarana*, *Tylerana*, and a suite of taxa of Ranidae now recognized at generic rank outside *Hylarana s.l.* (such as *Glandirana*, *Odorrana* and *Sanguirana*). Dubois (1992) also used large humeral glands to diagnose the subgenus *Humerana*. Frost et al. (2006) noted that the absence of humeral glands can be determined only by dissection, and stated that it is not clear from Dubois (1992) whether dissections were conducted in *Hylarana s.l.* to ascertain this. Our examination showed that humeral glands of some sort were usually discernable if adult males in breeding condition were examined. We could not conclude that these glands were generally absent in any subgeneric clade within *Hylarana s.l.* (e.g. *Chalcorana*, *Hylarana*, *Tylerana*). Lack of detailed homology

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Table 4
Biogeographic reconstructions from MLSAR, S-DIVA, and DEC analyses. Node numbers correspond to Fig. 3. Probabilities <0.05 are not listed. A – Africa; B – South Asia (India, Nepal, Sri Lanka); C – Southeast Asia (Myanmar, Thailand, Cambodia, Vietnam, Laos, China, Malaysia, Java, Sumatra); D – Sulawesi; E – Philippines; F – Australasia.

Node	MLSAR		S-DIVA		DEC	
	Area	Probability	Area	Probability	Area	Probability
1	C	0.99	CE	1.00	CE	1.00
2	C	0.99	C	0.50	C	0.82
			CE	0.50	CE	0.18
3	C	0.50	CE	0.50	CE	1.00
	E	0.50	E	0.50		
4	C	0.50	CE	1.00	CE	1.00
	E	0.50				
5	C	0.99	C	0.50	C	1.00
			CD	0.50		
6	C	0.50	D	0.50	CD	1.00
	D	0.50	CD	0.50		
7	C	0.50	CD	1.00	CD	1.00
	D	0.50				
8	C	0.99	BC	1.00	BC	1.00
9	A	0.99	AC	1.00	AC	1.00
10	C	0.99	BC	1.00	BC	1.00
11	C	0.99	BC	1.00	BC	1.00
12	C	0.95	CF	0.50	CF	0.82
			BCF	0.50	BCF	0.18
13	C	0.95	BC	1.00	BC	1.00

assessment of these glands makes their use complicated and problematic. We have here assumed that all of these variable gland configurations are related and homologous, because our examination of material from all subgenera did not produce an obvious distinction between them; they are all here generically called humeral glands (*sensu* Duellman and Trueb, 1986:59; Figs. 3–14). There is a need for a comprehensive, detailed study of body glands in *Hylarana* s.l., and in other closely related genera of Ranidae, which should include dissection of material. Despite their uncertain homology, we did note that the size and position of the humeral gland(s) along the forearm varies predictably between major clades (Table 3). Therefore, presence or absence of a humeral gland (or brachial gland) in itself may not be a useful character to define genera. Rather, more detailed attention needs to be paid to the exact position, shape and size of the humeral gland(s), and note whether they fail homology tests with other similar glands, in order to obtain any phylogenetic information of diagnostic value. Positional similarity is a well-known requirement for homology determinations (Patterson, 1982). Scott (2005) presented various arguments against imprecise character-state descriptions used verbatim from historical literature, which can adversely affect the informativeness of morphological characters in ranoid frogs.

Another set of characters that we observed to be potentially informative within these frogs is the position and shape of various accessory body glands in adults, particularly on the flanks and thighs, which Dubois (1992) used as diagnostic for *Chalcorana*. Dubois (1992) defined *Hylarana s.s.* as having dermal glands in larvae, although detailed species-level studies are few (see Gawor et al. (2009) for a regional study of *Hylarana s.l.* tadpoles, wherein differences in gland position in larvae were noted among species.). Presumably, these glands persist with a fair degree of positional similarity into adult frogs (there is no evidence that they fade or disappear at metamorphosis), particularly in the genera *Hydrophylax* (type: *H. malabarica*; clade I) and *Hylarana s.s.* (type: *H. erythraea*; clade F), and *Amnirana* (type: *A. amnicola*; clade D). Voucher specimens from our *Amnirana* and *Papurana* clades also demonstrated additional accessory body glands, which may be species-specific, and appear consistent within populations and putative species groups (L.A. Oliver, in prep.).

Additional external morphological characters of adults may prove informative to species diagnoses within clades of *Hylarana s.l.* The position, size, and shape of the rictal gland (Inger, 1966), or clusters of glands, behind the angle of the mouth can diagnose species in some *Hylarana s.l.* complexes, *sensu* Inger, 1966. We found that whether the upper and/or lower lip was uniformly white, or contained patterns or blotches, was consistent within species. Similarly, the general configuration of patterning present on the lateral flanks (including presence or absence of the dark 'eye-mask' only, or a continuous dark lateral band below the dorsolateral folds), is taxonomically useful, and has been noted previously in morphological work on *Papurana* (Kraus and Allison, 2007). Occasionally, the tympanic-border color appears as a useful taxonomic character. The extent and degree of development of the barring on the dorsal surface of the thigh, which can differ from both the barring on the dorsal surface of the shank and from the coloration of the posterior surface of the thighs, varies within clades and among species that we examined. The unique 'flash' patterning on the posterior surface of thighs in *Hylarana s.l.* varied regularly among species and remained consistent within species examined here, and may be similar to the species-specific variation in this pattern documented as being diagnostic among species of *Ptychadena* Boulenger, 1918 (Stewart, 1967). Particular attention should also be paid to the relative expansion of Digit 1 compared to Digits 3 and 4 on the hands, which we found varied among species, while the relative size of the discs on the hands and feet varied among genera. Further study should be invested into discerning the differences in expansion of discs and presence or absence of circummarginal grooves on certain digits in *Hylarana*, which was noted by Dubois (1992) and Biji et al. (2014). We hope that future studies will investigate these character systems in more detail within each clade.

4.3. Systematic account

Frogs currently placed in *Hylarana s.l.* have been apportioned among a number of subgenera, most of these created recently (Dubois, 1992; Fei et al., 1990, 2010). Our molecular analysis identifies a number of well-supported clades within *Hylarana s.l.* that correspond in varying degrees with several of these previously proposed subgenera while rejecting others. Our results now allow us to better sort among available morphological evidence to support formal recognition of several of these taxa. We believe that partition of *Hylarana s.l.* into multiple genera using these data better reflects the diverse biogeographic history of this large group than does retaining a single large genus spanning three continents. We expect it will also facilitate more-detailed investigations into these smaller clades. In particular, we believe that the two monophyletic invasions and radiations of *Hylarana s.l.* into Africa and Australasia over difficult-to-cross biogeographic barriers should be recognized taxonomically so as to emphasize the biological importance of those improbable events. Multiple invasions into India from southeastern Asia are also more easily highlighted and discussed with this revised taxonomic framework. Recognizing the African and Papuan clades, as well as the clades we retrieve that are clearly diagnosable morphologically, requires us to also taxonomically recognize a few additional clades that are more morphologically variable but supported by our molecular evidence so as to avoid leaving a paraphyletic *Hylarana.* Hence, we divide *Hylarana s.l.* into ten genera based on a combination of our monophyletic groupings, morphological diagnosability, biogeographical importance, and taxonomic precedence (Tables 1 and 3).

We raise Amnirana, Chalcorana, Humerana, Pulchrana, Papurana, and Sylvirana (Dubois, 1992), and Hydrophylax (Fitzinger, 1843) to generic rank. We retain Hylarana for the clade

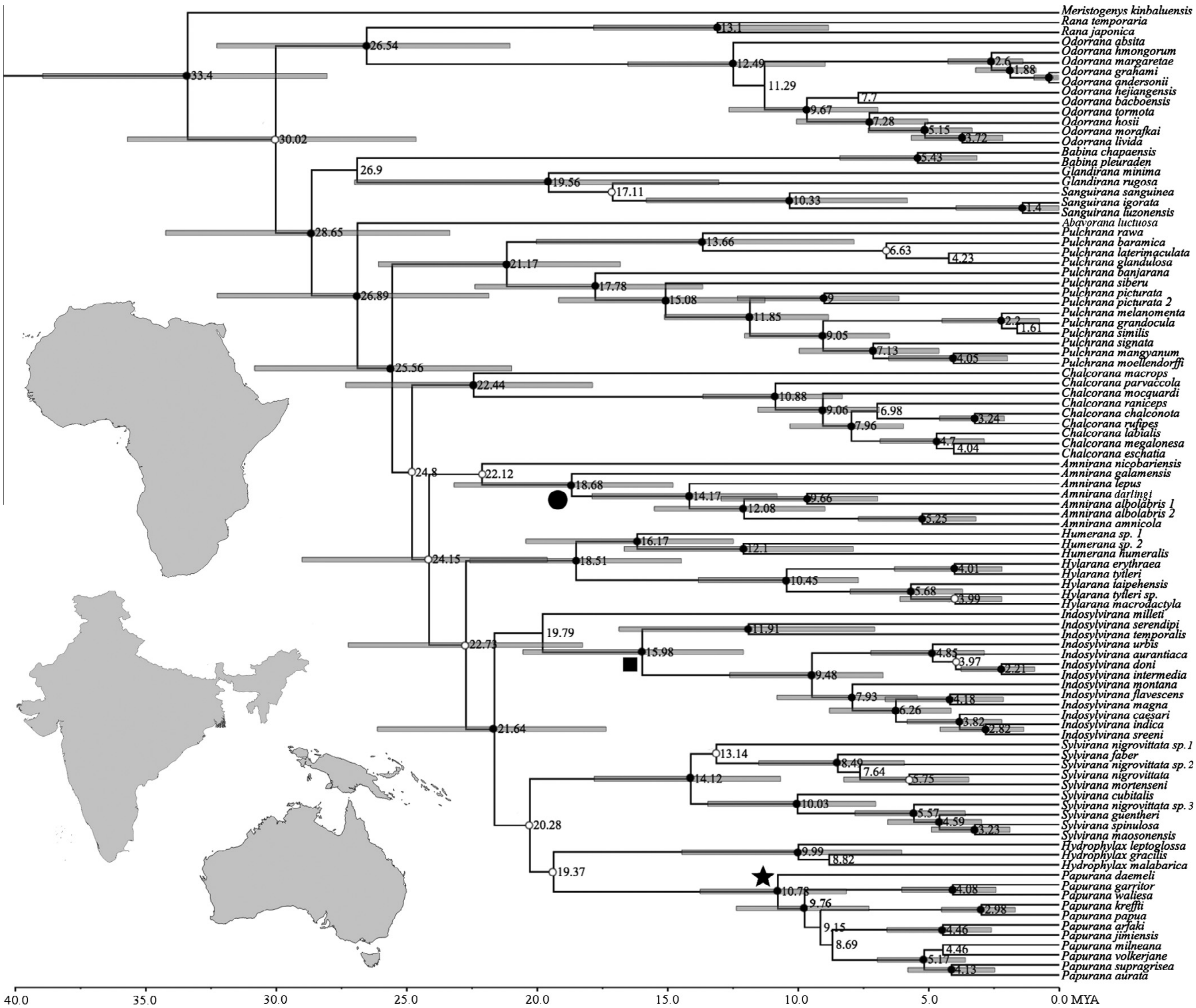

Fig. 4. Time-calibrated maximum clade credibility tree estimated using BEAST. Ages on nodes are in millions of years. Branch support values are BPP based on the topology recovered from the BEAST analysis. Node values ⩾0.95 have a black circle and nodes that are ⩾0.75 have a white circle. Nodes <0.75 are not labeled. Terminal names represent the revised taxonomy proposed in the Systematic Account. Three nodes have symbols corresponding with colonization events: large circle (Africa), square (first colonization of India), and star (Australasia).

containing *H. erythraea*, *H. macrodactyla*, *H. taipehensis*, and *H. tytleri*. We synonymize *Boulengerana*, *Tenuirana*, and *Tylerana* into *Sylvirana*, *Hylarana*, and *Papurana*, respectively. Additionally, we describe two new genera: one genus monotypic for *Hylarana luctuosa*, viz. *Abavorana* gen. nov., and the second, *Indosylvirana* gen. nov., containing *H. flavescens* plus *H. aurantiaca*, *H. intermedia*, *H. milleti*, *H. montana, H. temporalis*, and recently described Indian species (Biju et al., 2014). We tentatively assign untested species to clades based on suggestions of close relationships from the literature. However, these hypotheses need to be further tested with additional data for reliably identified voucher specimens. We briefly describe diagnostic morphological characters of each genus based on our voucher specimens (Table 3) and also from descriptions in the literature (Biju et al., 2014; Bortamuli et al., 2010; Boulenger, 1920; Brown and Guttman, 2002; Dubois, 1992; Kraus and Allison, 2007). The characters described are put forward as a preliminary delineation and require further exploration within each genus.

Family Ranidae Rafinesque 1814

Genus *Abavorana* gen. nov.

ETYMOLOGY: The name is derived from the Latin *avus*, meaning *grandfather*, the Latin prefix *ab-* indicating *away* or *from* (in the sense of *prior to*, in this case), and the Latin *rana*, meaning *frog*. The name can be interpreted, thus, as *ancestral frog* and is in recognition of this early phylogenetic separation from other frogs within our study clade.
TYPE SPECIES: *Limnodytes luctuosus* Peters, 1871 by monotypy.
MATERIAL EXAMINED: *Abavorana luctuosa* (FMNH 273219).
DIAGNOSIS: *Abavorana* can be diagnosed from other *Hylarana* *s.l.* by having the unique combination of absence of a vocal

sac, small pale spots on body and limbs, shagreened dorsum, red coloration on the dorsum, and absence of rictal ridges and dorsolateral folds.
TAXONOMIC NOTES: Additional description of *A. luctuosa* in Boulenger (1920). This species was earlier assigned to *Pulchrana* by Dubois (1992), but has been found here and in other studies to represent a separate lineage sister to remaining taxa in *Hylarana s.l.* (Pyron and Wiens, 2011; Wiens et al., 2009).
RANGE: Disjunct distribution in peninsular Thailand, Malaysia, Sumatra, and Borneo (Frost, 2014).

Genus *Amnirana* Dubois, 1992 stat. nov.:

TYPE SPECIES: *Hylarana amnicola* Perret, 1977 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *A. nicobariensis* and *A. amnicola*. By implication, the African taxa *Hylarana asperimma*, *H. fonensis*, *H. lemairei*, *H. longipes*, *H. occidentalis*, and *H. parkeriana* are provisionally included in *Amnirana*.
MATERIAL EXAMINED: *Amnirana amnicola* (AMNH 117606, 117621, 122818), *A. galamensis* (AMNH 23543, MVZ 234148, 245225), *A. lepus* (CAS 249985, 249987, USNM 584220), and *A. nicobariensis* (MVZ 239177, FMNH 266995).
TAXONOMIC NOTES: We recognize this clade based on its monophyletic status and biogeographic cohesion and isolation. Data available at this time do not allow for a morphological diagnosis due to high variability within the clade. Dubois (1992) placed the African taxa into two different sections of his classification of *Hylarana s.l.* based on the presence or absence of distinct humeral glands. However, the body glands in this genus are highly variable among species and, hence, cannot serve to define this clade. Another character previously considered informative at higher taxonomic levels is expansion of the tips of the fingers into discs, and character states of this are highly variable in *Amnirana*, and plesiomorphic in ranids (Scott, 2005). Furthermore, whether the posterior section of the abdominal skin is smooth or granular alternately occurs in different species of *Amnirana* (and differs across other clades of *Hylarana s.l.*) These variable characters partially explain why African *Hylarana s.l.* was placed into two sections in Dubois' (1992) classification. Dubois (1992) placed *A. galamensis* with *H. malabarica* in *Hydrophylax* due to similar unexpanded discs. We did not find the *Hydrophylax* clade to be closely related to *Amnirana* in our molecular analysis. We included only five of 11 described species of *Amnirana*, and included Biju et al. (2014)'s Indian *H. malabarica* sequences from GenBank. Our molecular analysis could not refute the monophyly of African *Amnirana*, nor the position of *A. nicobariensis* (previously placed in *Sylvirana*) as sister to this African clade. We are hesitant to raise *A. nicobariensis* to separate generic status, given that the non-molecular synapomorphies of *Amnirana* are not clear and external morphology provides no diagnostic characters at present. We concede that there is a huge biogeographic gap between *A. nicobariensis*' distribution and the rest of *Amnirana*. We defer any decision of excluding *A. nicobariensis* from *Amnirana* until further data are available to support a compelling decision. The range of variation in tadpole characters listed in Bortamuli et al. (2010) does not assist in explaining the placement of *A. nicobariensis* with the African species, but it is consistent with this placement.
RANGE: Western and central sub-Saharan Africa, and southern portions of the Horn of Africa, associated there with Central African Forests (Frost, 2014). *Amnirana nicobariensis* occurs in the Nicobar Islands, Peninsular Thailand, Sumatra, Java, Borneo, Sulu Archipelago, and Palawan (Frost, 2014).

Genus *Chalcorana* Dubois, 1992 stat. nov.:

TYPE SPECIES: *Hyla chalconotus* Schlegel, 1837 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *C. macrops* and *C. chalconota*. By implication, *Hylarana crassiovis*, *H. kampeni* and *H. scutigera* are also provisionally included in *Chalcorana*.
MATERIAL EXAMINED: *Chalcorana chalconota* (AMNH 107901–11) *C. eschatia* (FMNH 268851, 268859), *C. macrops* (MVZ 254478), *C. megalonesa* (FMNH 235641, 268981), *C. parvaccola* (FMNH 268613), and *C. rufipes* (FMNH 26857, 268579, 268587).
DIAGNOSIS: *Chalcorana* can be diagnosed as the only genus of *Hylarana s.l.* with 1st finger ⩽ 2nd finger, disc size on fingers ⩾ 2x width of the finger, and humeral gland 1/3 to 1/2 length of humerus. Additionally, they have a gracile body shape and many accessory body glands.
RANGE: Southern and Peninsular Thailand, Java, Sumatra, West Malaysia, northern and western Borneo, and Sulawesi (Frost, 2014).

Genus *Humerana* Dubois, 1992 stat. nov.:

TYPE SPECIES: *Rana humeralis* Boulenger, 1887 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *H.* sp. 1 (USNM 583186) and *H. humeralis*. By implication, *H. miopus* and *H. oatesii* are also provisionally included in *Humerana*.
MATERIAL EXAMINED: *Humerana oatesii* (AMNH 45579), *H. sp.* 1 (USNM 583186), and *H. sp.* 2 (USNM 583170).
DIAGNOSIS: *Humerana* can be diagnosed by its unique combination of having a mid-dorsal color line, 1st finger > 2nd finger, and disc expansion roughly equal to that of the width of the fingers.
RANGE: Myanmar, Peninsular Thailand and Malaysia, northeastern India, Nepal, Bangladesh, and Bhutan (Frost, 2014).

Genus *Hydrophylax* Fitzinger, 1843, stat. nov.:

TYPE SPECIES: *Rana malabarica* Tschudi, 1838 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *H. leptoglossa* and *H. malabarica*.
MATERIAL EXAMINED: *Hydrophylax gracilis* (AMNH 76991–93, 77496, 74235–37, 74281–82, 76990, 77497, 83646), *H. malabarica* (AMNH 84587, 89797, 38080–84, 38086–89, 40055–67, 63507–08), and *H. leptoglossa* (AMNH 53080, CAS 239886).
DIAGNOSIS: *Hydrophylax* can be diagnosed by its unique combination of having a postocular mask (not as distinct as in *Papurana*), robust body, rear of thighs with strong vermiculations, large rictal gland, prominent humeral glad (but not as prominent as in morphologically similar *Sylvirana*), and circum-marginal grooves sometimes absent on finger 1.
RANGE: Sri Lanka, India, Bangladesh, southern Myanmar, and western Thailand (Frost, 2014).

Genus *Hylarana* Tschudi, 1838 stat. nov.:

TYPE SPECIES: *Hyla erythraea* Schlegel, 1837 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *H. taipehensis* and *H. erythraea*.
SYNONYMS: *Tenuirana* Fei et al., 1990 syn. nov. Type species *Rana taipehensis* Fei et al., 1990.

MATERIAL EXAMINED: *Hylarana erythraea* (AMNH 168529, 168530, FMNH 263289), *H. macrodactyla* (AMNH 26221, 180616–732, FMNH 255186, USNM 583138, 583140), *H. taipehensis* (AMNH 163972–73, 168753–54), and *H. tytleri* (CAS 247465, USNM 583188, 583190).
DIAGNOSIS: *Hylarana* can be diagnosed by its unique combination of lacking a mid-dorsal color line (present in morphologically similar *Humerana*), 1st finger subequal to second, and disc expansion of 1.2 to 1.7x the width of the finger.
TAXONOMIC NOTES: *H. macrodactyla* and *H. taipehensis* (the two species previously placed in *Tenuirana*) were considered to be part of *Hylarana s.s.* by Dubois (1992).
RANGE: Bangladesh, India, Nepal, Bhutan, Cambodia, Laos, Peninsular Malaysia, Myanmar, Thailand, Vietnam, Java, Penang Perak, Borneo, Singapore, Taiwan, and southern China (Frost, 2014). *Hylarana s.s.* (*H. erythraea*) has also been introduced to the Philippines (Diesmos et al., 2002).

Genus *Indosylvirana* gen. nov.

ETYMOLOGY: The generic name is Latin, in recognition that the geographic range of the clade is largely restricted to India and that all included species were formerly assigned to *Sylvirana*.
TYPE SPECIES: *Rana flavescens* Jerdon, 1853.
DEFINITION: All descendants of the most recent common ancestor of *I. milleti* and *I. flavescens*.
MATERIAL EXAMINED: *Indosylvirana aurantiaca* (AMNH 78924–25, 80086–67) and *I. temporalis* (AMNH 74217–18, 76988–89, 77490–95).
DIAGNOSIS: *Indosylvirana* can be diagnosed by its unique combination of having a postocular mask (faded and not as distinct as in *Papurana*), thin and well-defined dorsolateral folds, and prominent humeral gland extending along ¾ length of arm.
TAXONOMIC NOTES: We were unable to examine voucher specimens of *I. milleti*, and the diagnosis does not include information for this species. All species of *Indosylvirana* were previously assigned to *Sylvirana* by Dubois (1992) but are found to be a separate clade in our analysis.
RANGE: All species except *I. milleti* are restricted to India and Sri Lanka. *Indosylvirana milleti* is located in southern Vietnam, southern Thailand, and southwestern Cambodia (Frost, 2014).

Genus *Papurana* Dubois, 1992 stat. nov.:

TYPE SPECIES: *Rana papua* Lesson, 1826 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *P. daemeli* and *P. papua*. By implication, New Guinean taxa *H. grisea* and *H. novaeguineae* are provisionally included in *Papurana* as all other New Guinean species of *Hylarana s.l.* are representatives of *Papurana*, and these species are morphologically similar to the remaining members of the genus. Dubois (1992) also placed *H. elberti*, *H. florensis*, and *H. moluccana* in *Papurana*. This hypothesis needs further testing using both molecular and morphological data, but we provisionally include them in *Papurana*.
SYNONYMS: *Tylerana* Dubois, 1992 syn. nov. Type species *Rana jimiensis* Tyler, 1963.
MATERIAL EXAMINED: *Papurana arfaki* (AMNH 79933–34, 191673), *P. daemeli* (AMNH 74863–68, 81292–93), *P. garritor* (AMNH 131003), *P. jimiensis* (AMNH 84583) *P. kreffti* (AMNH 35404), *P. novaeguineae* (AMNH 84566), *P. papua* (AMNH 98992–93), and *P. supragrisea* (AMNH 66616).
DIAGNOSIS: *Papurana* can be diagnosed by the unique combination of having a postocular eye mask, robust body shape, rear of thighs with strong vermiculations, and dorsolateral folds either absent or thin, with asperities.
TAXONOMIC NOTES: Kraus and Allison (2007) recorded various characters to distinguish among species of New Guinean *Hylarana*. *Papurana jimiensis* and *P. arfaki* were originally assigned to *Tylerana* by Dubois (1992). The greatest morphological variation in this genus exists between (*P. arfaki* + *P. jimiensis*) and all other New Guinean species of *Papurana*.
RANGE: New Guinea; D'Entrecasteaux Islands; Sudest, Louisiade Islands; Aru Islands; New Hanover Island; New Britain; Yapen; Seram; Manus; Waigeo; Solomon Islands; New Ireland; Cape York Peninsula, northeastern Queensland, Australia; and northeastern border of the Gulf of Carpentaria, Northern Territory, Australia (Frost, 2014). The ranges of the provisionally included species (*P. elberti*, *P. florensis*, and *P. moluccana*) include Flores, Sumba, Timor, Wetar, Babar, Tanimbar, Lombok, and Moluccas.

Genus *Pulchrana* Dubois, 1992 stat. nov.:

TYPE SPECIES: *Polypedates signatus* Günther, 1872 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *P. baramica* and *P. signata*. By implication, *H. centropeninsularis* and *H. debussyi* are also provisionally included in *Pulchrana*.
MATERIAL EXAMINED: *Pulchrana baramica* (AMNH 90514–17; FMNH 248217, 266574, 266927), *P. glandulosa* (AMNH 90542–49), *P. picturata* (FMNH 245786, 266946), *P. signata* (AMNH 90592–99, FMNH 273117, 269721), and *P. similis* (FMNH 266275).
DIAGNOSIS: *Pulchrana* can be diagnosed by its unique combination of weakly or strongly warty skin; a mottled to spotted dorsum, sometimes with bright coloration; fine or warty dorsolateral folds, also sometimes with bright coloration; and a large outer metatarsal tubercle.
TAXONOMIC NOTES: Brown and Guttman (2002) previously examined the *Pulchrana signata* complex using morphology and molecules. With the exception of *Abavorana luctuosa*, our study supports the original delineation of *Pulchrana* (Dubois, 1992).
RANGE: Southern Vietnam, Peninsular Thailand, Peninsular Malaysia, Java, Borneo, Siberut Island, Sumatra, Singapore, Bangka Island, Natuna Islands, Sulu Archipelago, and the Philippines (Frost, 2014).

Genus *Sylvirana* Dubois, 1992 stat. nov.:

TYPE SPECIES: *Lymnodytes nigrovittatus* Blyth, 1856 by original designation.
DEFINITION: All descendants of the most recent common ancestor of *S. spinulosa* and *S. nigrovittata*. *Hylarana hekouensis* and *H. menglaensis* were described as part of the *S. nigrovittata* group (Fei et al., 2008) and are also provisionally placed in *Sylvirana*. We were unable to include in our analyses several other mainland Southeast Asian and Indian species that have also been placed in *Sylvirana*. For these species, it is necessary to further test their taxonomic placement. It is likely, for instance, than one or more (especially among the Indian species) may be more closely related to *Indosylvirana* or *Hydrophylax*. These species are *H. attigua*, *H. celebensis*, *H. chitwanensis*, *H. garoensis*, *H. lateralis*, *H. latouchii*, *H. margariana*, and *H. montivaga*. We consider these *incertae sedis*.
SYNONYMS: *Boulengerana* Fei et al., 2010 syn. nov. Type species *Rana guentheri* Boulenger, 1882.

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MATERIAL EXAMINED: *Sylvirana cubitalis* (CAS 210634, FMNH 265818, 270736), *S. guentheri* (AMNH 16190, 161462–63, 163940–42), *S. mortenseni* (FMNH 263303), *S. nigrovittata* (AMNH 161270–75, USNM 583124–25, 583178), and *S. spinulosa* (MVZ 236683).

DIAGNOSIS: Similar to *Indosylvirana*, *Hydrophylax*, and *Papurana*, *Sylvirana* can be diagnosed by its unique combination of having a postocular eye mask, robust body shape, rear of thighs with strong vermiculations, thick dorsolateral folds, and a humeral gland that is less prominent than that seen in *Indosylvirana*, but more prominent than those in *Hydrophylax* and *Papurana*. It can be differentiated from *Papurana* based on thicker and better-developed dorsolateral folds, less developed postocular mask, and more prominent humeral gland; from *Hydrophylax* by its smaller rictal ridge, generally larger discs on the fingers, and more prominent humeral gland; and from *Indosylvirana* by its thicker dorsolateral folds and less prominent humeral gland.

TAXONOMIC NOTES: *Sylvirana guentheri* was the only species assigned to *Boulengerana*. We synonomize it with *Sylvirana* because it falls within that clade.

RANGE: Mainland China, Hainan Island, Taiwan, Myanmar, Thailand, Laos, Cambodia, Vietnam, Bhutan, Nepal, Bangladesh, and West Bengal (Frost, 2014).

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Appendix A

Taxa and vouchers used in this study. Samples that we sequenced are marked as "This Study" and sequences we downloaded from GenBank are cited by the original publication.

Accession No.	Genus	New Genus	Species	Country: Locality	Study
FMNH 256531	*Babina*	NA	*chapaensis*	Laos: Xieng Khouang Prov.	This study
FMNH 256532	*Babina*	NA	*chapaensis*	Laos: Xieng Khouang Prov.	This study
CAS 207510	*Babina*	NA	*pleuraden*	China: Yunnan Prov.	This study
CIB-HUI040003	*Glandirana*	NA	*minima*	China: Heilongjiang	Che et al. (2007)
NIBRAM0000000445	*Glandirana*	NA	*rugosa*	Korea	Jeong et al. (2013)
FMNH 273219	*Hylarana*	*Abavorana*	*luctuosa*	Malaysia: Sarawak	This study
UTA 44664	*Hylarana*	*Amnirana*	*albolabris 1*	Cameroon: East Province	This study
TMSA 84177	*Hylarana*	*Amnirana*	*albolabris 1*	Cameroon: Nguti	This study
ROM 19861	*Hylarana*	*Amnirana*	*albolabris 2*	Liberia: Sapo National Park	This study
ROM 19863	*Hylarana*	*Amnirana*	*albolabris 2*	Liberia: Sapo National Park	This study
CAS 229991	*Hylarana*	*Amnirana*	*albolabris sp.*	Sierra Leone: Kasewe Hills Forest Reserve	This study
AMNH 117606	*Hylarana*	*Amnirana*	*amnicola*	Cameroon: Southwest Prov.	This study
AMNH 117621	*Hylarana*	*Amnirana*	*amnicola*	Cameroon: Southwest Prov.	This study
AMNH 122818	*Hylarana*	*Amnirana*	*amnicola*	Cameroon: East Prov.	This study
PEM A6989	*Hylarana*	*Amnirana*	*darlingi*	Angola: Tazua Falls	This study
MVZ 234148	*Hylarana*	*Amnirana*	*galamensis*	Tanzania: Mara Region	This study
MVZ 245225	*Hylarana*	*Amnirana*	*galamensis*	Ghana: Greater Accra Region	This study
CAS 249985	*Hylarana*	*Amnirana*	*lepus*	Cameroon: Sanaga River Bank	This study
CAS 249987	*Hylarana*	*Amnirana*	*lepus*	Cameroon: Sanaga River Bank	This study
USNM 584220	*Hylarana*	*Amnirana*	*lepus*	Congo: Lekoumou	This study
FMNH 266995	*Hylarana*	*Amnirana*	*nicobariensis*	Indonesia: West Sumatra	This study
FMNH 266996	*Hylarana*	*Amnirana*	*nicobariensis*	Indonesia: West Sumatra	This study
MVZ 239177	*Hylarana*	*Amnirana*	*nicobariensis*	Indonesia: Sumatra	This study
MVZ 253938	*Hylarana*	*Amnirana*	*nicobariensis*	Indonesia: Java	This study

Appendix A (*continued*)

Accession No.	Genus	New Genus	Species	Country: Locality	Study
MVZ 239431	*Hylarana*	*Chalcorana*	*chalconota*	Indonesia: Sumatra	This study
CAS 229564	*Hylarana*	*Chalcorana*	*eschatia*	Myanmar: Pakchan Reserve Forest	This study
FMNH 268851	*Hylarana*	*Chalcorana*	*eschatia*	Thailand: Khao Luang National Park	This study
FMNH 268859	*Hylarana*	*Chalcorana*	*eschatia*	Thailand: Khao Phanom Bencha Park	This study
FRIM 1539	*Hylarana*	*Chalcorana*	*labialis*	Malaysia: Kedah	Stuart et al. (2006)
FRIM 1735	*Hylarana*	*Chalcorana*	*labialis*	Malaysia: Kedah	Stuart et al. (2006)
MVZ 254478	*Hylarana*	*Chalcorana*	*macrops*	Indonesia: Sulawesi	This study
FMNH 235641	*Hylarana*	*Chalcorana*	*megalonesa*	Malaysia: Sabah	This study
FMNH 268981	*Hylarana*	*Chalcorana*	*megalonesa*	Malaysia: Sarawak	This study
MVZ 254679	*Hylarana*	*Chalcorana*	*mocquardi*	Indonesia: Sulawesi	This study
MVZ 254762	*Hylarana*	*Chalcorana*	*mocquardi*	Indonesia: Sulawesi	This study
FMNH 268613	*Hylarana*	*Chalcorana*	*parvaccola*	Indonesia: West Sumatra	This study
FMNH 267961	*Hylarana*	*Chalcorana*	*raniceps*	Malaysia: Sarawak	Stuart et al. (2006)
FMNH 267962	*Hylarana*	*Chalcorana*	*raniceps*	Malaysia: Sarawak	Stuart et al. (2006)
FMNH 268575	*Hylarana*	*Chalcorana*	*rufipes*	Indonesia: West Sumatra	This study
SDBDU 2009.1094	*Hylarana*	*Humerrana*	*cf. humeralis*		Biju et al. (2014)
USNM 583186	*Hylarana*	*Humerrana*	*sp. 1*	Myanmar	This study
USNM 583170	*Hylarana*	*Humerrana*	*sp. 2*	Myanmar	This study
DZ 1156	*Hylarana*	*Hydrophylax*	*gracilis*	Sri Lanka: Ganemulla	Biju et al. (2014)
DZ 1164	*Hylarana*	*Hydrophylax*	*gracilis*	Sri Lanka: Hiyare	Biju et al. (2014)
CAS 239886	*Hylarana*	*Hydrophylax*	*leptoglossa*	Myanmar: Kyaukpyu District	This study
BNHS 5879	*Hylarana*	*Hydrophylax*	*malabarica*	India: Meladoor	Biju et al. (2014)
BNHS 5880	*Hylarana*	*Hydrophylax*	*malabarica*	India: Amboli	Biju et al. (2014)
FMNH 263289	*Hylarana*	*Hylarana*	*erythraea*	Cambodia: Koh Kong Prov.	This study
FMNH 255186	*Hylarana*	*Hylarana*	*macrodactyla*	Laos: Champasak Prov.	This study
USNM 583138	*Hylarana*	*Hylarana*	*macrodactyla*	Myanmar	This study
USNM 583140	*Hylarana*	*Hylarana*	*macrodactyla*	Myanmar	This study
AMNH 168754	*Hylarana*	*Hylarana*	*taipehensis*	Vietnam: Lao Cai	This study
AMNH 163973	*Hylarana*	*Hylarana*	*taipehensis*	Vietnam: Ha Giang	This study
SDBDU 2009.421	*Hylarana*	*Hylarana*	*tytleri sp.*	India	Biju et al. (2014)
CAS 229614	*Hylarana*	*Hylarana*	*tytleri*	Myanmar: Tanintharyi Div.	This study
CAS 247465	*Hylarana*	*Hylarana*	*tytleri*	Myanmar: Tanintharyi Div.	This study
USNM 583190	*Hylarana*	*Hylarana*	*tytleri*	Myanmar	This study
USNM 583188	*Hylarana*	*Hylarana*	*tytleri*	Myanmar	This study
BNHS 5811	*Hylarana*	*Indosylvirana*	*aurantiaca*	India: Chathankod	Biju et al. (2014)
SDBDU 2011.520	*Hylarana*	*Indosylvirana*	*aurantiaca*	India:Chathankod	Biju et al. (2014)
BNHS 5842	*Hylarana*	*Indosylvirana*	*caesari*	India: Humbarli	Biju et al. (2014)
SDBDU 2004.4527	*Hylarana*	*Indosylvirana*	*caesari*	India: Amboli	Biju et al. (2014)
BNHS 5815	*Hylarana*	*Indosylvirana*	*doni*	India: Padagiri	Biju et al. (2014)
BNHS 5818	*Hylarana*	*Indosylvirana*	*doni*	India: Parambikulam	Biju et al. (2014)
BNHS 5844	*Hylarana*	*Indosylvirana*	*flavescens*	India: Settukunnu	Biju et al. (2014)
BNHS 5845	*Hylarana*	*Indosylvirana*	*flavescens*	India: Sairandhri	Biju et al. (2014)
BNHS 5848	*Hylarana*	*Indosylvirana*	*indica*	India: Charmadi Ghats	Biju et al. (2014)
BNHS 5855	*Hylarana*	*Indosylvirana*	*indica*	India: Meenmutty	Biju et al. (2014)
BNHS 5832	*Hylarana*	*Indosylvirana*	*intermedia*	India: Kalpetta	Biju et al. (2014)
BNHS 5836	*Hylarana*	*Indosylvirana*	*intermedia*	India: Kakkayam	Biju et al. (2014)
BNHS 5857	*Hylarana*	*Indosylvirana*	*magna*	India: Pandimotta	Biju et al. (2014)
SDBDU 2002.2050	*Hylarana*	*Indosylvirana*	*magna*	India: Kakkachi	Biju et al. (2014)
ROM 34429	*Hylarana*	*Indosylvirana*	*milleti*	Vietnam: Gia Lai	This study
BNHS 5862	*Hylarana*	*Indosylvirana*	*montana*	India: Bhagamandala	Biju et al. (2014)
BNHS 5865	*Hylarana*	*Indosylvirana*	*montana*	India: Bygoor	Biju et al. (2014)
DZ 1144	*Hylarana*	*Indosylvirana*	*serendipi*	Sri Lanka: Kudawa	Biju et al. (2014)
DZ 1145	*Hylarana*	*Indosylvirana*	*serendipi*	Sri Lanka: Kudawa	Biju et al. (2014)
BNHS 5869	*Hylarana*	*Indosylvirana*	*sreeni*	India: Kuddam	Biju et al. (2014)
BNHS 5871	*Hylarana*	*Indosylvirana*	*sreeni*	India: Kaikatti	Biju et al. (2014)
DZ 1141	*Hylarana*	*Indosylvirana*	*temporalis*	Sri Lanka: Kudawa	Biju et al. (2014)
DZ 1153	*Hylarana*	*Indosylvirana*	*temporalis*	Sri Lanka: Panwila	Biju et al. (2014)
BNHS 5837	*Hylarana*	*Indosylvirana*	*urbis*	India: Kadavanthra	Biju et al. (2014)
BNHS 5841	*Hylarana*	*Indosylvirana*	*urbis*	India: Meladoor	Biju et al. (2014)
BPBM 19463	*Hylarana*	*Papurana*	*arfaki*	Papua New Guinea: Central Prov.	This study
RG 7637	*Hylarana*	*Papurana*	*arfaki*	Indonesia: Papua Prov., Wondiwoi Mts	This study

(*continued on next page*)

Appendix A (*continued*)

Accession No.	Genus	New Genus	Species	Country: Locality	Study
RG 6548	*Hylarana*	*Papurana*	*aurata*	Indonesia: Papua Prov., Nabire	This study
RG 7588	*Hylarana*	*Papurana*	*aurata*	Indonesia: Papua Prov., Nabire	This study
BPBM 36024	*Hylarana*	*Papurana*	*daemeli*	Papua New Guinea: East Sepik Prov.	This study
BPBM 36025	*Hylarana*	*Papurana*	*daemeli*	Papua New Guinea: East Sepik Prov.	This study
BPBM 15488	*Hylarana*	*Papurana*	*garritor*	Papua New Guinea: Gulf Prov.	This study
BPBM 15489	*Hylarana*	*Papurana*	*garritor*	Papua New Guinea: Gulf Prov.	This study
BPBM 22831	*Hylarana*	*Papurana*	*jimiensis*	Papua New Guinea: West Sepik Prov.	This study
BPBM 22832	*Hylarana*	*Papurana*	*jimiensis*	Papua New Guinea: West Sepik Prov.	This study
BPBM 22402	*Hylarana*	*Papurana*	*kreffti*	Papua New Guinea: East New Britain	This study
BPBM 22403	*Hylarana*	*Papurana*	*kreffti*	Papua New Guinea: East New Britain	This study
BPBM 15749	*Hylarana*	*Papurana*	*milneana*	Papua New Guinea: Milne Bay Prov.	This study
BPBM 16361	*Hylarana*	*Papurana*	*milneana*	Papua New Guinea: Milne Bay Prov.	This study
BPBM 20741	*Hylarana*	*Papurana*	*milneana*	Papua New Guinea: Milne Bay Prov.	This study
BPBM 22844	*Hylarana*	*Papurana*	*papua*	Papua New Guinea: West Sepik Prov.	This study
LSUMZ 97639	*Hylarana*	*Papurana*	*papua*	Papua New Guinea: Madang Prov.	This study
BPBM 24218	*Hylarana*	*Papurana*	*supragrisea*	Papua New Guinea: Central Prov.	This study
BPBM 39587	*Hylarana*	*Papurana*	*supragrisea*	Papua New Guinea: Northern Prov.	This study
RG 7636	*Hylarana*	*Papurana*	*volkerjane*	Indonesia: Papua Prov., Wondiwoi Mts	This study
RG 7724	*Hylarana*	*Papurana*	*volkerjane*	Indonesia: Papua Prov., Wondiwoi Mts	This study
BPBM 16384	*Hylarana*	*Papurana*	*waliesa*	Papua New Guinea: Milne Bay Prov.	This study
BPBM 16398	*Hylarana*	*Papurana*	*waliesa*	Papua New Guinea: Milne Bay Prov.	This study
ZRC8326	*Hylarana*	*Pulchrana*	*banjarana*	Malaysia: Peninsular, Pahang	Brown and Siler, 2014
FMNH 248217	*Hylarana*	*Pulchrana*	*baramica*	Brunei: Belait District	This study
FMNH 266574	*Hylarana*	*Pulchrana*	*baramica*	Malaysia: Sarawak	This study
FMNH 266927	*Hylarana*	*Pulchrana*	*baramica*	Indonesia: West Sumatra	This study
FMNH 248254	*Hylarana*	*Pulchrana*	*glandulosa*	Brunei: Belait District	Brown and Siler (2014)
FMNH 266573	*Hylarana*	*Pulchrana*	*glandulosa*	Malaysia: Sarawak	Stuart (2008)
KU 302375	*Hylarana*	*Pulchrana*	*grandocula*	Philippines: Camiguin Sur Island	Brown and Siler (2014)
KU 302378	*Hylarana*	*Pulchrana*	*grandocula*	Philippines: Camiguin Sur Island	Brown and Siler (2014)
KUHE 17593	*Hylarana*	*Pulchrana*	*laterimaculata*	Malaysia: Sarawak	Matsui et al. (2012)
KU 303577	*Hylarana*	*Pulchrana*	*mangyanum*	Philippines: Mindoro Island	Brown and Siler (2014)
KU 303578	*Hylarana*	*Pulchrana*	*mangyanum*	Philippines: Mindoro Island	Brown and Siler (2014)
ELR 164	*Hylarana*	*Pulchrana*	*melanomenta*	Philippines: Tawi-tawi Island	Brown and Siler (2014)
ELR 165	*Hylarana*	*Pulchrana*	*melanomenta*	Philippines: Tawi-tawi Island	Brown and Siler (2014)
KU 309009	*Hylarana*	*Pulchrana*	*moellendorffi*	Philippines: Palawan Island	Brown and Siler (2014)
KU 327050	*Hylarana*	*Pulchrana*	*moellendorffi*	Philippines: Palawan Island	Brown and Siler (2014)
FMNH 245786	*Hylarana*	*Pulchrana*	*picturata*	Malaysia: Sabah	This study
FMNH 266946	*Hylarana*	*Pulchrana*	*picturata 2*	Indonesia: West Sumatra	This study
MZB Amp 14565	*Hylarana*	*Pulchrana*	*rawa*	Indonesia: Sumatra	Matsui et al. (2012)
BJE 202	*Hylarana*	*Pulchrana*	*siberu*	Indonesia: Siberut Island	Brown and Siler (2014)
BJE 236	*Hylarana*	*Pulchrana*	*siberu*	Indonesia: Siberut Island	Brown and Siler (2014)
FMNH 273117	*Hylarana*	*Pulchrana*	*signata*	Malaysia: Sarawak	This study
FMNH 266275	*Hylarana*	*Pulchrana*	*similis*	Philippines: Luzon, Zambales	This study
CAS 210634	*Hylarana*	*Sylvirana*	*cubitalis*	Myanmar: Shan State	This study
FMNH 265818	*Hylarana*	*Sylvirana*	*cubitalis*	Thailand: Loei, Phu Rua	This study
FMNH 270736	*Hylarana*	*Sylvirana*	*cubitalis*	Thailand: Nan Prov., Pua District	This study
FMNH 267767	*Hylarana*	*Sylvirana*	*faber*	Cambodia: Pursat Prov.	Stuart (2008)
AMNH 163940	*Hylarana*	*Sylvirana*	*guentheri*	Vietnam: Ha Giang	This study
AMNH 163941	*Hylarana*	*Sylvirana*	*guentheri*	Vietnam: Ha Giang	This study

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Appendix A (*continued*)

Accession No.	Genus	New Genus	Species	Country: Locality	Study
FMNH 255637	*Hylarana*	*Sylvirana*	*maosonensis*	Vietnam: Nghe An	This study
FMNH 263303	*Hylarana*	*Sylvirana*	*mortenseni*	Cambodia: Koh Kong Prov.	This study
FMNH 266318	*Hylarana*	*Sylvirana*	*mortenseni*	Cambodia: Koh Kong Prov.	This study
USNM 583178	*Hylarana*	*Sylvirana*	*nigrovittata*	Myanmar	This study
USNM 583124	*Hylarana*	*Sylvirana*	*nigrovittata sp. 1*	Myanmar	This study
USNM 583125	*Hylarana*	*Sylvirana*	*nigrovittata sp. 1*	Myanmar	This study
AMNH 161290	*Hylarana*	*Sylvirana*	*nigrovittata sp. 2*	Vietnam: Ha Tinh	This study
AMNH 161299	*Hylarana*	*Sylvirana*	*nigrovittata sp. 2*	Vietnam: Ha Tinh	This study
AMNH 161280	*Hylarana*	*Sylvirana*	*nigrovittata sp. 3*	Vietnam: Ha Tinh	This study
MVZ 236683	*Hylarana*	*Sylvirana*	*spinulosa*	China: Hainan Prov.	This study
ROM 44390	*Hylarana*	*Sylvirana*	*spinulosa*	China: Hainan Prov.	This study
FMNH 268503	*Limnonectes*	NA	*kochangae*		This study
FMNH 258107	*Odorrana*	NA	*absita*	Laos: Xe Kong Prov.	Stuart (2008)
CAS 233900	*Odorrana*	NA	*andersonii*	China: Yunnan Prov.	This study
CAS 233901	*Odorrana*	NA	*andersonii*	China: Yunnan Prov.	This study
FMNH 255611	*Odorrana*	NA	*bacboensis*	Vietnam: Nghe An Prov.	Stuart (2008)
CAS 207505	*Odorrana*	NA	*grahami*	China: Yunnan Prov.	Stuart (2008)
SCUM0405180CJ	*Odorrana*	NA	*hejiangensis*	China: Hejiang, Sichuan	Che et al. (2007)
ROM 26370	*Odorrana*	NA	*hmongorum*	Vietnam: Lao Cai Prov.	Stuart (2008)
FMNH 273209	*Odorrana*	NA	*hosii*	Malaysia: Sarawak	This study
FMNH 263415	*Odorrana*	NA	*livida*	Thailand: Prachuap Kirikhan Prov.	Stuart et al. (2006)
FMNH 233029	*Odorrana*	NA	*margaretae*	China: Sichuan Prov.	Stuart (2008)
ROM 39907	*Odorrana*	NA	*morafkai*	Vietnam: Tram Lap	Stuart (2008)
No voucher	*Odorrana*	NA	*tormota*	China: Anhui Prov.	Stuart (2008)
CAS 245414	*Rana*	NA	*japonica*	Myanmar: Myitkyina Dist.	This study
FMNH 259496	*Sanguirana*	NA	*igorata*	Philippines: Luzon, Kalinga	Stuart (2008)
USNM 512317	*Sanguirana*	NA	*luzonensis*	Philippines: Polillo Island	This study
RMB 3011	*Sanguirana*	NA	*sanguinea*	Philippines: Palawan	Bossuyt et al. (2006)

Institutional abbreviations: American Museum of Natural History (AMNH); Bombay Natural History Society Museum (BNHS); Bernice Pauahi Bishop Museum (BPBM); Ben J Evans field number (BJE); California Academy of Sciences (CAS);Chengdu Institute of Biology, the Chinese Academy of Sciences (CIBHU); Department of Zoology, University of Peradeniya (DZ); Edmund B. Leo Rico field number (ELR); Field Museum of Natural History (FMNH); Forest Research Institute of Malaysia (FRIM); Kansas University Biodiversity Institute (KU) ;Kyoto University (KUHE); Louisiana State University Museum of Natural Science (LSUMZ); Museum of Vertebrate Zoology at Berkeley (MVZ); Museum Zoologicum Bogoriense (MZB); National Institute of Biological Resources South Korea (NIBR); Rainer Günther field number (RG); Rafe M. Brown (RMB); Royal Ontario Museum (ROM); Systematics Lab, University of Delhi (SBDU); Sichuan University Museum (SCUM); Ditsong NationalMuseum of Natural History (TMSA); National Museum of Natural History (USNM); University Texas at Austin (UTA); Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC).

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