

# An investigation into the taxonomy of *Abavorana luctuosa* (Peters, 1871) (Anura, Ranidae) and the resurrection of *Rana decorata* Mocquard, 1890 from Borneo

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## Abstract

The taxonomic status of the ranid frog *Abavorana luctuosa* (Peters, 1871) was investigated using a combination of molecular and morphological data. The analyses revealed that *A. luctuosa sensu lato* is composed of two species in Borneo. One of these species agrees with the description of *Rana decorata* Mocquard, 1890 which is resurrected in the combination *Abavorana decorata* comb. nov. (Mocquard, 1890). *Abavorana decorata* is recovered as the sister lineage to the remainder of *Abavorana* and differs by a 16.0–17.0 % uncorrected pairwise sequence divergence from its congeners *A. nazgul* and *A. luctuosa*, respectively. It is distinguishable morphologically from *A. luctuosa* and *A. nazgul* by its ventral pattern (bold, black and white reticulations on its venter along with bold banding on the underside of hind limbs vs. generally immaculate and spotted in the latter two species), and a prominent white streak beneath the eye and/or tympanum extending to the corner of the jaw. *Abavorana decorata* further differs from *A. luctuosa* by having a significantly wider head and snout, larger interorbital and tympanum diameters, longer femur in both sexes, and various combinations of other mensural characters. Both species are sympatric in Borneo and this discovery adds to a growing number of widespread Sundaic species shown to be species complexes with distinct forms in Borneo.

## Key words

amphibia, biodiversity, conservation, endemic, herpetofauna, phylogeny, Sundaland, systematics

## Introduction

The Mahogany frog (*Abavorana luctuosa*) is a colourful riparian species heard at night calling from tangled thickets along the edges of small streams and rivers as well as standing bodies of water such as ponds, pig wallows and pools in intermittent streams on the Thai-Malay Peninsula and Borneo. *Abavorana luctuosa* was described by Peters in 1871 from an unspecified location in Sarawak, East Malaysian Borneo (Capoccia 1957). It was once thought to be a single wide-ranging species across Sundaland until a second species *A. nazgul*, was recently described from Gunung Jerai in Peninsular Malaysia (Quah et al. 2017). In their analyses, Quah et al. (2017) also recovered populations of *A. luctuosa* from Sabah as polyphyletic and only distantly related to one another.

Building upon these preliminary findings, we hypothesize that these populations are distinct evolutionary lineages and test this hypothesis with increased sample sizes from Borneo, Thailand, Peninsular Malaysia and detailed morphological, colour pattern, and genetic analyses based on the mitochondrial genes 16S, ND1 and flanking tRNAs (tRNA-Leu, tRNA-Ile, and tRNA-Gln). Given the results from the preponderance of data analyses herein, we rescind Boulenger's synonymization of *Rana decorata* Mocquard, 1890 with *Abavorana luctuosa* and resurrect the species in the combination *Abavorana decorata* comb. nov. (Mocquard, 1890).

## Materials and methods

### DNA extraction and amplification

Nine additional specimens of *Abavorana luctuosa* *sensu lato* from Borneo were sequenced (Table 1). Genomic DNA was isolated from liver or skeletal muscle stored in 95% ethanol using a SPRI magnetic bead extraction protocol (<https://github.com/phyletica/lab-protocols/blob/master/extraction-spri.md>). A combined fragment (1443 bp) of the mitochondrial genes 16S, ND1 and flanking tRNAs (tRNA-Leu, tRNA-Ile, and tRNA-Gln) was amplified using a double stranded polymerase chain reaction (PCR) under the following conditions: 1.0 µl genomic DNA (10–30 µg), 1.0 µl (concentration 10 µM) light strand primer 16S-frog 5' TTACCTGGGGATAACAG-CGCAA-3' (Camargo et al. 2006), 1.0 µl (concentration 10 µM) heavy strand primer tmet-frog 5'-TTGGGGTAT-GGGCCAAAAGCT-3' (Camargo et al. 2006), 1.0 µl dinucleotide pairs (1.5 µM), 2.0 µl 5x buffer (1.5 µM), 1.0 µl MgCl 10x buffer (1.5 µM), 0.1 µl Taq polymerase (5 units/µl), and 6.4 µl ultra-pure H<sub>2</sub>O. All PCR reactions were carried out on an Axygen Maxygene II gradient thermocycler under the following thermal profile: initial denaturation at 94°C for 2 min 30s, followed by 30 cycles of a secondary denaturation at 94°C for 1 min, annealing at 54°C for 1 min, elongation at 72°C for 1.5

min. PCR products were visualized via a 1.0% agarose gel electrophoresis. Successful PCR products were sent to GENEWIZ® for PCR purification, cycle sequencing, sequencing purification, and sequencing using the same primers as in the amplification. Sequences were analysed from both the 3' and the 5' ends separately to confirm congruence between reads. All forward and reverse sequences were uploaded and edited in Geneious™ version v11 (Kearse et al. 2012). Following sequence editing, 16S, ND1 and flanking tRNAs were aligned using the MAFFT v7.017 (Katoh et al. 2002) plugin under the default settings in Geneious™ (Kearse et al. 2012). Sequences were checked in Mesquite v3.5 (Maddison & Maddison, 2019) to ensure the correct amino acid reading frame for the coding region ND1.

### Phylogenetic analysis

The new sequences were added to the molecular phylogenetic dataset of Quah et al. (2017) along with additional GenBank sequences from Shimada et al. (2011) (Table 1). Ingroup samples consisted of 30 individuals representing three nominal species of *Abavorana* (Table 1). Outgroups species used to root the tree were *Pulchrana sundabarai* Chan, Abraham, Grismer & Brown, and *Meristogenys stenocephalus* Shimada, Matsui, Yambun & Sudin, based in part on the relationships of Quah et al. (2017). New sequence data generated for this study are deposited on GenBank (Table 1).

Maximum likelihood (ML) and Bayesian Inference (BI) were used to generate phylogenetic trees. The data were partitioned into four partitions (ND1 by codon positions [1–3] and 16S+tRNAs) and best-fit models of evolution were determined in the IQ-TREE webserver version (Nguyen et al. 2015; Trifinopoulos et al. 2016) using the Bayesian information criterion (BIC; Schwarz 1978) implemented in ModelFinder (Kalyaanamoorthy et al. 2017). The model K2P+G4 was the best-fit model of evolution for ND1 codon position 1, HKY+I for codon position 2, TN+I for codon position 3 and TIM2e+G4 for 16S+ tRNAs. The ML analysis was performed using the IQ-TREE webserver (Trifinopoulos et al. 2016) with 1000 bootstrap pseudoreplicates using the ultrafast bootstrap (UFBoot) option (Minh et al. 2013; Hoang et al. 2017). The Bayesian analysis was performed in BEAST v2.5.1 (Bouckaert et al. 2014) using bModelTest (Bouckaert & Drummond 2017) to numerically integrate over uncertainty in models of substitution, while estimating the phylogeny using Markov chain Monte Carlo (MCMC). The models selected by bModelTest for ND1 codon position 1 was 123141 (posterior support 35.22%), codon position 2, 121131 (posterior support 6.22%), codon position 3, 121131 (posterior support 29.94%) and 123454 (posterior support 29.01%) for the noncoding partition 16S+tRNAs. We ran the MCMC chain for 100 million generations while sampling every 10,000 generations. Stationarity was checked with Tracer v1.7 (Rambaut et al. 2018) and the effective sample sizes for all parameters were greater than 200. A maximum clade credibility tree was generat-

**Table 1.** Specimens used for the molecular phylogenetic analyses.

Taxon	Locality	Voucher	GenBank no.	Reference
Outgroups				
<i>Meristogenys stenocephalus</i>	Borneo, Sabah, Crocker Range National Park	UMS:BORNEENSIS 8684	AB526612.1	Shimada et al. 2011
<i>Pulchrana sundabarat</i>	West Malaysia, Kelantan, Pergau	USMHC 1468	KY982540	Quah et al. 2017
<b>Ingroup</b>				
<i>Abavorana decorata</i>	Borneo, Sabah, Lahad Datu district, Danum Valley	FMNH 231052	KY982535	Quah et al. 2017
<i>Abavorana nazgul</i>	West Malaysia, Kedah, Gunung Jerai	LSUHC 10512	KY982537	Quah et al. 2017
<i>Abavorana nazgul</i>	West Malaysia, Kedah, Gunung Jerai	LSUHC 10513	KY982538	Quah et al. 2017
<i>Abavorana nazgul</i>	West Malaysia, Kedah, Gunung Jerai	LSUHC 10514	KY982539	Quah et al. 2017
<i>Abavorana luctuosa</i>	Borneo, Sabah, Sipitang district, Mendolong	FMNH 234972	KY982536	Quah et al. 2017
<i>Abavorana luctuosa</i>	Borneo, Sabah, Sipitang district, Mendolong	FMNH 235295	MW478376	This study
<i>Abavorana luctuosa</i>	Borneo, Sabah, Sipitang district, Mendolong	FMNH 238720	MW478379	This study
<i>Abavorana luctuosa</i>	Borneo, Sarawak, Bintulu division, Tubau Camp	FMNH 269008	MW478378	This study
<i>Abavorana luctuosa</i>	Borneo, Sarawak, Bintulu division, Tubau Camp	FMNH 269142	MW478383	This study
<i>Abavorana luctuosa</i>	Borneo, Sarawak, Bintulu division, Tubau Camp	FMNH 269143	MW478380	This study
<i>Abavorana luctuosa</i>	Borneo, Sarawak, Bintulu division, Bukit Kana	FMNH 273216	MW478384	This study
<i>Abavorana luctuosa</i>	Borneo, Sarawak, Bintulu division, Bukit Kana	FMNH 273217	MW478377	This study
<i>Abavorana luctuosa</i>	Borneo, Sarawak, Bintulu division, Bukit Kana	FMNH 273218	MW478381	This study
<i>Abavorana luctuosa</i>	Borneo, Sarawak, Bintulu division, Samarakan	FMNH 273220	MW478382	This study
<i>Abavorana luctuosa</i>	West Malaysia, Kelantan, Gunung Stong	LSUHC 11087	KY982519	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Kedah, Sungai Sedim	LSUHC 9731	KY982520	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Penang, Penang Hill	USMHC 1649	KY982521	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Penang, Penang Hill	USMHC 1650	KY982522	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Penang, Penang Hill	USMHC 1651	KY982523	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Penang, Penang Hill	USMHC 1652	KY982524	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Selangor, Gombak	LSUHC 6580	KY982525	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Selangor, Gombak	LSUHC 6585	KY982526	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Fraser's Hill	LSUHC 12679	KY982527	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Fraser's Hill	LSUHC 12680	KY982528	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Fraser's Hill	LSUHC 12681	KY982529	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Genting Highlands	LSUHC 11663	KY982530	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Genting Highlands	LSUHC 11664	KY982531	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Genting Highlands	LSUHC 11665	KY982532	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Genting Highlands	LSUHC 11666	KY982533	Quah et al. 2017
<i>Abavorana luctuosa</i>	West Malaysia, Pahang, Genting Highlands	USMHC 1662	KY982534	Quah et al. 2017

ed by summarizing the posterior distribution of trees after discarding the first 25%, using mean node heights with TreeAnnotator v2.5.1 (Bouckaert et al. 2014). We considered Bayesian posterior probabilities (BPP) of 0.95 and above and ultrafast bootstrap support values (UFBoot) of 95 and above as strong nodal support (Huelsenbeck et al. 2001; Minh et al. 2013). Uncorrected pairwise sequence divergences (p-distance) were calculated in MEGA v6.06 using default settings which used pairwise deletion for the treatment of gaps and missing data in the dataset (Tamura et al. 2013) (Table 2).

## Morphological analysis

Morphological data from 62 adult specimens (34 males; 28 females) of *Abavorana luctuosa sensu lato* from 21 populations throughout the Thai-Malay Peninsula and Borneo (Appendix 1), and eight specimens of *A. nazgul* (seven males; one female) from the type locality in Penin-

sular Malaysia, were taken following the methodology of Quah et al. (2017) (Table 3). Notes on colour pattern were taken from digital images of living and euthanized specimens prior to preservation. Sex was determined by the presence of the humeral glands in adult male *Abavorana* as they lack vocal sacs and nuptial pads (Inger 1966). The following characters were measured by ESHQ with a Control Company digimatic caliper to the nearest 0.01 mm on the right side of the body for symmetrical characters: snout-vent length (**SVL**), from the tip of snout to the vent; head length (**HL**), from the posterior margin of mandible to the tip of snout; head width (**HW**), measured at the level of the jaw articulation points; snout length (**SL**), from the anterior margins of eyes to the tip of snout; snout width (**SW**), distance between the anterior margins of eyes; interorbital diameter (**IOD**), distance across the top of the head between the medial margins of the upper eyelids at their closest points; internarial distance (**IND**), distance between the medial margins of the nostrils; eye diameter (**ED**), distance between the anterior and poste-

**Table 2.** Uncorrected *p*-distances of the genus *Abavorana*. Mean (min–max) uncorrected *p*-distances (%) within examined populations of the genus *Abavorana* Oliver, Prendini, Kraus & Raxworthy 2015 computed in MEGA v6.06 (Tamura et al. 2013). Distances in bold are intraspecific distances, and distances below the diagonal are interspecific distances. n = number of individuals

	n	<i>A. decorata</i>	<i>A. nazgul</i>				<i>A. luctuosa</i> (Pen. Malaysia)				<i>A. luctuosa</i> (Borneo)			
<i>A. decorata</i>	1	—	—				—				—			
<i>A. nazgul</i>	3	0.17	<b>0.00</b>				—				—			
<i>A. luctuosa</i> (Pen. Malaysia)	16	0.16	0.08				<b>0.00</b> (0.00–0.02)				—			
<i>A. luctuosa</i> (Borneo)	10	0.16 (0.16–0.17)	0.08 (0.07–0.08)				0.02 (0.02–0.03)				<b>0.01</b> (0.00–0.03)			

**Table 3.** Measurements of *Abavorana decorata*, *A. nazgul* and different populations of *A. luctuosa*. Abbreviations are listed in the Materials and methods.

Catalog no.	Species	SVL	HL	HW	SL	SW	IOD	IND	ED	TD	BL	FAL	ML	FL	CL	TL	PL	HG
ZRC 1.709	<i>A. decorata</i>	58.42	23.71	20.87	8.52	10.87	6.60	6.67	5.72	5.27	9.00	11.68	13.12	30.42	30.93	13.4	27.92	♀
SP02100	<i>A. decorata</i>	29.66	12.23	10.62	4.69	6.25	3.91	3.68	4.04	2.27	6.81	5.79	8.36	17.19	17.28	8.52	14.72	♀
SP02810	<i>A. decorata</i>	57.67	22.05	20.03	9.46	10.98	6.78	6.72	6.17	5.36	10.35	13.94	14.95	29.74	32.00	15.84	30.45	♀
SP20695	<i>A. decorata</i>	57.92	22.76	21.07	9.31	11.68	6.05	6.77	6.58	5.63	10.27	12.71	14.79	31.34	32.50	16.00	31.49	♀
SP26873	<i>A. decorata</i>	46.21	19.14	17.66	7.76	9.91	5.95	6.16	5.56	4.54	8.51	10.77	12.2	25.58	24.74	13.13	23.44	3.25
FMNH 109935	<i>A. decorata</i>	55.00	19.05	18.57	7.99	10.36	6.12	6.21	5.42	4.46	9.53	11.47	14.00	25.81	29.83	14.98	27.50	♀
FMNH 109936	<i>A. decorata</i>	56.00	19.05	19.53	8.22	10.71	5.39	6.09	5.93	4.6	10.06	11.18	15.00	26.1	29.33	14.98	28.00	3.89
FMNH 231052	<i>A. decorata</i>	33.69	13.9	11.92	6.42	7.07	4.29	4.48	3.94	2.78	6.89	6.59	9.33	17.25	17.74	9.19	17.12	♀
USMHC 2231	<i>A. nazgul</i>	43.99	17.14	15.83	7.44	8.70	4.48	5.54	3.86	3.80	8.87	8.13	11.00	23.11	24.01	11.84	24.08	2.51
USMHC 2232	<i>A. nazgul</i>	41.56	16.56	14.88	7.10	8.04	4.47	5.76	4.15	3.52	8.34	8.07	11.08	23.08	23.77	11.70	23.40	2.76
USMHC 2233	<i>A. nazgul</i>	44.10	16.68	14.72	7.16	8.02	3.99	5.45	4.06	3.61	8.76	8.29	11.05	22.56	23.85	11.30	22.76	2.41
LSUHC 10512	<i>A. nazgul</i>	41.51	16.50	14.63	7.13	8.11	4.33	5.80	3.93	3.60	8.49	7.54	10.37	22.31	22.83	10.70	22.1	2.4
LSUHC 10513	<i>A. nazgul</i>	42.70	16.50	15.03	7.25	8.39	4.12	5.73	4.24	3.58	8.48	7.84	10.90	22.20	23.52	11.14	23.18	2.47
LSUHC 10514	<i>A. nazgul</i>	52.51	19.65	18.57	8.69	9.59	4.94	6.61	4.80	4.10	12.02	10.17	13.41	27.80	28.77	14.42	28.84	♀
USMHC 2572	<i>A. nazgul</i>	43.92	16.36	15.60	7.54	8.60	4.05	5.56	4.36	4.01	8.98	8.23	11.53	23.22	23.93	11.31	24.46	2.55
USMHC 2573	<i>A. nazgul</i>	41.61	16.52	15.41	7.57	7.98	3.94	5.67	4.56	3.91	8.32	8.39	11.25	22.43	23.26	10.95	23.22	2.98
FMNH 135347	<i>A. luctuosa</i> Malay Peninsula	44.39	15.20	13.83	6.48	8.75	4.81	6.41	5.05	3.24	9.49	9.23	11.24	21.92	24.69	12.39	22.52	♀
USMHC 2576	<i>A. luctuosa</i> Malay Peninsula	46.12	16.84	14.66	7.80	9.19	4.12	5.42	5.04	3.90	9.91	9.20	12.42	23.95	24.94	12.44	25.38	♀
USMHC 2577	<i>A. luctuosa</i> Malay Peninsula	44.17	16.69	15.58	7.56	8.62	4.59	5.44	4.60	3.32	7.99	7.90	10.58	19.82	21.59	11.61	21.72	3.40
USMHC 2310	<i>A. luctuosa</i> Malay Peninsula	41.27	16.37	14.50	6.99	8.52	4.33	5.27	4.10	3.54	7.80	7.66	10.25	21.27	22.03	11.02	22.03	3.36
LSUHC 9731	<i>A. luctuosa</i> Malay Peninsula	37.20	14.70	13.39	6.75	8.21	4.03	5.08	3.80	3.41	8.03	8.14	10.46	19.80	22.14	10.92	20.50	3.89
LSUHC 11087	<i>A. luctuosa</i> Malay Peninsula	48.7	19.59	15.98	8.29	9.38	4.93	6.72	4.75	3.82	9.11	9.64	13.72	25.14	27.29	14.30	27.32	♀
ZRC 1.11129	<i>A. luctuosa</i> Malay Peninsula	49.75	19.35	16.84	8.07	8.37	5.20	6.04	5.21	3.96	7.67	9.38	12.50	24.52	26.48	14.56	26.30	♀
ZRC 1.3145	<i>A. luctuosa</i> Malay Peninsula	43.89	17.96	15.12	7.47	8.29	3.80	5.75	4.38	3.58	6.69	8.87	11.23	21.55	25.72	12.74	23.5	♀
LSUHC 13479	<i>A. luctuosa</i> Malay Peninsula	51.06	19.15	16.17	8.24	9.25	5.49	6.53	5.19	4.24	9.37	11.39	12.55	26.37	28.75	14.52	27.86	♀
LSUHC 13486	<i>A. luctuosa</i> Malay Peninsula	45.71	17.09	16.32	7.64	9.04	4.92	5.90	4.40	4.14	7.80	9.84	10.01	21.91	23.88	12.36	22.55	♀
LSUHC 13487	<i>A. luctuosa</i> Malay Peninsula	43.06	15.85	14.58	6.95	8.18	5.14	5.70	4.20	3.66	7.08	8.55	9.83	20.78	23.49	12.26	22.55	4.41
LSUHC 13488	<i>A. luctuosa</i> Malay Peninsula	49.50	18.05	16.76	8.30	8.97	5.64	5.87	4.97	3.93	8.48	11.07	11.60	23.72	26.39	13.14	25.46	♀
LSUHC 13535	<i>A. luctuosa</i> Malay Peninsula	49.13	18.43	16.57	8.14	8.99	5.13	6.17	5.01	4.07	8.70	10.00	12.29	25.00	27.03	13.49	26.05	♀
LSUHC 13549	<i>A. luctuosa</i> Malay Peninsula	46.08	16.08	14.74	7.37	8.21	5.15	5.73	4.65	3.79	8.57	8.96	10.92	23.67	24.95	12.25	25.15	♀
LSUHC 13550	<i>A. luctuosa</i> Malay Peninsula	44.27	16.41	14.45	7.17	8.16	4.38	5.48	4.07	3.59	7.43	7.73	11.13	22.04	23.73	12.35	23.11	3.80
USMHC 2574	<i>A. luctuosa</i> Malay Peninsula	46.89	17.23	16.48	8.19	8.82	5.06	6.13	4.91	3.87	8.6	9.10	12.75	24.4	25.18	12.79	25.14	♀

**Table 3** continued.

Catalog no.	Species	SVL	HL	HW	SL	SW	IOD	IND	ED	TD	BL	FAL	ML	FL	CL	TL	PL	HG
USMHC 2575	<i>A. luctuosa</i> Malay Peninsula	40.56	16.26	14.34	7.43	8.12	4.59	5.14	4.70	3.41	7.37	8.81	10.69	21.91	22.36	11.30	22.00	2.58
FMNH 141734	<i>A. luctuosa</i> Malay Peninsula	40.17	14.45	13.78	6.62	7.58	3.25	5.30	4.15	2.62	8.85	8.27	10.34	18.62	21.43	10.72	20.83	2.81
FMNH 141735	<i>A. luctuosa</i> Malay Peninsula	38.09	14.96	14.51	6.43	8.04	4.11	5.07	4.31	3.24	8.84	8.30	10.54	20.54	21.28	10.66	19.62	3.50
FMNH 141736	<i>A. luctuosa</i> Malay Peninsula	40.77	15.75	13.94	6.70	8.26	4.21	5.88	4.38	3.12	8.14	8.01	9.65	19.58	20.75	10.00	20.58	3.09
FMNH 141738	<i>A. luctuosa</i> Malay Peninsula	37.83	14.94	13.35	6.20	7.11	4.89	4.93	4.17	3.05	8.34	7.55	9.68	18.38	21.03	10.31	20.59	3.09
ZRC 1.11943	<i>A. luctuosa</i> Borneo	37.78	15.92	13.49	6.33	7.52	3.80	4.66	4.09	3.00	5.78	7.98	8.69	17.82	19.70	10.69	18.40	3.87
ZRC 1.11938	<i>A. luctuosa</i> Borneo	43.58	17.60	14.96	7.30	7.71	4.70	5.10	4.33	3.77	7.38	9.55	10.33	20.10	23.72	12.82	21.97	♀
ZRC 1.2270	<i>A. luctuosa</i> Borneo	42.71	16.51	14.67	6.97	8.06	4.90	4.75	4.82	3.38	8.14	9.32	10.10	21.44	22.63	11.69	21.16	♀
FMNH 234985 (SP00897)	<i>A. luctuosa</i> Borneo	37.43	15.75	13.69	6.54	7.83	4.56	5.03	4.00	2.81	6.93	7.83	8.69	18.99	20.83	11.05	19.96	4.05
FMNH 242884 (SP01905)	<i>A. luctuosa</i> Borneo	45.19	16.26	15.74	6.99	9.02	5.60	5.99	4.79	3.63	8.47	9.89	11.29	23.09	24.98	13.48	23.73	♀
SP02676	<i>A. luctuosa</i> Borneo	39.83	15.78	13.73	6.64	7.94	4.63	5.32	4.50	3.61	6.68	8.92	9.94	21.31	21.94	11.22	19.69	3.65
FMNH 234972	<i>A. luctuosa</i> Borneo	39.51	15.26	13.58	6.90	7.95	4.70	5.58	4.59	3.40	7.86	8.01	10.59	21.25	22.06	11.75	20.88	3.96
FMNH 234973	<i>A. luctuosa</i> Borneo	37.22	13.53	13.27	6.09	7.59	3.83	4.76	3.65	3.35	7.20	7.50	9.20	19.04	19.53	9.86	19.01	3.06
FMNH 234974	<i>A. luctuosa</i> Borneo	37.05	14.84	12.71	6.61	7.65	4.15	5.01	4.08	2.95	8.87	8.50	9.22	19.13	21.63	11.29	21.29	♀
FMNH 234975	<i>A. luctuosa</i> Borneo	38.86	15.15	13.64	6.67	7.69	3.78	5.26	4.33	3.11	8.56	7.22	10.10	19.81	20.72	10.28	20.32	3.92
FMNH 234976	<i>A. luctuosa</i> Borneo	36.30	14.16	13.17	5.66	7.33	4.13	4.89	3.98	2.50	7.37	7.25	9.49	18.31	20.11	10.19	19.53	3.12
FMNH 234977	<i>A. luctuosa</i> Borneo	35.41	14.72	12.92	6.35	7.77	4.22	5.04	4.18	2.75	7.38	7.77	8.73	19.13	20.29	10.71	19.21	3.95
FMNH 234978	<i>A. luctuosa</i> Borneo	35.05	14.25	12.28	6.39	7.47	4.10	5.41	4.20	3.26	8.65	7.36	8.79	18.53	20.82	10.39	20.55	2.50
FMNH 234979	<i>A. luctuosa</i> Borneo	36.78	14.54	12.25	6.26	7.57	4.10	5.01	4.30	3.05	8.92	7.23	9.03	17.81	21.22	10.84	20.09	2.22
FMNH 234980	<i>A. luctuosa</i> Borneo	38.19	14.44	13.39	6.01	7.57	4.00	4.90	4.40	3.34	8.53	7.51	9.36	19.43	20.91	11.27	20.50	3.85
FMNH 234981	<i>A. luctuosa</i> Borneo	38.22	15.27	12.90	6.50	7.65	4.59	5.05	4.12	3.07	8.96	7.13	9.47	19.32	20.93	10.86	21.28	3.79
FMNH 234982	<i>A. luctuosa</i> Borneo	39.74	15.98	13.93	6.75	7.84	4.62	5.44	4.54	3.04	9.06	8.13	9.55	20.63	21.39	11.36	20.87	3.58
FMNH 234983	<i>A. luctuosa</i> Borneo	37.27	15.51	13.25	6.96	7.90	4.53	5.50	3.79	3.06	8.42	7.42	9.13	19.86	21.5	11.55	20.93	3.22
FMNH 234984	<i>A. luctuosa</i> Borneo	38.37	15.04	12.80	6.62	8.22	4.41	5.28	4.05	3.00	8.94	7.27	9.43	20.12	21.23	11.27	21.82	4.16
FMNH 238720	<i>A. luctuosa</i> Borneo	39.01	15.74	13.65	6.63	8.02	4.19	5.38	3.95	3.16	9.05	7.49	9.03	20.98	21.36	10.97	20.96	3.33
FMNH 242882	<i>A. luctuosa</i> Borneo	45.01	17.49	15.52	7.40	8.79	4.86	5.80	5.22	3.67	10.2	9.92	10.61	23.68	24.27	13.11	22.82	♀
FMNH 242883	<i>A. luctuosa</i> Borneo	45.2	17.45	14.85	7.00	8.72	4.72	5.77	4.81	3.41	9.95	8.82	10.91	22.66	24.64	12.83	23.25	♀
FMNH 242885	<i>A. luctuosa</i> Borneo	43.75	17.06	14.51	7.34	8.71	4.65	5.74	4.54	3.47	10.13	9.01	11.08	22.17	22.99	12.71	23.01	♀
FMNH 242886	<i>A. luctuosa</i> Borneo	45.11	17.57	15.14	7.13	8.81	4.55	5.98	4.74	3.64	10.29	8.25	11.29	22.55	25.02	12.69	23.69	♀
FMNH 269008	<i>A. luctuosa</i> Borneo	42.18	17.72	13.92	6.93	7.75	4.58	5.31	4.75	3.18	8.11	9.11	10.65	21.05	19.83	11.71	22.00	♀
FMNH 269142	<i>A. luctuosa</i> Borneo	38.46	15.62	13.41	6.98	7.40	4.28	5.20	3.73	2.88	6.85	8.01	11.00	19.78	20.99	11.22	20.34	2.18

**Table 3** continued.

Catalog no.	Species	SVL	HL	HW	SL	SW	IOD	IND	ED	TD	BL	FAL	ML	FL	CL	TL	PL	HG
FMNH 269143	<i>A. luctuosa</i> Borneo	39.18	16.08	13.97	6.69	8.00	4.14	5.33	4.39	3.24	9.37	8.52	10.39	21.57	21.42	11.18	21.71	2.29
FMNH 269144	<i>A. luctuosa</i> Borneo	39.56	16.78	13.44	7.03	7.72	3.80	5.23	4.23	3.83	9.56	7.56	10.40	20.58	20.68	10.40	19.45	2.67
FMNH 273216	<i>A. luctuosa</i> Borneo	39.32	15.06	13.72	6.76	7.66	4.59	4.95	4.35	3.40	7.68	8.03	10.36	20.48	21.24	10.48	20.44	2.46
FMNH 273217	<i>A. luctuosa</i> Borneo	44.93	15.81	15.09	7.86	8.04	4.62	5.37	4.81	3.18	8.81	8.25	11.78	21.66	23.15	12.30	23.32	♀
FMNH 273218	<i>A. luctuosa</i> Borneo	40.87	17.33	14.49	7.36	8.41	4.31	5.70	4.67	3.59	10.00	8.23	11.36	21.55	22.37	11.21	22.53	♀
FMNH 273219	<i>A. luctuosa</i> Borneo	37.25	14.80	13.60	6.62	7.53	4.25	5.10	4.30	3.19	7.97	7.45	10.22	19.28	19.5	10.17	19.49	3.14
FMNH 273220	<i>A. luctuosa</i> Borneo	40.55	16.12	14.41	6.79	7.90	3.95	5.13	4.28	3.38	9.45	8.22	10.79	19.9	20.95	10.8	20.82	2.73

**Table 4.** Pairwise matrix of statistically significant characters among species of the genus *Abavorana*. Pairwise matrix of statistically significant mean differences of characters among *Abavorana decorata*, *A. nazgul*, and *A. luctuosa* populations from the Malay Peninsula and Borneo. Abbreviations are in the Materials and methods.

		<i>A. decorata</i>		<i>A. nazgul</i>		<i>A. luctuosa</i> Malay Peninsula		<i>A. luctuosa</i> Borneo	
		♂	♀	♂	♀	♂	♀	♂	♀
<i>A. decorata</i>	♂	—	—	—	—	—	—	—	—
	♀	—	—	—	—	—	—	—	—
<i>A. nazgul</i>	♂	HL, HW, SL, IOD, ED, TD, FAL, TL, PL, SW, IND, ML, CL, FL, HG	—	—	—	—	—	—	—
	♀	—	HW, IOD, IND, FL, PL, SL, BL	—	—	—	—	—	—
<i>A. luctuosa</i> Malay Peninsula	♂	HL, HW, SL, IOD, ED, TD, FAL, TL, PL, SW, IND, ML, FL, CL	—	HL, HW, SL, TD, PL, IND, ML, FL, CL, HG	—	—	—	—	—
	♀	—	HW, SW, IOD, TD, FL	—	HL, HW, SW, ML, FL, CL, PL, SL, BL, TL	—	—	—	—
<i>A. luctuosa</i> Borneo	♂	HL, HW, SL, IOD, ED, TD, TL, PL, SW, IND, FAL, ML, CL, FL	—	SVL, HL, HW, SL, TD, PL, SW, IND, ML, FL, CL, HG	—	SVL, HW, SL, PL, ML, CL	—	—	—
	♀	—	HW, HL, SW, IOD, TD, FAL, ML, FL, CL, PL, ED	—	HL, HW, SW, IND, TD, FAL, ML, FL, CL, PL, SL, BL, TL	—	HW, SW, IND, TD, FAL, ML, FL, CL, PL, SL, TL	—	—

rior margins of the eyeball; tympanum diameter (**TD**), the horizontal width of the tympanum at its widest point; brachium length (**BL**), distance from the axilla to most distal point of inflection on flexed elbow; forearm length (**FAL**), distance from outer margin of flexed elbow to the base of the inner metacarpal tubercle; manus length (**ML**), distance from the proximal edge of the outer metacarpal tubercle to the tip of the third finger; femur length (**FL**),

distance from the vent to the outer margin of the flexed knee; crus length (**CL**), distance from the outer face of flexed knee to the outer margin of tarsal inflection; tarsal length (**TL**), the outer margin of flexed tarsus to the base of the inner metatarsal tubercle; pes length (**PL**), measured from the proximal edge of the inner metatarsal tubercle to the tip of fourth toe; humeral gland length (**HG**), the horizontal length of the humeral gland. Discrete co-

lour pattern data, along with univariate and multivariate analyses of morphological data (see statistical analyses below) were then used to search for characters and morphospatial patterns bearing statistically significant differences that were consistent with the previous designations of the species-level hypotheses, thus providing independent diagnoses to complement the molecular analyses.

## Repositories, Institutional acronyms or Institutional abbreviations

Museum abbreviations are: **FMNH** (Field Museum of Natural History, Chicago, Illinois); **LSUHC** (La Sierra University Herpetological Collection, Riverside, California); **MNHN** (Muséum National d'Histoire Naturelle, Paris); **MSNG** (Museo Civico di Storia Naturale “Giacomo Doria”, Genova); **SP** (Sabah Parks Collection, Sabah, Malaysia); **USMHC** (Universiti Sains Malaysia Herpetological Collection); and **ZRC** (Zoological Reference Collection, Lee Kong Chian Natural History Museum [LKCINHM], Singapore).

## Statistical analyses

All analyses were performed using the platform R version 3.2.1 (R Core Team 2015). Owing to a lack of genetic material from the type locality of *Rana decorata* at Mount Kinabalu, Sabah, an *a priori* decision as to the membership to which species to assign specimens prior to additional downstream analyses was based on the colour pattern of their venters which has been shown to be a distinguishing characteristic for the genus (Fig. 9; Quah et al. 2017). Specimens with bold black and white reticulations along flanks, and banding on the underside of their legs are identified as the *decorata* pattern morph, while those with generally immaculate venters are identified as the *luctuosa* pattern morph. To reduce allometric bias as a result of ontogeny, the characters of each species were scaled using the following equation:  $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$ , where  $X_{adj}$  = adjusted value;  $X$  = measured value;  $\beta$  = unstandardized regression coefficient for each population;  $SVL$  = measured snout-vent length;  $SVL_{mean}$  = overall average  $SVL$  of all samples (Thorpe, 1983; Lleonart et al. 2000). Each species was scaled separately and the data concatenated so as not to conflate interpopulational variation. The measurements for the sexes were analysed separately to eliminate bias caused by sexual dimorphism. All raw measurements are presented in Table 3.

A MANOVA analysis was performed to test for significantly different ( $p < 0.05$ ) multivariate structure in the mensural data and subsequently viewed in a principal component analysis (PCA). PCA and discriminant analysis of principal components (DAPC) were performed using the ADEGENET package in R (Jombart et al. 2010) to determine if the morphospatial position of Bornean *Abavorana luctuosa* populations with boldly marked venters and other populations of *A. luctuosa* with generally immaculate venters from Borneo and the Thai-Malay

Peninsula coincided with the putative species boundaries delimited by the molecular phylogenetic analyses. All mensural data were incorporated in the analyses except HG which is absent in females. Principal components of the DAPC with eigenvalues accounting for 90–99% of the variation in the data were retained for the DAPC according to the criterion of Jombart et al. (2010). For this analysis, the first seven PCs out of 17 (males) and 16 (females) were retained which accounted for 94.9% (males) and 97.6% (females) of the variation.

Independent of the MANOVA, an analysis of variance (ANOVA) was conducted on mensural characters. Since the species and population sample sizes were unequal, a Levene's test for homogeneity of variances among the mensural characters was conducted prior to an analysis of variance (ANOVA). A Welch's ANOVA was conducted on characters with unequal variances ( $p \geq 0.05$ ) and a standard ANOVA was conducted on characters with equal variances ( $p \leq 0.05$ ) to test for the presence of statistically significant mean differences ( $p \leq 0.05$ ) between all combinations of species or population pairs in the data set. Characters with equal variances and bearing statistical differences were subjected to a TukeyHSD test to ascertain which population pairs differed significantly from each other for those characters (Table 4). Characters with unequal variances bearing statistical differences were subjected to a Games-Howell test to ascertain which population pairs differed significantly from each other for those characters (Table 4). Summary statistics were generated for the mensural data (Table 5).

## Results

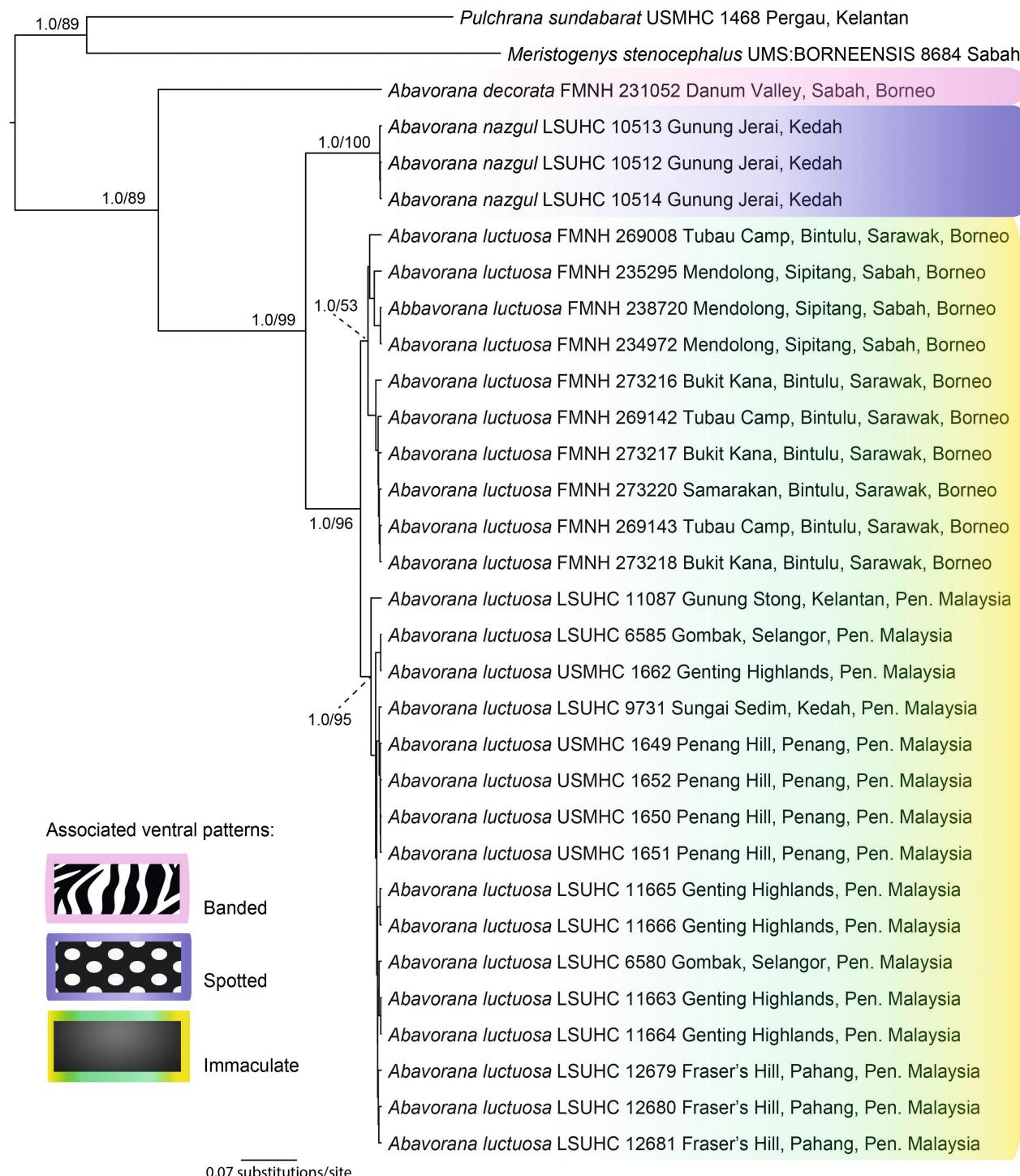
### Phylogeny and genetic divergence

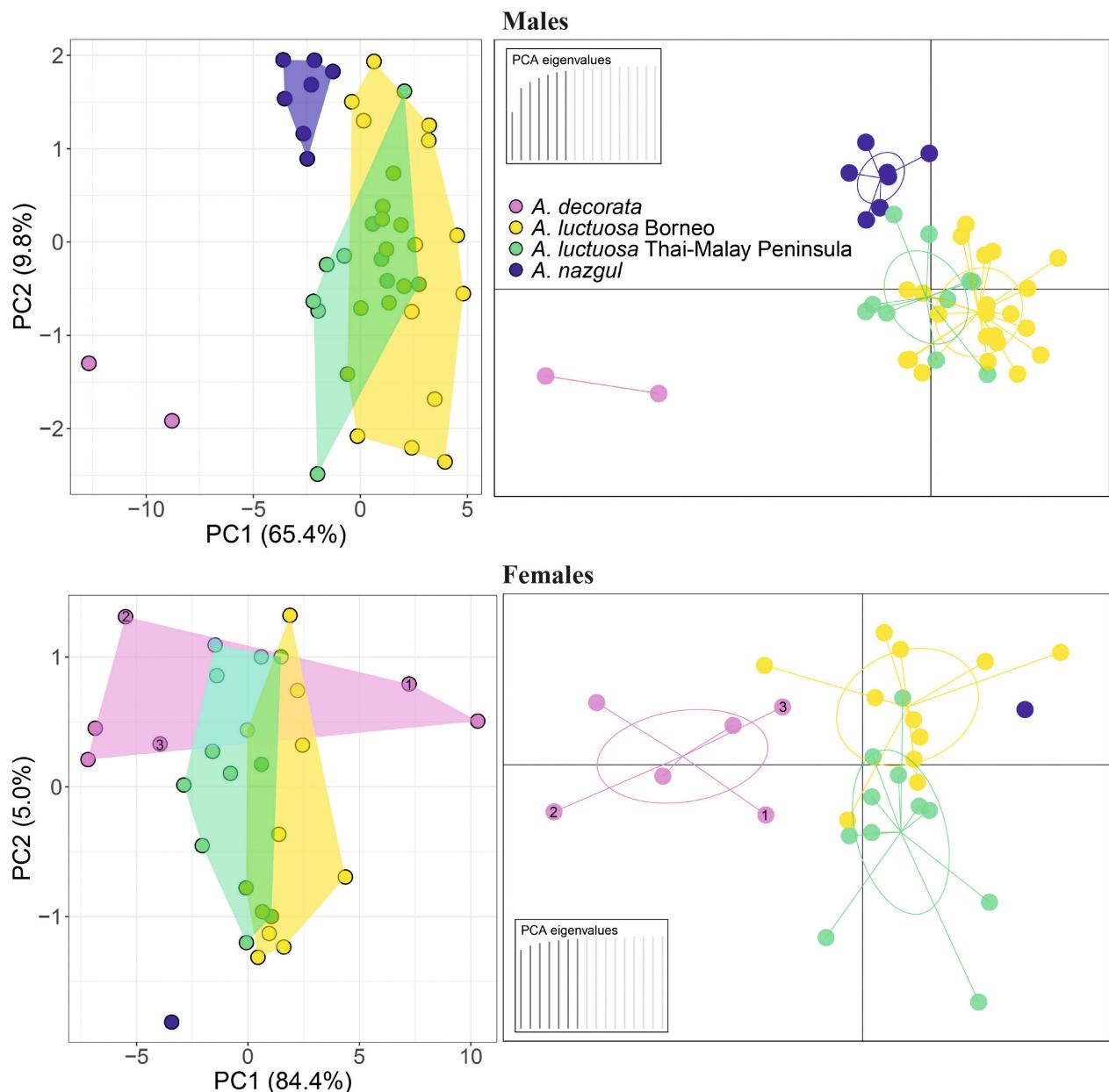
The BI and ML analyses recovered trees with identical topologies. Specimen FMNH 231052 with bold black and white mottling on the ventral side of its flanks and banding on the underside of its legs from Danum Valley, Sabah (Fig. 6A & B) was recovered as the strongly supported (BPP=1.0, Ufboot=89) sister lineage of the remaining *Abavorana* (Fig. 1). The remaining *A. luctuosa sensu lato* from the Thai-Malay Peninsula and Borneo bearing generally immaculate venters and underside of their legs (Figs 1, 4) formed a strongly supported (BPP=1.0, Ufboot=96) clade, and were recovered as the sister species to *A. nazgul* (BPP=1.0, Ufboot=99). FMNH 231052 differs by an uncorrected pairwise sequence divergence of 16.0–17.0 % from *A. nazgul* and other *A. luctuosa* populations, respectively (Table 2). With the inclusion of additional Bornean specimens in this study, two reciprocally monophyletic lineages (BPP=1.0, Ufboot=96) of *A. luctuosa* with generally immaculate venters and underside of hind limbs were recovered—one from Peninsular Malaysia and another from Borneo (Fig. 1). Nevertheless, these populations differ from each other by only a 2.0–3.0 % uncorrected pairwise sequence divergence (Table 2).

**Table 5.** Summary statistics and ventral colour pattern among members of the genus *Abavorana*. Summary statistics and ventral colour pattern for *Abavorana decorata*, *A. nazgul*, and *A. luctuosa* populations from the Malay Peninsula and Borneo, SD = standard deviation, N = sample size, / = no data. Humeral gland only present in males and all measurements in mm.

**Table 5** continued.

	<i>A. decorata</i>		<i>A. nazgul</i>		<i>A. luctuosa</i> Malay Peninsula		<i>A. luctuosa</i> Borneo	
mean ( $\pm$ SD)	3.57 ( $\pm$ 0.45)	/	2.58 ( $\pm$ 0.21)	/	3.39 ( $\pm$ 0.54)	/	3.26 ( $\pm$ 0.66)	/
range	3.25–3.89	/	2.40–2.98	/	2.58–4.41	/	2.18–4.16	/
<b>Pattern of venter</b>	Belly usually mottled with black and white reticulations along the flanks; limbs with bold black and white bands or reticulations	Spotted		Immaculate to very faint, sparse speckling		Immaculate to very faint, sparse speckling		

**Figure 1.** Phylogenetic tree of the genus *Abavorana*; Maximum likelihood phylogram for species of the genus *Abavorana*. Nodal support is indicated by Bayesian posterior probability (BPP) / Ultrafast bootstrap (UFboot) respectively.



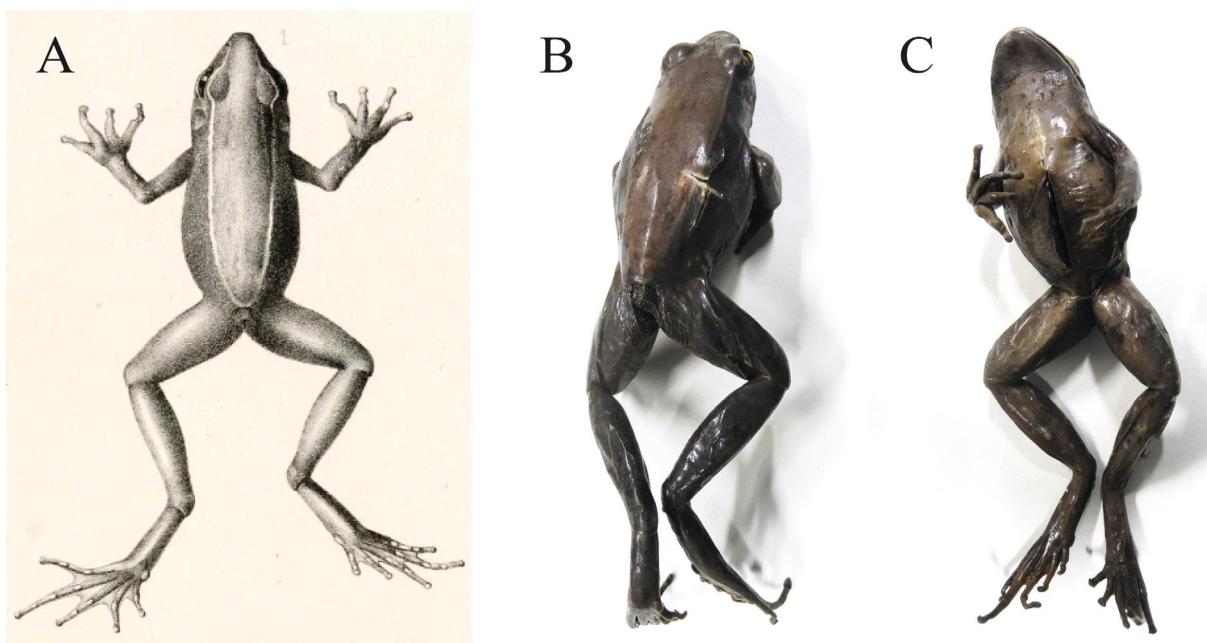
**Figure 2.** PCA and DAPC for the genus *Abavorana*; PCAs (left) with convex hull polygons and DAPCs (right) showing the morphospatial relationships of male (top) and female (bottom) *Abavorana decorata*, *A. nazgul*, and *A. luctuosa* populations from the Malay Peninsula and Borneo. 1 = FMNH 231052, 2 = ZRC 1.709 and 3 = FMNH 109935.

## Morphometric and statistical analyses

The MANOVA indicated there were significant (Wilks' lambda,  $p=2.2 \times 10^{-6}$ ) differences in mensural data between both sexes of the two pattern morphs of *Abavorana luctuosa sensu lato* and *A. nazgul*, as visualized in the PCA and DAPC (Fig. 2). For males, the PCA and DAPC showed distinct separation between both the *decorata* and *luctuosa* pattern morph populations. In the PCA, the males of both phenotypes were clearly separated along PC1. PC1 accounts for 65.4% of the variation (Fig. 2), and loads most heavily for SVL, HW and CL (Appendix 2). In females, the PCA did not show a separation between the two pattern morphs as there was significant overlap along PC1 and PC2. However, the DAPC showed complete separation in the 66% confidence ellipses between the females of both

phenotypes (Fig. 2). FMNH 231052 bearing the *decorata* pattern morph from Danum Valley, Sabah clustered in morphospace with topotypic material referable to *Rana decorata* from Mount Kinabalu, Sabah (FMNH 109935 and ZRC 1.709) in the DAPC. In both sexes, the *luctuosa* pattern morph populations from Borneo and the Thai-Malay Peninsula overlapped in both the PCA and DAPC analyses.

The analyses also revealed that both venter phenotypes also differ in a number of statistically significant mensural metrics (Table 4 & 5). Across both sexes, the two phenotypes differed significantly in their head width, snout width, interorbital diameter, tympanum diameter, and femur length. The specimens with the reticulated venters and boldly banded undersides of their legs (i.e. the *decorata* pattern morph) that match the descriptions of *Rana decorata* presented:



**Figure 3.** Holotype of *Abavorana luctuosa*; A: Original illustration of the holotype of *Abavorana luctuosa* from Peters (1872). B: Dorsum of the holotype of *A. luctuosa* (MSNG 29344). C: Venter of the holotype of *A. luctuosa* (MSNG 29344). Photographs by Giuliano Doria.

Significantly wider heads in both sexes, with HW of adult males 17.66–19.53 mm, mean  $18.60 \pm SD 1.32$ ,  $n = 2$  (vs. 12.25–14.41 mm, mean  $13.39 \pm SD 0.52$ ,  $n = 22$ ,  $P < 0.001$ , in Bornean *Abavorana luctuosa*, and 13.35–15.58 mm, mean  $14.24 \pm SD 0.66$ ,  $n = 10$ ,  $P < 0.001$ , in Malay Peninsula *A. luctuosa*) and adult females 10.62–21.07 mm, mean  $17.18 \pm SD 4.68$ ,  $n = 6$  (vs. 12.71–15.74 mm, mean  $14.69 \pm SD 0.83$ ,  $n = 11$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 13.83–16.84 mm, mean  $15.77 \pm SD 1.01$ ,  $n = 11$ ,  $P < 0.01$ , in Malay Peninsula *A. luctuosa*); significantly wider snouts in both sexes, with SW of adult males 9.91–10.71 mm, mean  $10.31 \pm SD 0.57$ ,  $n = 2$  (vs. 7.33–8.22 mm, mean  $7.73 \pm SD 0.23$ ,  $n = 22$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 7.11–8.62 mm, mean  $8.08 \pm SD 0.44$ ,  $n = 10$ ,  $P < 0.001$ , in Malay Peninsula *A. luctuosa*) and adult females 6.25–11.68 mm, mean  $9.54 \pm SD 2.28$ ,  $n = 6$  (vs. 7.65–9.02 mm, mean  $8.33 \pm SD 0.51$ ,  $n = 11$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 8.21–9.38 mm, mean  $8.84 \pm SD 0.40$ ,  $n = 11$ ,  $P < 0.05$ , in Malay Peninsula *A. luctuosa*); significantly wider interorbital diameter in both sexes, with IOD of adult males 5.59–5.95 mm, mean  $5.67 \pm SD 0.40$ ,  $n = 2$  (vs. 3.78–4.70 mm, mean  $4.24 \pm SD 0.30$ ,  $n = 22$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 3.25–5.14 mm, mean  $4.35 \pm SD 0.52$ ,  $n = 10$ ,  $P < 0.001$ , in Malay Peninsula *A. luctuosa*) and adult females 3.91–6.78 mm, mean  $5.63 \pm SD 1.22$ ,  $n = 6$  (vs. 4.15–5.60 mm, mean  $4.69 \pm SD 0.37$ ,  $n = 11$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 3.80–5.64 mm, mean  $4.93 \pm SD 0.54$ ,  $n = 11$ ,  $P < 0.001$ , in Malay Peninsula *A. luctuosa*); significantly wider tympanum diameter in both sexes, with TD of adult males 4.54–4.60 mm, mean  $4.57 \pm SD 0.04$ ,  $n = 2$  (vs. 2.50–3.83 mm, mean  $3.16 \pm SD 0.29$ ,  $n = 22$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 2.62–3.66 mm, mean  $3.30 \pm SD 0.31$ ,  $n = 10$ ,  $P < 0.001$ , in Malay Peninsula *A. luctuosa*) and adult females 2.27–5.63 mm, mean  $4.30 \pm SD 0.40$ ,  $n = 6$  (vs. 2.50–3.83 mm, mean  $3.16 \pm SD 0.29$ ,  $n = 22$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 2.62–3.66 mm, mean  $3.30 \pm SD 0.31$ ,  $n = 10$ ,  $P < 0.001$ , in Malay Peninsula *A. luctuosa*).

SD 1.43,  $n = 6$  (vs. 2.95–3.77 mm, mean  $3.44 \pm SD 0.25$ ,  $n = 11$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 3.24–4.24 mm, mean  $3.87 \pm SD 0.27$ ,  $n = 11$ ,  $P < 0.05$ , in Malay Peninsula *A. luctuosa*); and significantly longer femur length in both sexes, FL of adult males 25.58–26.10 mm, mean  $25.84 \pm SD 0.37$ ,  $n = 2$  (vs. 17.81–21.57 mm, mean  $19.72 \pm SD 1.08$ ,  $n = 22$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 18.38–22.04 mm, mean  $20.27 \pm SD 1.26$ ,  $n = 10$ ,  $P < 0.001$ , in Malay Peninsula *A. luctuosa*) and adult females 17.19–31.34 mm, mean  $25.29 \pm SD 6.53$ ,  $n = 6$  (vs. 19.13–23.68 mm, mean  $21.73 \pm SD 1.32$ ,  $n = 11$ ,  $P < 0.001$ , in Bornean *A. luctuosa*, and 21.55–26.37 mm, mean  $23.83 \pm SD 1.51$ ,  $n = 11$ ,  $P < 0.05$ , in Malay Peninsula *A. luctuosa*). In addition to these, the phenotypes differed significantly from each other and *A. nazgul* by a suite of other mensural characters (Table 4 & 5).

## Taxonomy of *Abavorana*

### Systematics and nomenclature

The analyses demonstrate unequivocally that *Abavorana luctuosa* on Borneo are composed of two genetically and morphologically distinct forms. *Abavorana luctuosa* described by Peters (1871) on the basis of a single female specimen from Sarawak (Fig. 3) has only very faint speckling on its venter and underside of the limbs. Therefore, specimens from southern Thailand, Peninsular Malaysia, and Borneo that possess this phenotype shall be referred to as *A. luctuosa* (Figs 4, 7E–H, 8A–F, 9A–B). The second lineage is readily identifiable by the reticulated pattern on their venters and boldly banded underside



**Figure 4.** Bornean *Abavorana luctuosa*; Dorsal (A & C) and ventral (B & D) pattern of *Abavorana luctuosa* from Borneo. A & B: Top row (from left to right); FMNH 234972, FMNH 234973, FMNH 234975 and FMNH 234977 (all specimens from Sipitang District, Sabah). Bottom row (from left to right); FMNH 234980 (Sipitang District, Sabah), FMNH 269142, FMNH 273216 and FMNH 273217 (specimens from Bintulu Division, Sarawak). C & D (from left to right): ZRC 1.11938, ZRC 1.11943 (both from Kubah, Sarawak) and ZRC 1.22270 (unspecified location in Borneo).

of their hind limbs, and is endemic to Borneo. Nine specimens examined from the states of Sabah (Mount Kinabalu, Kota Belud, Maliau Basin, Tambunan and Danum Valley) and Sarawak (Barito) bear this ventral colour pattern and match the description of *Rana decorata* Mocquard, 1890 that was described from Mount Kinabalu, Sabah, East Malaysian Borneo. They resemble the colour pattern of the type series (MNHN 1889.226–28) (Figs 5, 6, 7A–D, 9C–D). *Rana decorata* was synonymised with *A. luctuosa* by Boulenger (1891) without clear justification yet followed in subsequent works (e.g., Boulenger 1920; Van Kampen 1923; Quah et al. 2017 and references therein). Thus, given the preponderance of data, *R. decorata* Mocquard, 1890, in the combination *Abavorana decorata* comb. nov. (Mocquard, 1890) is resurrected for the populations bearing this phenotype.

### ***Abavorana luctuosa* (Peters, 1871)**

Common Mahogany Frog

Figs 3, 4, 7E–H, 8A–F, 9A–B

*Limnodytes luctuosus*: Peters 1871:579, 1872:43 & pl. 6; Capoccacia 1957:208 & 215.

*Rana luctuosa* (in part): Boulenger 1882:68, 1891:341, 1912:238, 1920:183 & 184; Flower 1896:904, 1899:896 & 897; Hanitsch 1900:73; Butler 1904:199 & 200; Van Kampen 1923:196 & 197; Smith 1930:94 & 103, 1931:16; Capoccacia 1957: 215; Taylor & Elbel 1958:1040; Taylor 1962:451–453; Inger 1954:250, 1966:206–208, 1978:312, 1985:iii, 5, 38, 40, 56, 57, 76; Grandison 1972:66 & 67; Berry 1975:74 & 75; Dring 1979:200; Inger & Stuebing 1992:42, 2005:19, 27, 33, 149 & 150; Inger & Tan 1996:563; Inger et al. 1996:363; Manthey & Grossmann 1997:111 & 112; Khonsue & Thirakhupt 2001:73; Malkmus et al. 2002: 163–165; Das 2006a:5; Jaafar et al. 2008:39.

*Rana (Limnodytes) luctuosa*: Mocquard 1890:122.

*Rana (Hylorana) luctuosa* (in part): Boulenger 1920:126.

*Rana (Hylarana) luctuosa* (in part): Van Kampen 1923:196 & 197; Bourret 1942:360; Dubois, 1987: 42.

*Hylorana luctuosa* (in part): Deckert 1938:144.

*Rana (Pulchrana) luctuosa* (in part): Dubois 1992:326.

*Pulchrana luctuosa* (in part): Frost et al. 2006:369; Fei et al. 2010:33.

*Hylarana luctuosa* (in part): Manthey 1983:22; Che et al. 2007: 1–13 (by implication); Das et al. 2007:159, 160, 167, 170, fig. 7d; Imbun 2014:99.

*Abavorana luctuosa*: Oliver et al. 2015:186 (in part); Quah et al. 2017: 272–288 (in part); Zainudin et al. 2017:876–891 (in part); Chan et al. 2019:1057, 1062.

*Hylarana (Abavorana) luctuosa* (in part): Inger et al. 2017:147 & 148.

**Holotype.** Adult female (MSNG 29344) collected by Giacomo Doria and Odoardo Beccari from “Sarawak”, (Borneo) Malaysia (Capoccacia 1957) (Fig. 3).

**Diagnosis.** Body robust, medium-sized; head moderate; snout short, rounded, canthus rostralis smoothly rounded; interorbital space broader than the upper eyelid; tympanum distinct, not quite two-thirds the size of the eye with no pale colouration on the margins of the tympanum; no

vocal sacs in males; vomerine teeth in two small oblique patches on a level with the posterior edge of the choanae; length of 1st finger greater than 2nd finger; disc width to finger width ratios of finger 3 and toe 4 is 1–1.5; dorsolateral fold indistinct or absent; the humeral gland in males is prominent, raised and centrally positioned on the ventral surface of the upper arm; a weak or absent radial ridge; outer metatarsal tubercle weak or absent; subarticular tubercles moderate; skin of dorsum smooth or finely shagreened; throat, abdomen, and flanks smooth; posterior section of venter and back of the thigh rugose; dorsum reddish-orange to chocolate-brown, encircled by a white or cream coloured dorsolateral line that encircles the snout, canthus rostralis, outer edge of the upper eyelids, and dorsum along the dorsolateral fold to the vent; lower flanks dark-brown or black below the dorsolateral line grading into a paler venter; dorsal colouration of the limbs same as the flanks with whitish or light-grey speckles or stripes. *Abavorana luctuosa* can be easily differentiated from its congeners on the basis of its ventral colour pattern which is usually immaculate or with only very faint, sparse, light speckling (Figs 3, 4, 9A–B). Adult males with SVL 35.05–44.27 mm, adult females with SVL 37.05–51.06 mm; adult males with SW 7.11–8.62 mm, adult females with SW 7.65–9.38 mm; adult males with IOD 3.25–5.14 mm, adult females with IOD 3.80–5.64 mm; adult males with TD 2.50–3.83 mm, adult females with TD 2.95–4.24 mm; adult males with FL 17.81–22.04 mm, adult females with FL 19.13–26.37 mm (Table 5).

**Distribution.** Its distribution spans southern Peninsular Thailand, Peninsular Malaysia, Borneo, and Sumatra (Manthey & Grossmann 1997; Oliver et al. 2015; Quah et al. 2017). Within Borneo it is confirmed from Sabah state: Imbak Canyon and Sipitang; Sarawak state: Bukit Kana, Samarakan and Tubau in Bintulu Division and Kubah National Park where it is sympatric with *Abavorana decorata* (Fig. 10). The species is expected to range across Borneo.

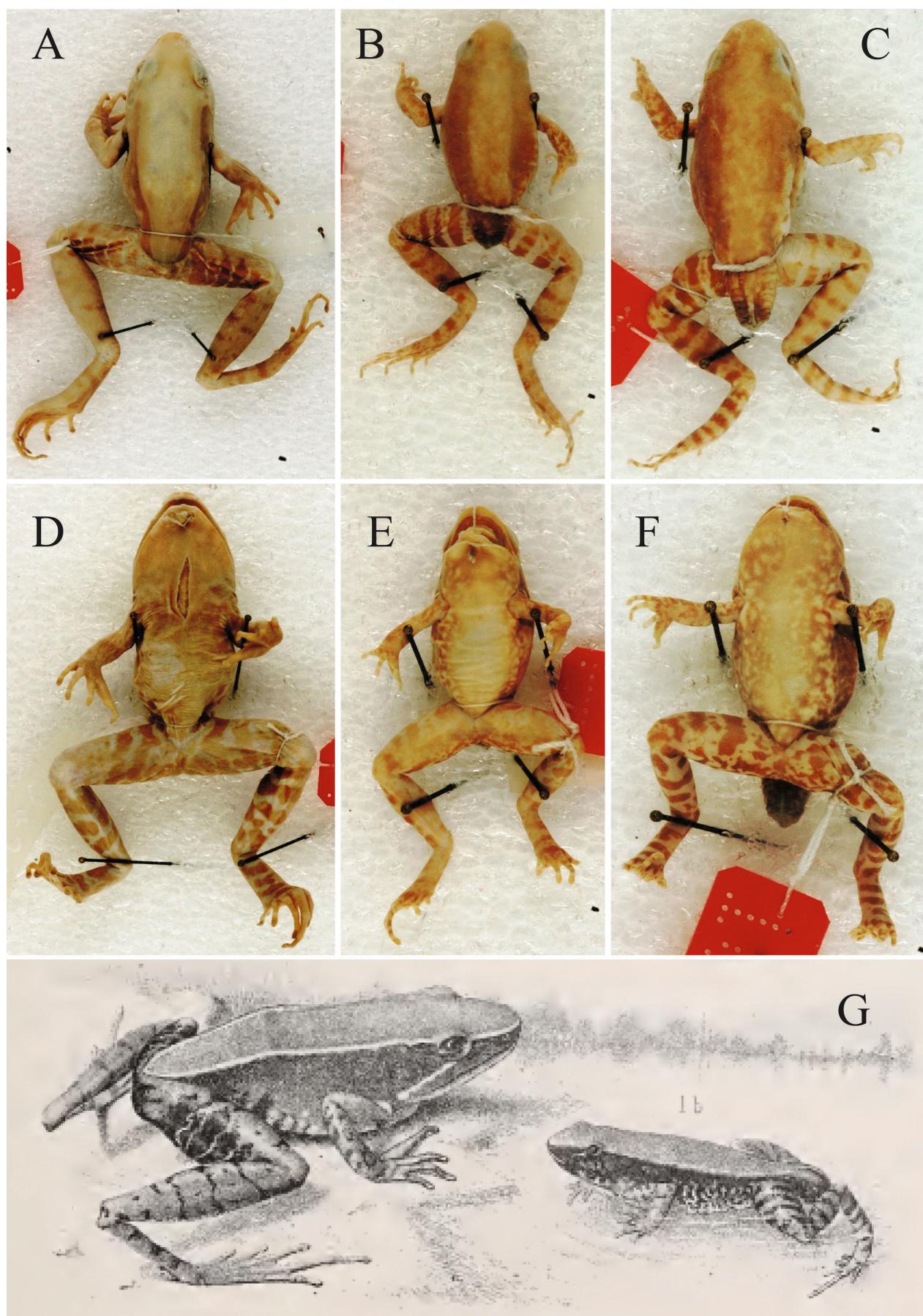
### ***Abavorana decorata* comb. nov. (Mocquard, 1890)**

Decorated Mahogany Frog

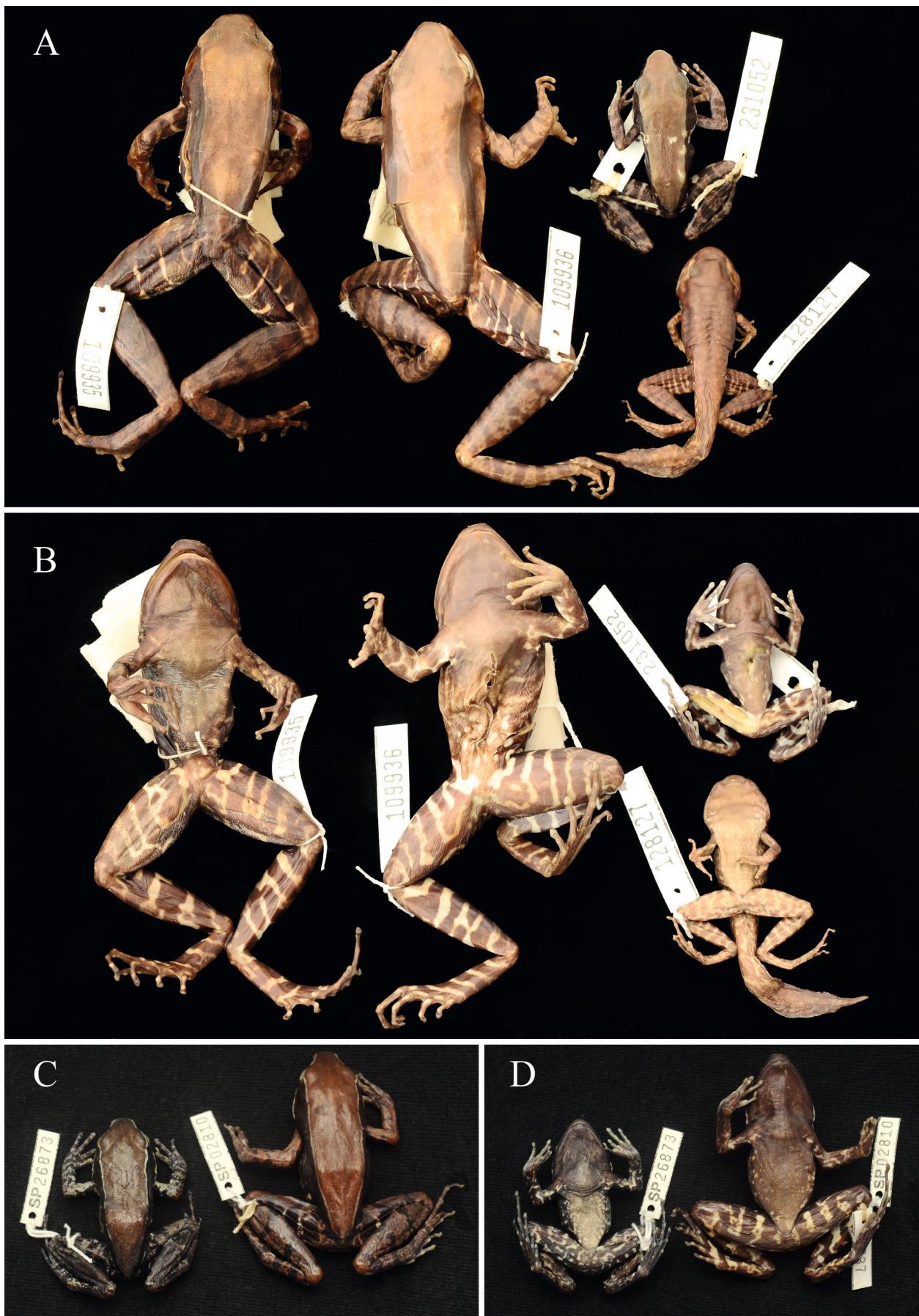
Figs 5, 6, 7A–D, 9C–D

*Rana decorata*: Mocquard 1890:145–146; Guibé 1950:41

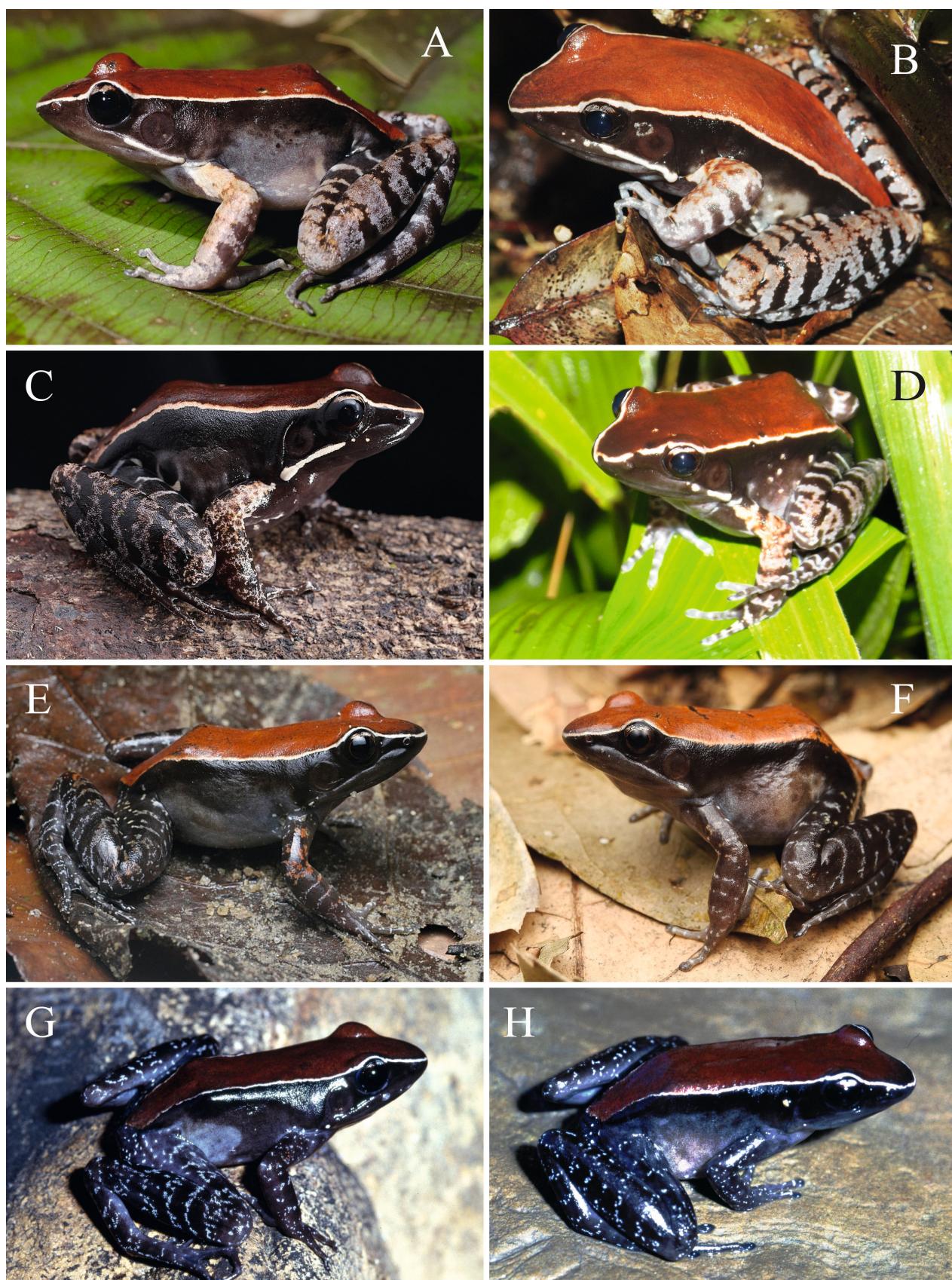
*Rana luctuosa* (in part): Boulenger 1891:341 & 342, 1912:238, 1920:183 & 184; Flower 1896:904, 1899:896 & 897; Hanitsch 1900:73; Butler 1904:199; Smith 1931:16; Van Kampen 1923:196 & 197; Taylor 1962:451–453; Inger 1954:250, 1966:206–208, 1978:312, 1985:iii, 5, 38, 40, 56, 57, 76; Grandison 1972:66 & 67; Berry 1975:74 & 75, Fig. 50 (right); Matsui 1979:333; Inger & Stuebing 1992:42, 2005:19, 27, 33, 149 & 150; Inger & Tan 1996:563; Inger et al. 1996:363; Malkmus 1994:244; Manthey & Grossmann 1997:111 & 112; Khonsue & Thirakhupt 2001:73; Malkmus et al. 2002: 163–165, figs 159, 160; Das 2006a:5.



**Figure 5.** Syntypes of *Abavorana decorata*; A & D: Dorsum and venter of MNHN-RA-1889.226. B & E: Dorsum and venter of MNHN-RA-1889.227. C & F: Dorsum and venter of MNHN-RA-1889.228 (Photographs by Christine Reinhardt). G: Original illustration of the syntypes of *Abavorana decorata* from Mocquard (1890). Illustrations assignable to specimen MNHN-RA-1889.226 (left) and MNHN-RA-1889.228 (right).



**Figure 6.** Examined *Abavorana decorata* specimens; Dorsal (A & C) and ventral (B & D) pattern of *Abavorana decorata* from Borneo. A & B (from left to right): FMNH 109935 from Kiau, Mount Kinabalu, Sabah (left), FMNH 109936 from Kiau, Mount Kinabalu, Sabah (middle), FMNH 231052 from Danum Valley Research Center, Lahad Datu District, Sabah (top right), FMNH 128127 from Bario, Sarawak (bottom right). C & D: SP 26873 from Tawau Hills, Sabah (left) and SP 02810 from Maliau Basin, Sabah.



**Figure 7.** Living specimens of *Abavorana decorata* and Bornean *A. luctuosa*; A: *Abavorana decorata* from Tawau Hills, Sabah, East Malaysia. B: *A. decorata* from Maliau Basin, Sabah, East Malaysia. C: *A. decorata* from Kubah National Park, Sarawak, East Malaysia. D: *A. decorata* from Melawi Regency, West Kalimantan Province, Indonesia. E & F: *A. luctuosa* from Kubah National Park, Sarawak, East Malaysia. G: *A. luctuosa* (FMNH 238720) from Sipitang, Sabah, East Malaysia. H: *A. luctuosa* (FMNH 242883) from Sipitang, Sabah, East Malaysia. (Photographs by Alexander Haas [A, C & E], Paul Bertner [B], Muhammad Aini [D], Chien C. Lee [F], and Robert F. Inger [G & H], Figs G & H ©Field Museum of Natural History. Created by Field Museum of Natural History, Amphibian and Reptile Collection and licensed under CC-BY-SA 4.0).

*Rana (Hylorana) luctuosa* (in part): Boulenger 1920:126.  
*Rana (Hylarana) luctuosa* (in part): Van Kampen 1923:196 & 197;  
 Bourret 1942:360; Dubois, 1987: 42.  
*Hylorana luctuosa* (in part): Deckert 1938:144  
*Rana (Pulchrana) luctuosa* (in part): Dubois 1992:326  
*Pulchrana luctuosa* (in part): Frost et al. 2006:369; Fei et al. 2010:33.  
*Hylarana luctuosa* (in part): Manthey 1983:22; Che et al. 2007: 1–13  
 (by implication); Das et al. 2007:159, 160, 167, 170; Imbun 2014:99.  
*Abavorana luctuosa*: Oliver et al. 2015:186 (in part); Quah et al. 2017:  
 272–288 (in part); Zainudin et al. 2017:876–891 (in part); Haas et al.  
 2018:92, 93, 100, fig. 4b.  
*Hylarana (Abavorana) luctuosa* (in part): Inger et al. 2017:147 & 148.

**Syntypes.** MNHNP 1889.226–28 from “Bornéo Kina Ba-lu”, Sabah (Borneo), Malaysia. (Guibé 1950) (Fig. 5).

**Diagnosis.** In addition to its phylogenetic placement (Fig. 1), *Rana decorata* is reassigned as a member of the genus *Abavorana* based on the combination of having a robust, medium-sized body; no vocal sacs in males; length of 1st finger greater than 2nd finger; disc width to finger width ratios of finger 3 and toe 4 is 1–1.5; dorsolateral fold indistinct or absent; the colour of the dorsolateral line being white or yellow; the humeral gland in males is prominent, raised and centrally positioned on the ventral surface of the upper arm; a weak or absent rictal ridge; outer metatarsal tubercle weak or absent; skin of dorsum smooth or finely shagreened; throat, abdomen and flanks smooth; posterior section of venter and back of the thigh rugose; no pale colouration on the margins of the tympanum; flanks dark-brown or black below the dorsal fold grading into a pale venter (Inger 1966; Oliver et al. 2015; Quah et al. 2017). Dorsum reddish-orange to rust-brown, encircled by a white or cream coloured dorsolateral line that encircles the snout, canthus rostralis, outer edge of the upper eyelids, and dorsum along the dorsolateral fold to the vent; lower flanks dark-brown or black below the dorsolateral line grading into a paler venter; dorsal colouration of the limbs light-grey or brown with speckling and prominent dark-brown or black bands. *Abavorana decorata* can be differentiated from its congeners on the basis of its ventral colour pattern which is reticulated in black and white especially on the lower flanks, underside of the limbs (especially hind-limbs) are boldly banded in black and white, and a prominent white streak under the eye and/or tympanum to the corner of the jaw (Figs 5, 6, 9C–D). Adult males with SVL 46.21–56.0 mm, adult females with SVL 29.66–58.42 mm; adult males with SW 9.91–10.71 mm, adult females with SW 6.25–11.68 mm; adult males with IOD 5.59–5.95 mm, adult females with IOD 3.91–6.78 mm; adult males with TD 4.54–4.60 mm, adult females with TD 2.27–5.63 mm; adult males with FL 25.58–26.10 mm, adult females with FL 17.19–31.34 mm (Table 5).

**Distribution (Fig 10).** Endemic to Borneo. The species is known from Sabah state, Malaysian Borneo: Mount Kinabalu, Kampung Kiau Taburi, Danum Valley, Tawau Hills Park, Maliau Basin, Tambunan and Penampang (CalPhotos ID: 0000 0000 0912 1159); Sarawak state,

Malaysia Borneo: Kubah National Park (Fig. 7C) and Barito (Fig. 6A–B); and West Kalimantan, Indonesia: Melawi Regency (Fig. 7D). The species is expected to be wider ranging on the island.

## *Abavorana nazgul* Quah, Shahrul Anuar, Grismer, Wood, Siti Azizah & Muin 2017

Gunung Jerai Black Stream-Frog

Figs 8G–H, 9E–F

*Rana luctuosa* Sukumaran, J. 2005: 38

**Holotype.** An adult male (USMHC 2231) collected on 9 April 2016 from Gunung Jerai, Kedah, Peninsular Malaysia ( $5^{\circ}47.719'N$ ;  $100^{\circ}26.222'E$ , 948 m in elevation) by Evan S.H. Quah and David Chan.

**Diagnosis.** *Abavorana nazgul* can be differentiated from its congeners by the following combination of characters: adult males 41.51–44.1 mm SVL and single adult female 52.51 mm; adult males with SW 7.98–8.70 mm, single adult female SW 9.59 mm; adult males with IOD 3.94–4.48 mm, single adult female IOD 4.94 mm; adult males with TD 3.52–4.01 mm, single adult female TD 4.10 mm; adult males with FL 22.20–23.22 mm, single adult female FL 27.80 mm; nuptial pads absent in males; humeral glands in males small (2.4–2.98 mm) (Table 5); dorsolateral stripe continuous, orange to yellow in colour; dorsum between dorsolateral stripes black, with or without faint orange or yellow speckles; flanks black, colouration unstratified; distinct cream-colored spots on flanks, dorsal surfaces of limbs, and upper lip; venter grey-brown with prominent light spots on throat and belly, smaller spots on underside of thigh (Fig. 9E–F; Quah et al. 2017).

**Distribution.** *Abavorana nazgul* is thus far confirmed from the upper elevations of Gunung Jerai, Kedah, Peninsular Malaysia (Quah et al. 2017). Specimens resembling this species have been photographed at Thale Ban National Park, Satun Province in southern Thailand at approximately 500–600m in elevation around wild boar wallows but are only tentatively identified as *A. cf. nazgul* pending positive evidence (Fig. 8H).

## Discussion

Prior to this study and that of Quah et al. (2017), Inger (1966) and Grandison (1972) noted that Peninsular Malaysian *Abavorana luctuosa* were smaller than Bornean populations and lacked stripes on the undersides of their limbs but did not realise they were comparing two different species, *A. luctuosa* and *A. decorata*. *Abavorana decorata* is recovered as the sister species to the remainder



**Figure 8.** Peninsular Malaysian, Thai and Sumatran *Abavorana luctuosa*, and *A. nazgul*; A: *A. luctuosa* from Sungai Durian Forest Reserve, Kelantan, Peninsular Malaysia. B: *A. luctuosa* from Janda Baik, Pahang, Peninsular Malaysia. C: *A. luctuosa* from Semenyih, Selangor, Peninsular Malaysia. D: *A. luctuosa* from Fraser's Hill, Pahang, Peninsular Malaysia. E: *A. luctuosa* from Hala-Bala Wildlife Sanctuary, Thailand. F: *A. luctuosa* from Sumatra, Indonesia. G: *A. nazgul* (USMHC 2572) from Gunung Jerai, Kedah, Peninsular Malaysia. H: *A. cf. nazgul* from Thale Ban National Park, Satun Province, Thailand. (Photographs by Zaharil Dzulkafly [A], Steven Wong [B], Kurt H.P. Guek [C], Evan Quah [D & G], Ian Dugdale [E], Hellen Kurniati [F] & Bunyarat Dechochai [H]).



**Figure 9.** Colour pattern comparison among species of the genus *Abavorana*; Dorsum (A,C & E) and venter (B,D & F) in life of *A. luctuosa* (USMHC 2576) (A & B) from Penang Hill, Penang Island, Malaysia, *A. decorata* from Maliau Basin, Sabah, East Malaysia, Borneo (C & D) and *A. nazgul* (USMHC 2233) (E & F) from Gunung Jerai, Kedah, West Malaysia. (Photographs by Evan Quah [A, B, E & F] and Stefan T. Hertwig [C & D].)

of the genus and this study suggests that the ancestor of the genus possibly originated in Borneo before dispersing across Sundaland where one lineage gave rise to *A. nazgul* in the uplands of northwestern Peninsular Malaysia and possibly southern Thailand, and the second lineage gave rise to the widespread *A. luctuosa*. These findings lend credence to the out-of-Borneo hypothesis that has been postulated for a number of other herpetofaunal taxa and other biotic groups (de Bruyn et al. 2014; Grismer et al. 2016; Quah et al. 2020b). Alternatively, the present-day

endemism of *A. decorata* on Borneo might be the result of extinction in other parts of Southeast Asia, the mainland in particular. *Abavorana decorata* may have had a far more extensive distribution across Sundaland previously. Nevertheless, both hypotheses can be explored in greater detail in the future with biogeographic range evolution analysis based on larger molecular datasets and broader taxon sampling for both *Abavorana* and other related genera across Sundaland.



**Figure 10.** Distribution map of *Abavorana decorata* and *A. luctuosa* in Borneo; Known distribution of *Abavorana decorata* (red) and *A. luctuosa* (blue) in Borneo. Star = type locality.

Borneo has long been a focal point of herpetological research in Southeast Asia (Das 2006b, 2007; Inger et al. 2017; Malkmus et al. 2002; Stuebing et al. 2014 and references within), and new discoveries continue to be made especially with the aid of molecular data and careful taxonomic reappraisals (for example, Davis et al. 2019; Grismer et al. 2018; Hertwig et al. 2012; Karin et al. 2018; Matsui et al. 2020; Mediyansyah et al. 2019; Munir et al. 2019; Pui et al. 2017; Quah et al. 2019a, 2020a). Our findings continue to lend support to the growing evidence that widely distributed species tend to be complexes and that their true diversity is not fully realised in the region

(such as Arifin et al. 2018; Chan et al. 2020a,b; Grismer et al. 2018; Mediyansyah et al. 2019; Munir et al. 2019; Quah et al. 2019a, 2020a). Our data also reveal some significant differences in the measurements of *Abavorana luctuosa* populations from the Thai-Malay Peninsula and Borneo which, along with the genetic data and their allopatry, indicates that these populations are evolving on separate evolutionary trajectories, which makes them candidates for their recognition as distinct species. However, we continue to consider them as conspecific due to their low genetic divergence (2.0–3.0 %) based on ND1, 16S and tRNAs of mitochondrial DNA. We are adopting

a conservative approach for now pending a more extensive genetic examination as other studies using genomic datasets have revealed past hybridization events between

Bornean and Thai-Malay Peninsula populations of other anuran species complexes (Chan et al. 2020c).

## Key to the species of the genus *Abavorana*

- 1 Mid-dorsal region of dorsum orange or reddish-brown ..... 2
- Mid-dorsal region of dorsum generally black, sometimes with faint orange or yellow speckles, venter with light spots ..... *A. nazgul*
- 2 Venter immaculate or with only very fine, light speckling on flanks and underside of legs, and absence or only faint white streak under the eye and/or tympanum to the corner of the jaw ..... *A. luctuosa*
- Venter with light and dark spots or reticulations especially along the flanks, and underside of legs boldly marked with black and white reticulations or barring, and a prominent white streak under the eye and/or tympanum to the corner of the jaw ..... *A. decorata*

## Acknowledgements

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## Supplementary material 1

### Appendix 1

**Authors:** Evan S.H. Quah, L. Lee Grismer, Perry L. Wood Jr., Kelvin K.P. Lim, Paul Y. Imbun, M.S. Shahru Anuar

**Data type:** .docx

**Explanation note:** Specimens of *Abavorana* that were examined for morphology in this study. \*metamorph specimen that was not measured for comparison.

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**Link:** <https://doi.org/10.3897/vz.71.e60921.suppl1>

## Supplementary material 2

### Appendix 2

**Authors:** Evan S.H. Quah, L. Lee Grismer, Perry L. Wood Jr., Kelvin K.P. Lim, Paul Y. Imbun, M.S. Shahru Anuar

**Data type:** .docx

**Explanation note:** Summary statistics and principal component analysis scores among male *Abavorana decorata*, *A. nazgul*, and *A. luctuosa* populations from the Malay Peninsula and Borneo. Abbreviations are in the Materials and methods.

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**Link:** <https://doi.org/10.3897/vz.71.e60921.suppl2>

## Supplementary material 3

### Appendix 3

**Authors:** Evan S.H. Quah, L. Lee Grismer, Perry L. Wood Jr., Kelvin K.P. Lim, Paul Y. Imbun, M.S. Shahru Anuar

**Data type:** .docx

**Explanation note:** Principal component analysis scores among female *Abavorana decorata*, *A. nazgul*, and *A. luctuosa* populations from the Malay Peninsula and Borneo. Abbreviations are in the Materials and methods.

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**Link:** <https://doi.org/10.3897/vz.71.e60921.suppl3>

## Supplementary material 4

### Appendix 4

**Authors:** Evan S.H. Quah, L. Lee Grismer, Perry L. Wood Jr., Kelvin K.P. Lim, Paul Y. Imbun, M.S. Shahru Anuar

**Data type:** .docx

**Explanation note:** *P*-values of the ANOVA tests on male and female morphometric datasets. Asterisks (\*) denote characters that were found to be significantly different based on  $\alpha=0.05$ .

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**Link:** <https://doi.org/10.3897/vz.71.e60921.suppl4>