Zootaxa 4320 (2): 272–288
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4320.2.4
http://zoobank.org/urn:lsid:zoobank.org:pub:0BFEF3CC-D02B-4265-BD12-22F8487C5F48

A new species of frog of the genus *Abavorana* Oliver, Prendini, Kraus & Raxworthy 2015 (Anura: Ranidae) from Gunung Jerai, Kedah, northwestern Peninsular Malaysia

EVAN S.H. QUAH[1,5], SHAHRUL ANUAR, M.S.[1,2], L.L. GRISMER[3,5], PERRY L. WOOD JR.[4], SITI AZIZAH M.N.[1] & MOHD ABDUL MUIN[1]

[1] *School of Biological Sciences, Universiti Sains Malaysia, 11800 Minden, Penang, Malaysia.*
E-mail: evanquah@yahoo.com, sanuar@usm.my, sazizah@usm.my, mamuin@gmail.com
[2] *Center for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 Minden, Penang, Malaysia.*
[3] *Department of Biology, La Sierra University, Riverside, California, USA. E-mail: lgrismer@lasierra.edu*
[4] *Department of Biology, Brigham Young University, 150 East Bulldog Boulevard, Provo, Utah 84602 USA. E-mail: pwood@byu.edu*
[5] *Corresponding authors*

Abstract

The recently erected ranid genus *Abavorana* is thought to contain one nominal species, *A. luctuosa,* that ranges from the Thai-Malay Peninsula to Borneo and Sumatra. A melanistic form from Gunung Jerai, Peninsular Malaysia previously thought to be the same species is new to science and herein described based on new specimens and data. Based on morphology, colour pattern, and phylogenetic analyses using the mitochondrial genes 16s, ND1 and three tRNAs (tRNA-leu, tRNA-lle, and tRNA-gln), we determine that this new species, *Abavorana nazgul* **sp. nov**., is the sister lineage to other populations of *A. lucutosa* from Peninsular Malaysia and one from Borneo. It differs from *A. luctuosa* by a minimum sequence divergence of 7.5% and the following combination of morphological and colour pattern characteristics: (1) SVL 42.1–50.0 mm in adult males; (2) prominent but small humeral glands in males (2.3–2.5 mm); (3) dorsolateral stripe continuous, orange to yellow in colour; (4) mid-dorsal region of dorsum black, with or without faint orange or yellow speckles; (5) flanks with distinct cream spots; (6) dorsal surfaces of limbs with cream spots–bar; and (7) venter grayish brown, with prominent light spots on throat and belly. The discovery of yet another endemic species from the upland regions of Peninsular Malaysia highlights the rich diversity of these habitats and the need for more studies in montane areas throughout the region.

Key words: Herpetofauna, montane, new species, taxonomy, conservation, systematics

Introduction

The ranid genus *Abavorana* Oliver, Prendini, Kraus & Raxworthy 2015 is thought to contain a single species, the Mahogany frog (*Abavorana luctuosa* [Peters, 1871]). Its distribution spans southern Thailand, Peninsular Malaysia, Borneo, and Sumatra (Manthey & Grossmann 1997; Oliver *et al*. 2015). It is a distinctive looking frog with a conspicuous reddish brown dorsal colouration outlined with a sharply defined, light-coloured, dorsolateral stripe that extends through the eyes to the tip of the snout, separating the brown dorsum from the dark sides of the head and flanks (Malkmus *et al*. 2002; Inger & Stuebing 2005). The species is terrestrial and found in the leaf litter of forested areas where they usually gather around rain pools or muddy ponds to breed during the mating season (Malkmus *et al*. 2002; Inger & Stuebing 2005). This species has been reported from various localities throughout Peninsular Malaysia (Berry 1975; Chan *et al*. 2009; Flower 1896; Grandison 1972; Grismer *et al*. 2010; Leong & Lim 2003; Lim *et al*. 2002; Manthey & Grossmann 1997) (Fig. 6). Sukumaran (2005) reported finding *A. luctuosa* (reported as *Rana luctuosa*) at Gunung Jerai, Kedah and noted that this populations is melanistic and postulated they were an upland specialist.

Accepted by J. Rowley: 12 Jul. 2017; published: 15 Sept. 2017

A total evidence approach was adopted, combining morphology and molecular phylogenetics to evaluate the taxonomic and phylogenetic placement of this population. Both molecular and morphological data support the assignment of this population to the genus *Abavorana* and the results also indicate that it represents a genetically distinct lineage that differs from *A. luctuosa* by a suite of unique morphological and colour pattern characters. Under the unified species concept (De Queiroz 2005), we consider this separately evolving lineage as a new species that is morphologically distinct and is described below.

Materials and methods

Morphological analysis. Notes on colouration and pattern were taken from digital images of living and euthanized specimens prior to preservation. The sex of the specimens was determined by the presence of the humeral gland in adult males as the males of this genus lack vocal sacs and nuptial pads (Inger 1966). The following characters were measured by ESHQ with a Mitutoyo digimatic calliper to the nearest 0.1 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 supraorbital regions at their closest points; internarial distance (IND), distance between the medial margins of the nostrils; eye diameter (ED), distance between the anterior and posterior 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 flexed elbow; forearm length (FAL), 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 flexed knee to the 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. Toe webbing formula follows Savage & Heyer (1997). The type series is deposited at the Universiti Sains Malaysia Herpetological Collection (USMHC) and the La Sierra University Herpetological Collection (LSUHC), La Sierra University, Riverside, California, USA. Other institutional abbreviations are as follow: FMNH, Field Museum of Natural History Chicago, Illinois, USA. Images of specimens; FMNH 231052 & FMNH 234972 were examined by EQSH to confirm their species identities prior to subsequent molecular analyses.

DNA extraction and amplification. Genomic DNA was isolated from liver tissue stored in 95% ethanol and extracted using the animal tissue protocol provided by the iNtRON Biotechnology G-spinTM total DNA Extraction Kit (Korea). ND1 was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions:1.0 µl genomic DNA (concentration 10–30 µg of DNA), 0.5 µl light strand primer (5µM) 16S-frog 5'–TTACCCTGGGGATAACAGCGCAA–3' (Camargo *et al*. 2006), 0.5 µl heavy strand primer (5µM) tmet-frog 5'–TTGGGGTATGGGCCCAAAAGCT–3' (Camargo *et al*. 2006), 2.5 µl of iNtRON MgCl2-free PCR Buffer, 2.5 µl of iNtRON 15 mM MgCl2, 0.2 µl iNtRON Taq DNA Polymerase, 0.5 µl dNTP Mix 10 mM each dNTP, and 17.3 µl nuclease free H2O. PCR reactions were completed using a G-Storm GS482 Thermal Cycler with the following reaction conditions: initial denaturation at 94°C for 2 min 30s, second denaturation at 94°C for 1min, annealing at 53– 55°C for 1 min followed by an extension cycle at 72°C for 1 min 30s per cycle for 30 cycles. PCR products were visualized using gel electrophoresis using a 2.0% agarose gel. PCR products that had a distinct band with the correct molecular weight based on the standardized ladder were purified using iNtRON Biotechnology MEGAquick-spinTM Total Fragment DNA Purification Kit (Korea) and sequenced through the MyTACG Bioscience Enterprise sequencing facility (Taiwan). Sequences were analysed from both the 3' and 5' ends independently to ensure congruence between the sequences. Both the forward and the reverse sequences were assembled and edited in MEGA v5.05 (Tamura *et al*. 2011). Sequences were aligned by eye and to ensure the correct amino acid reading frame and Mesquite v3.04 (Maddison & Maddison 2015) was used to check for premature stop codons.

Phylogenetic analysis. Phylogenetic trees were constructed using Bayesian Inference (BI) and Maximum Likelihood (ML). In both, data were split into three partitions corresponding to codon positions. A partitioned ML analysis was conducted using IQTREE software on the webserver (Trifinopoulos *et al.* 2016) with models of molecular evolution estimated for each partition and codon position (16s plus tRNAs [leu, lle, and gln]= TIM2e+G4, 1st codon= K2P+I, 2nd codon= HKY+G, 3rd codon= TN+I). To assess nodal support, 1000 bootstrap pseudoreplicates via the ultrafast bootstrap approximation algorithm was employed (Minh *et al.* 2013). ML ultrafast bootstrap support values (ML) of >95 indicate well-supported nodes (Minh *et al.* 2013). The partitioned Bayesian (BI) analysis was implemented in MrBayes v3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) following the default priors using the closest models of molecular evolution estimated in IQTREE. Four simultaneous runs were performed with eight chains per run, seven hot and one cold. The analysis was run for 5,000,000 generations and sampled every 500 generations from the Markov Chain Monte Carlo (MCMC). The analysis was halted after the average standard deviation split frequency fell below 0.01. The first 25% of the trees were discarded as a burn-in. A consensus tree was computed from the two parallel runs using the *sumt* function in MrBayes. Nodes that had Bayesian posterior probabilities (BPP) >0.95 were considered well supported (Huelsenbeck & Ronquist 2001; Wilcox *et al.* 2002). Nodal support values for all analyses are reported in the order of BPP/ML. Populations whose haplotypes formed strongly supported lineages restricted to particular regions were considered as putative species. Uncorrected pairwise percent sequence divergences (p-distance) for 16s, ND1 and flanking tRNAs were calculated using MEGA v5.2.2 (Tamura *et al*. 2011).

TABLE 1. Information for specimens used in this study.

Voucher #	Species	Locality	GenBank #
LSUHC 11087	*Abavorana luctuosa*	West Malaysia, Kelantan, Gunung Stong	KY982519
LSUHC 9731	*Abavorana luctuosa*	West Malaysia, Kedah, Sungai Sedim	KY982520
USMHC 1649	*Abavorana luctuosa*	West Malaysia, Penang, Penang Hill	KY982521
USMHC 1650	*Abavorana luctuosa*	West Malaysia, Penang, Penang Hill	KY982522
USMHC 1651	*Abavorana luctuosa*	West Malaysia, Penang, Penang Hill	KY982523
USMHC 1652	*Abavorana luctuosa*	West Malaysia, Penang, Penang Hill	KY982524
LSUHC 6580	*Abavorana luctuosa*	West Malaysia, Selangor, Gombak	KY982525
LSUHC 6585	*Abavorana luctuosa*	West Malaysia, Selangor, Gombak	KY982526
LSUHC 12679	*Abavorana luctuosa*	West Malaysia, Pahang, Fraser's Hill	KY982527
LSUHC 12680	*Abavorana luctuosa*	West Malaysia, Pahang, Fraser's Hill	KY982528
LSUHC 12681	*Abavorana luctuosa*	West Malaysia, Pahang, Fraser's Hill	KY982529
LSUHC 11663	*Abavorana luctuosa*	West Malaysia, Pahang, Genting Highlands	KY982530
LSUHC 11664	*Abavorana luctuosa*	West Malaysia, Pahang, Genting Highlands	KY982531
LSUHC 11665	*Abavorana luctuosa*	West Malaysia, Pahang, Genting Highlands	KY982532
LSUHC 11666	*Abavorana luctuosa*	West Malaysia, Pahang, Genting Highlands	KY982533
USMHC 1662	*Abavorana luctuosa*	West Malaysia, Pahang, Genting Highlands	KY982534
FMNH 231052	*Abavorana luctuosa*	East Malaysia, Sabah, Lahad Datu district	KY982535
FMNH 234972	*Abavorana luctuosa*	East Malaysia, Sabah, Sipitang district	KY982536
LSUHC 10512	*Abavorana nazgul* **sp. nov.**	West Malaysia, Kedah, Gunung Jerai	KY982537
LSUHC 10513	*Abavorana nazgul* **sp. nov.**	West Malaysia, Kedah, Gunung Jerai	KY982538
LSUHC 10514	*Abavorana nazgul* **sp. nov.**	West Malaysia, Kedah, Gunung Jerai	KY982539
USMHC 1468	*Pulchrana picturata*	West Malaysia, Kelantan, Pergau	KY982540

Results

The BI and ML analyses produced trees with the same topology and we are presenting the Bayesian tree with ML support values mapped onto it (Fig. 1). The tree indicates that the Gunung Jerai population is a separate lineage sister to the remaining samples except for FMNH 231052 (1.0/100) and is not conspecific with or even most closely related to *A. luctuosa* populations from Peninsular Malaysia or Borneo. Both analyses strongly indicate (1.0/96) it is the sister species to a clade containing populations of *A. luctuosa* from Peninsular Malaysia and a specimen from Sipitang, Sabah in Borneo (FMNH 234972). Sister to these populations is a specimen from Lahad Datu, Sabah (FMNH 231052), indicating that *A. luctuosa* is paraphyletic with more than one species present in Borneo. The Gunung Jerai population differs from all other peninsular Malaysian populations by a mean p-distance of 8.1%. The p-distance among other *A. luctuosa* populations within Peninsular Malaysia ranges from 0.1–1.2% (Table 2). The specimen from Sipitang, Sabah differs from the Gunung Jerai population by a p-distance of 7.5% but to other Peninsular Malaysian populations by a p-distance range of only 2.2–2.5% (Table 2). The most distantly related population from Lahad Datu, Sabah has a minimum p-distance value of 18.4% from all the other populations. The morphological data support the molecular data indicating that the Gunung Jerai population is discretely diagnosable from all other populations studied by having unique suite of characters (Table 3), and is therefore described herein as a new species.

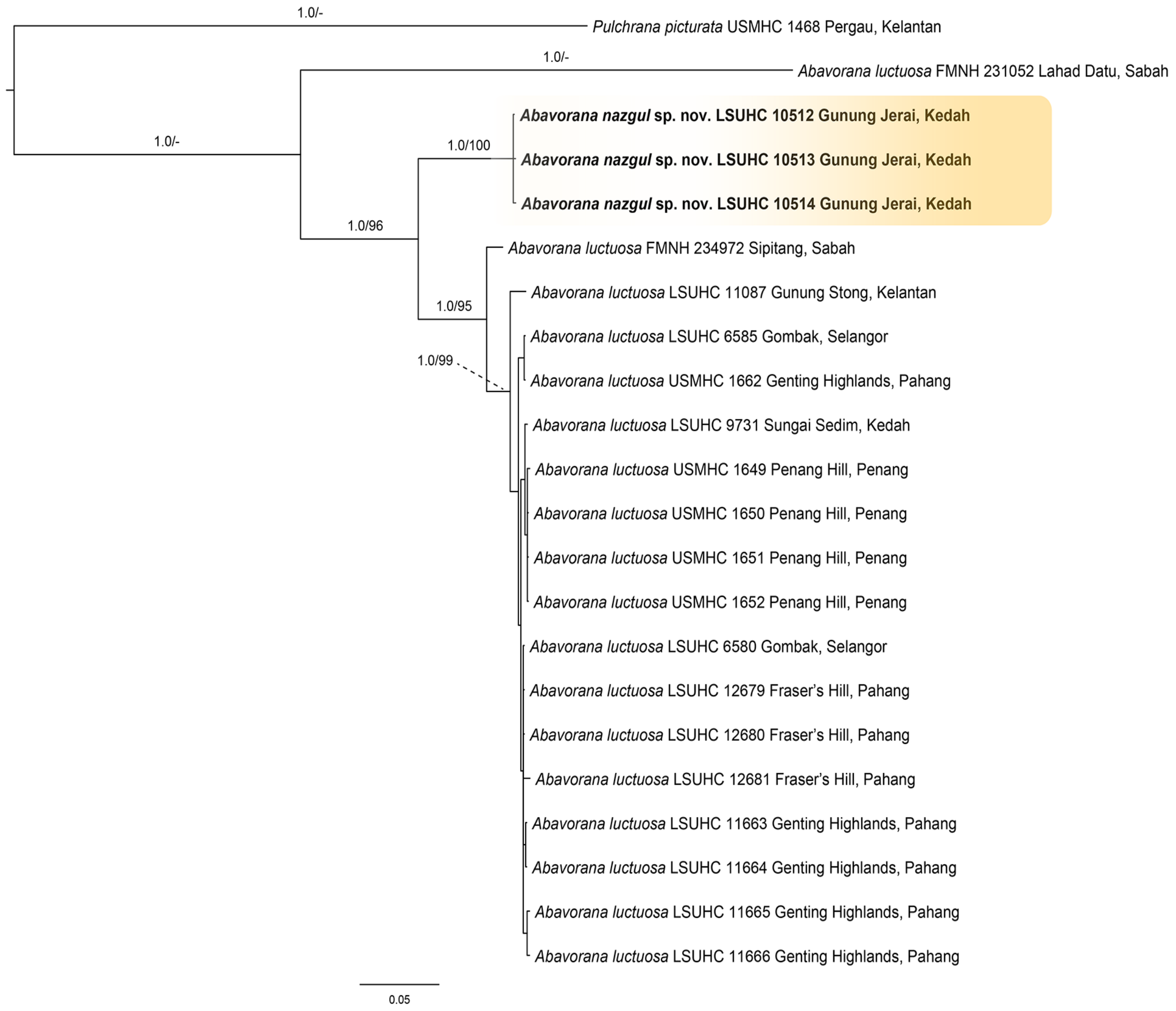

FIGURE 1. A Bayesian Inference (BI) phylogram of the relationships of the genus *Abavorana* based on the ND1 gene and flanking tRNAs. Numbers above the branches represent BI posterior probabilities and ML bootstrap support values, respectively.

TABLE 2. Uncorrected p-distances (%) for the examined populations of the genus *Abavorana* Oliver, Prendini, Kraus & Raxworthy 2015 computed in MEGA v5.1 (Tamura *et al.* 2011). Distances in bold are intraspecific distances, and distances below the diagonal are interspecific distances.

	Gunung Jerai, Kedah	Gunung Stong, Kelantan	Genting Highlands, Pahang	Gombak, Selangor	Sungai Sedim, Kedah	Penang Hill, Penang Island	Sipitang, Sabah	Lahad Datu, Sabah	Fraser's Hill, Pahang
Gunung Jerai, Kedah	**0.0**								
Gunung Stong, Kelantan	8.4	–							
Genting Highlands, Pahang	8.1	1.1	**0.3**						
Gombak, Selangor	8.0	1.1	0.3	**0.4**					
Sungai Sedim, Kedah	8.1	1.1	0.3	0.3	–				
Penang Hill, Penang Island	8.0	1.2	0.4	0.4	0.1	**0.0**			
Sipitang, Sabah	7.5	2.5	2.2	2.2	2.3	2.4	–		
Lahad Datu, Sabah	19.1	18.7	18.4	18.4	18.4	18.4	18.4	–	
Fraser's Hill, Pahang	8.1	1.0	0.1	0.2	0.2	0.3	2.2	18.5	**0.0**

Taxonomy

Abavorana nazgul sp. nov.

Gunung Jerai Black Stream-Frog
Fig. 2, 4 & 6

Rana luctuosa Sukumaran, J. 2005: 38.

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

Paratypes. Paratypes USMHC 2232 & USMHC 2233 bear the same locality data as the holotype. Paratype LSUHC 10512 was collected on 8 October 2011 while paratypes LSUHC 10513 and LSUHC 10514 were collected on 28 October 2011 by Evan S.H. Quah, M.A. Muin and Yusof Omar.

Diagnosis. Morphological analyses of the newly collected material from Gunung Jerai confirms the placement of this population in the genus *Abavorana* based on the combination of having a medium-sized, robust 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 ventrum 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 ventrum; dorsal surface of hind limbs speckled or mottled; posterior surface of thigh mottled (Inger 1966; Oliver *et al.* 2015). *Abavorana nazgul* **sp. nov.** can be differentiated from its congeners by the following combination of characters: adult males 42.1–50.0 mm SVL; nuptial pads absent in males; humeral glands in males small (2.3–2.5 mm); dorsolateral stripe continuous, orange to yellow in colour; mid-dorsal region of dorsum black, with or without faint orange or yellow speckles; flanks black, colouration unstratified; distinct cream 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.

Description of holotype. Adult male, SVL 50.0 mm; head longer than wide (HL/HW=1.19); snout wider than long (SW/SL=1.38), longer than eye diameter (SL/ED=2.00), slightly projecting beyond lower jaw, dorsally concave, gradually tapering with a slight median point in dorsal view, slightly rounded and posteroventrally, sloping downward in lateral view; canthus rostralis distinct, lores vertical, slightly concave; nares open laterally, just below canthus, positioned closer to rostrum than eye, distance between nares smaller than snout length (IND/SL=0.78), approximately one-half of snout width (IND/SW=0.56); eyes large, slightly protruding beyond lips in dorsal view, diameter less than snout length (ED/SL=0.50) and interorbital distance (ED/IOD=0.43); pupils circular; interorbital region flat, distance smaller than snout width (IOD/SW=0.85) but greater than snout length (IOD/SL=1.17); tympanum distinct, round, as tall as wide, horizontal diameter equal to eye diameter (TD/ED=1.00); choanae subcircular, separated by distance larger than their diameter; vomerine teeth small, indistinct; and tongue elongate, broadening posteriorly with a central terminal notch, posterior ⅓ free.

Forelimbs relatively long, slender (BL/SVL=0.14; FAL/SVL=0.15; ML/SVL=0.23), brachial and forearm length subequal (BL/FAL=0.93); enlarged humeral glands present on ventral surfaces of brachia; order of fingers from shortest to longest: II<IV<I<III (fingers I and IV subequal); fingers lack webbing; finger tips dilated into small, rounded discs bearing circummarginal grooves; numbers of subarticular tubercles are digit I(1), II(1), III(2), IV(2); subarticular tubercles prominently raised, oval, opaque on toes I and II and base of toes III and IV, second subarticular tubercles of toes III and IV indistinct; supernumerary tubercles absent; inner metacarpal tubercle large, oval, translucent; palmar tubercle oval, translucent, slightly smaller and not in contact with inner metacarpal tubercle; outer metacarpal tubercle oval, translucent, in contact, similar in size to palmar tubercle; nuptial pads absent. Hind limbs long, slender (FL/SVL =0.47; CL/SVL= 0.49; TL/SVL= 0.24), tibia slightly longer than femur (CL/FL =1.04); order of toes from shortest to longest: I<II<V<III<IV (toes III and V subequal); toe tips slightly dilated into small, rounded discs bearing circummarginal grooves; webbing formula: I1–1½ II 1–2 III 1½–3½ IV 3½–2½ V; subarticular tubercles prominently raised, translucent; number of subarticular tubercles on each toe varies by toe number: I(1), II(1), III(2), IV(3), V(2); inner metatarsal tubercle elongate, raised, translucent; outer metatarsal tubercle absent.

Dorsum, upper eyelid, interorbital region, snout, flanks and surface of limbs finely shagreened, lacking tubercles; dorsolateral and tympanic folds absent. Rictal glands absent, only a weak rictal ridge present; throat, stomach and ventral surfaces of limbs finely shagreened. Measurements of types are presented in Table 3.

Colouration in life (Fig. 2). The dorsum is black with faint orange specks along the vertebral line. A complete orange dorsolateral stripe extends from the rostrum (stripe yellowish-orange on the snout), along the canthus, lateral margin of palpebrae, and dorsolateral part of dorsum, and terminates at the sacrum where it forms a nearly complete loop. The lateral margins of the snout, anterior portion of the flanks, and dorsal surface of the limbs are black and gradually transition to dark-grey on the lower flanks. Along the upper lips are a single row of cream spots that form a streak beneath the tympanum and extend to the corner of the jaw. The tympanum is dark-brown. The flanks and dorsal side of the limbs bear round, creamy yellow spots, some of which connect to form short, elongate bars especially on the hind limbs. The venter is grey-brown and covered in whitish spots. The spots on the throat and belly are larger than those on the ventral surface of the thigh.

Colouration in preservation (Fig. 4). The dorsum, dorsal side of limbs and upper flanks are dark-grey while the dorsolateral stripe and spots–bars are cream. The lower flanks, fingers and toes are a lighter shade of grey. The venter is light grey-brown with the spots on throat, belly, and underside of the thighs whitish.

Variation. All paratypes closely resemble holotype in overall external morphology, colouration, and patterning. In a single paratype (USMH 2232) the narrow stripe outlining the snout and dorsolateral margin of the body is yellow instead of orange. In addition, the stripe along the snout of this specimen is discontinuous (Fig. 2D). Juveniles have a bolder colour pattern than the adults where the colour of the dorsum is darker and lacks any light mottling or faint specks. Juveniles also have fewer spots on the flanks of and no spots at the corners of the upper labial margins and the narrow stripe outlining the snout and dorsolateral margin of the body is bright orange or vermillion (Fig. 2F). In the female paratype (LSUHC 10514), the texture of the skin around the vent, posterior and ventral regions of the thighs is more rugose compared the male specimens. In addition, paratypes (LSUHC 10513 and 10514) have a small, weak, indistinct, round, outer metatarsal tubercle. This is not surprising as Inger (1966) reported observing the presence of a metatarsal tubercle in only approximately one-half of the *A. luctuosa* specimens he examined. Measurements showing variation in size within the type series are shown in Table 3.

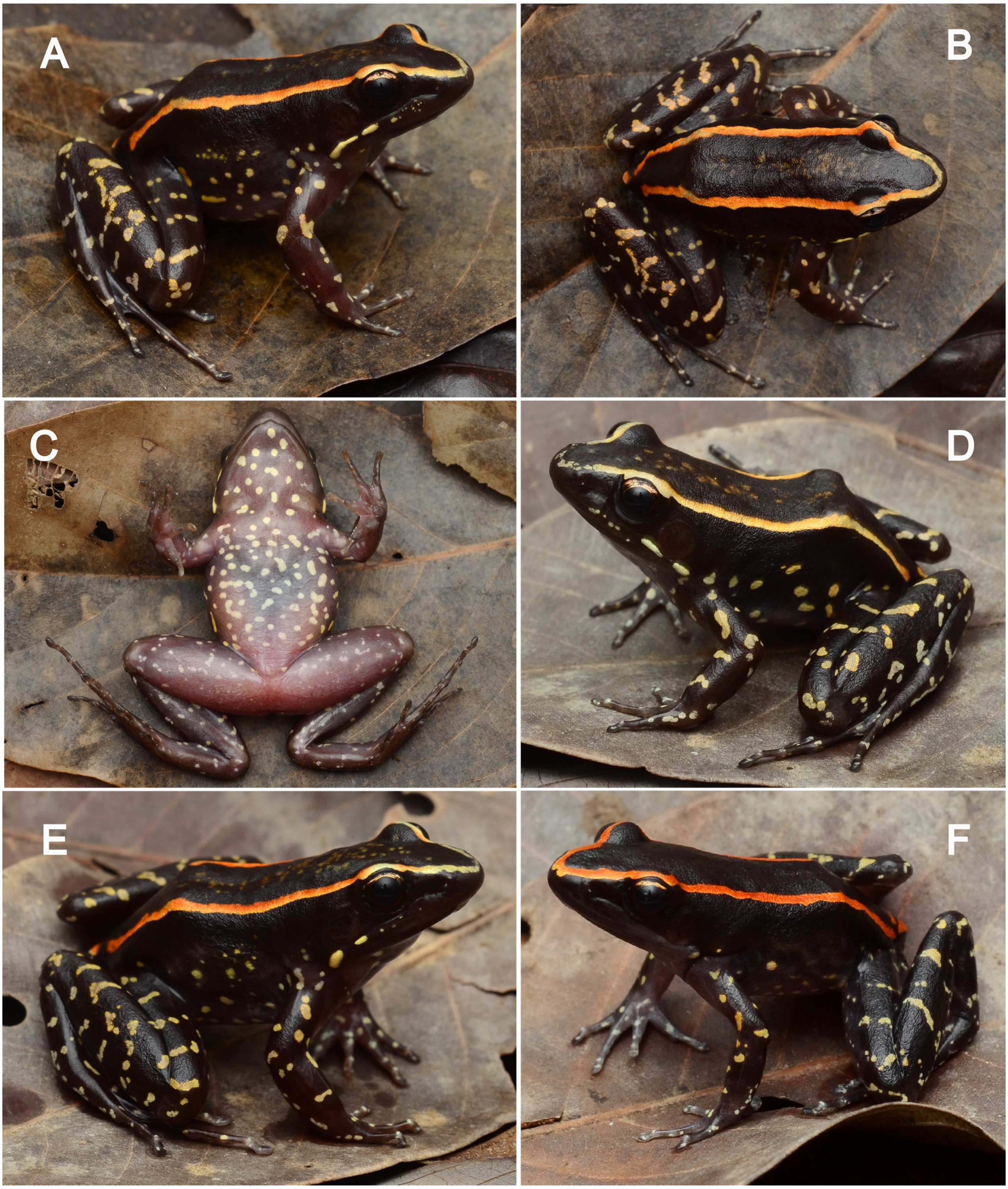

FIGURE 2. (A) Holotype of *Abavorana nazgul* **sp. nov.** (USMHC 2231). (B) Dorsal pattern of the holotype of *A. nazgul* **sp. nov.** (USMHC 2231). (C) Ventral pattern of the holotype of *A. nazgul* **sp. nov.** (USMHC 2231). (D) Paratype of *A. nazgul* **sp. nov.** (USMHC 2232). (E) Paratype of *A. nazgul* **sp. nov.** (USMHC 2233). (F) Juvenile *A. nazgul* **sp. nov.** from Gunung Jerai, Kedah. All photographs by Evan Quah.

Comparison. Morphological data for species comparison was obtained from Inger (1966) and the material examined (Appendix). *Abavorana nazgul* **sp. nov.** is differentiated from Peninsular Malaysian populations of *A. luctuosa* by the following characters: colouration of the dorsum (a black dorsum, with or without faint, fine orange or yellow speckling versus an orange or reddish-brown dorsum; dorsolateral stripes that are yellow or orange versus white or cream); spots on the upper lips (present, large yellow spots, especially prominent below the tympanum versus absent or only faint white spot at the corner of the jaws); pattern along the flanks (prominent yellow or cream spots versus an absence of spots or very fine, white spots); pattern on the upper surface of the limbs (large, prominent, cream or yellow spots or short bars versus fine white or greyish-blue spots or bars); pattern of venter (large, prominent cream or yellow spots versus an immaculate venter or with occasional fine, inconspicuous spots or reticulations on the belly or underside of the thigh) (Figs. 2–6). Occasionally, very dark individuals of *A. luctuosa* may be encountered or specimens with orange spots present on the dorsal surface of forearm, however these specimens can still be differentiated from *A. nazgul* **sp. nov.** by their immaculate flanks and venter or only very fine white spots present on the flanks (Figs. 3C & D), as well as their phylogenetic position. The difference in colour pattern between *A. nazgul* **sp. nov.** and Bornean populations of *A. luctuosa* is similar to those of Peninsular Malaysia with the exception being that the underside of the limbs in Bornean specimens have bold, cream-coloured bars (Inger 1966; see Fig. 159 in Malkmus *et al*. 2002). Examination of juveniles of both species shows that the juveniles resemble the adults (Figs. 2F, 3E, 3F), suggesting no ontogenetic changes in colouration for both *A. nazgul* **sp. nov.** and *A. luctuosa*. In addition to colour pattern, *A. nazgul* **sp. nov**. can be differentiated from Peninsular Malaysian populations of *A. luctuosa* by their larger size in adult males (42.1–50.0 mm SVL versus 42.7–44.5 mm SVL) and their smaller humeral glands (2.4 mm in 42.1 mm male versus 3.8mm in 42.0 mm male; Inger 1966). In comparison, Bornean male *A. luctuosa* are larger than *A. nazgul* **sp. nov**. (53.0–58.8 mm SVL versus 42.1–50.0 mm SVL) (Inger 1966). The size range reported for female *A. luctuosa* are between 53.0–60.0 mm SVL (Inger & Stuebing 2005) which is larger than the single female *A. nazgul* **sp. nov**. (LSUHC 10514) examined (52.8mm SVL).

Abavorana luctuosa was previously grouped with frogs of the genus *Pulchrana* (Dubois 1992) prior to recent taxonomic revision (Oliver *et al*. 2015). However, *A. nazgul* **sp. nov.** can be differentiated from members of the *Pulchrana picturata* complex by the following characteristics; dorsolateral line (indistinct versus a fine or warty and poorly developed); position of humeral gland (ventral surface versus anteroventral surface of brachium); rictal ridge (weak versus a medium to well-developed); outer metatarsal tubercle (absent or weak versus present and large); and texture of flanks (smooth versus weakly warty) (Oliver *et al*. 2015). *Abavorana nazgul* **sp. nov**. can be further differentiated from *P. centropeninsularis,* a species with a similar colour pattern, by the following combination of characters; dorsum in adults that is black with faint orange or yellow speckles versus dorsum that is black and unmarked; orange or yellow versus bright vermillion dorsolateral stripe; larger size of adult males (42.1–50.0 mm vs. 37.4–37.6 mm SVL); a small humeral gland on the ventral surface of the brachium versus large humeral gland on lateroventral surface of brachium; and absence versus presence of indistinct, translucent, supernumerary tubercles at the base of first phalanx on each finger. *Pulchrana centropeninsularis* is also a lowland species recorded from 90–105 m in elevation from central Peninsular Malaysia in the state of Pahang whereas *A. nazgul* **sp. nov**. is a montane species found only above 800 m in elevation at Gunung Jerai, Kedah (Chan *et al*. 2014a).

Distribution and natural history. *Abavorana nazgul* **sp. nov.** is only known from the upper elevations of Gunung Jerai, Kedah (Fig. 6). Sukumaran (2005) reports finding this species from 800–1200 m in elevation at three different locations, Mushroom Creek, Caecilian Stream, and Batu Kapal. The specimens we found were at the stream close to Telaga Tok Sheikh. This species is riparian and found in the vicinity of streams (Fig. 7). At night, frogs can be found hiding in the leaf litter, vegetation, tangled roots or overhanging banks along streams. Similar to observations by Sukumaran (2005), males can be heard calling from the banks of the stream, sometimes hidden among the roots of plants or in crevices. The males had a distinctive “mew”-like call and Sukumaran (2005) reports finding gravid females between November to March. He also reported observing tadpoles during this period that were found in deeper, sediment-bottomed, open pool sections of the creek during this same time period. We found recently emerged juveniles in April that indicates this species breeds in the later months and the beginning of the year which is the dry season in the Northwestern region of Peninsular Malaysia (Sukumaran 2005). Along the same stream where *A. nazgul* **sp. nov.** was found, *Phrynoidis asper, Limnonectes blythii, L. khasianus* and *Odorrana hosii* were observed. In the nearby vegetation, *Polypedates leucomystax, Philautus petersi,* and *Roarchestes parvulus* were also observed. These species were also noted by Sukumaran (2005).

Etymology. The specific epithet “nazgul” is a noun in apposition in reference to the “Nazgûl”, characters created by J.R.R. Tolkien in *The Lord of the Rings* (1954). Also known as Ring-wraiths, they were nine men who succumbed to Sauron’s power and were transformed into white ghostly figures wearing black cloaks—the colouration that the new population being described herein shares.

TABLE 3. Selected measurements (mm) of the type series of *Abavorana nazgul* **sp. nov.** and *A. luctuosa*. Please see methods for abbreviations.

	Abavorana nazgul **sp. nov.**							*Abavorana luctuosa*		
Character	USMHC 2231 Holotype	USMHC 2232 Paratype	USMHC 2233 Paratype	LSUHC 10512 Paratype	LSUHC 10513 Paratype	Mean ± Std Error (Min–Max)	LSUHC 10514 Paratype	LSUHC 9731	USMHC 2310	LSUHC 11087
SVL	50.0	48.0	45.0	42.1	43.0	45.6 ± 3.3 (42.1–50.0)	52.8	42.0	46.0	56.0
HL	17.2	16.5	16.3	16.6	16.3	16.6 ± 0.4 (16.3–17.2)	19.2	14.8	16.4	20.2
HW	14.4	12.9	13.1	12.9	13.1	13.3 ± 0.6 (12.9–14.4)	17.1	12.4	12.5	15.2
SL	7.5	7.1	7.1	7.2	7.2	7.2 ± 0.2 (7.1–7.5)	9.0	6.7	6.7	8.5
SW	10.4	9.8	10.2	9.9	10.1	10.1 ± 0.2 (9.8–10.4)	12.5	9.6	8.3	11.3
IOD	8.8	8.7	8.2	8.6	8.7	8.6 ± 0.2 (8.2–8.8)	9.9	7.6	7.8	9.0
IND	5.9	5.5	5.3	5.3	5.5	5.5 ± 0.3 (5.3–5.9)	6.0	5.1	5.2	6.7
ED	3.8	4.0	4.0	3.9	4.1	4.0 ± 0.1 (3.8–4.1)	4.8	3.5	4.2	4.7
TD	3.8	3.8	3.9	3.6	3.4	3.7 ± 0.2 (3.4–3.9)	4.1	3.2	3.5	3.8
BL	6.9	6.4	6.4	6.4	6.7	6.6 ± 0.2 (6.4–6.9)	8.8	6.2	6.4	8.0
FAL	7.4	7.6	7.3	7.4	7.5	7.4 ± 0.1 (7.3–7.6)	10.2	7.7	8.54	9.5
ML	11.4	11.1	11.1	10.8	11.0	11.1 ± 0.2 (10.8–11.4)	13.9	10.0	10.9	13.6
FL	23.4	23.0	22.8	22.4	22.8	22.9 ± 0.4 (22.4–23.4)	28.4	19.0	19.8	25.4
CL	24.4	24.2	24.3	23.2	23.8	24.0 ± 0.5 (23.2–24.4)	29.5	22.2	22.0	27.5
TL	12.0	11.8	11.4	10.7	11.2	11.4 ± 0.5 (11.2–12.0)	14.9	11.8	11.0	14.0
PL	24.1	23.6	23.5	22.3	23.4	23.4 ± 0.7 (22.3–24.1)	29.2	20.5	22.3	27.3
HG	2.5	2.5	2.3	2.4	2.5	2.4 ± 0.1 (2.3–2.5)	-	3.79	3.7	-
Sex	Male	Male	Male	Male	Male	Males (n=5)	Female	Male	Male	Female
Pattern of venter	Spotted	Spotted	Spotted	Spotted	Spotted	-	Spotted	Throat & chest immaculate. Stomach and limbs faintly mottled	Throat & chest immaculate. Stomach and limbs faintly mottled	Throat & chest immaculate. Stomach and limbs faintly mottled

FIGURE 3. (A) Adult *Abavorana luctuosa* (LSUHC 11087) from Gunung Stong, Kelantan (Photograph by L.L. Grismer). (B) Adult *A. luctuosa* (LSUHC 9731) from Sungai Sedim, Kedah (Photograph by L.L. Grismer). (C) Adult *A. luctuosa* (USMHC 2310) from Penang Hill, Penang. (D) Ventral pattern of adult *A. luctuosa* (USMHC 2310) from Penang Hill, Penang. (E) Juvenile *A. luctuosa* (USMHC 2192) from Fraser's Hill, Pahang. (F) Metamorph *A. luctuosa* (USMHC 1662) from Genting Highlands, Pahang. Photographs by Evan Quah.

FIGURE 4. Type series of *Abavorana nazgul* **sp. nov.** Top: View of the dorsum. Bottom: View of the venter.

FIGURE 5. Comparison of dorsum (top) and venter (bottom) of *Abavorana luctuosa* from Peninsular Malaysia.

Discussion

The discovery of *Abavorana nazgul* **sp. nov.** adds to the growing number of new species being described from the mountains of Peninsular Malaysia (Chan *et al*. 2014b; Davis *et al*. 2016; Grismer *et al*. 2012, 2013a,b, 2014a,b, 2015a,b, 2016; Grismer & Quah 2015; Loredo *et al*. 2013; Matsui *et al*. 2009, 2014; Wood *et al*. 2008, 2009; Zug 2010). Its discovery is especially interesting because it had been considered a melanistic form of *A. luctuosa* (Sukumaran 2005), and despite many surveys at other montane locations around the country, no other *A. luctuosa* populations with a melanistic pattern have ever been found. Within Peninsular Malaysia, *A. luctuosa* is a widely distributed species (Fig. 6) and has been recorded from lowland sites such as Sungai Sedim and Pasoh Forest Reserve as well as sub-montane locations such as at Fraser's Hill where we have found them close to the Jeriau waterfall at approximately 1000 m in elevation and at Awana trail, Genting Highlands, at approximately 800 m in elevation. Malkmus *et al*. (2002) reports the altitudinal distribution of *A. luctuosa* to be between 150–1400 m in elevation.

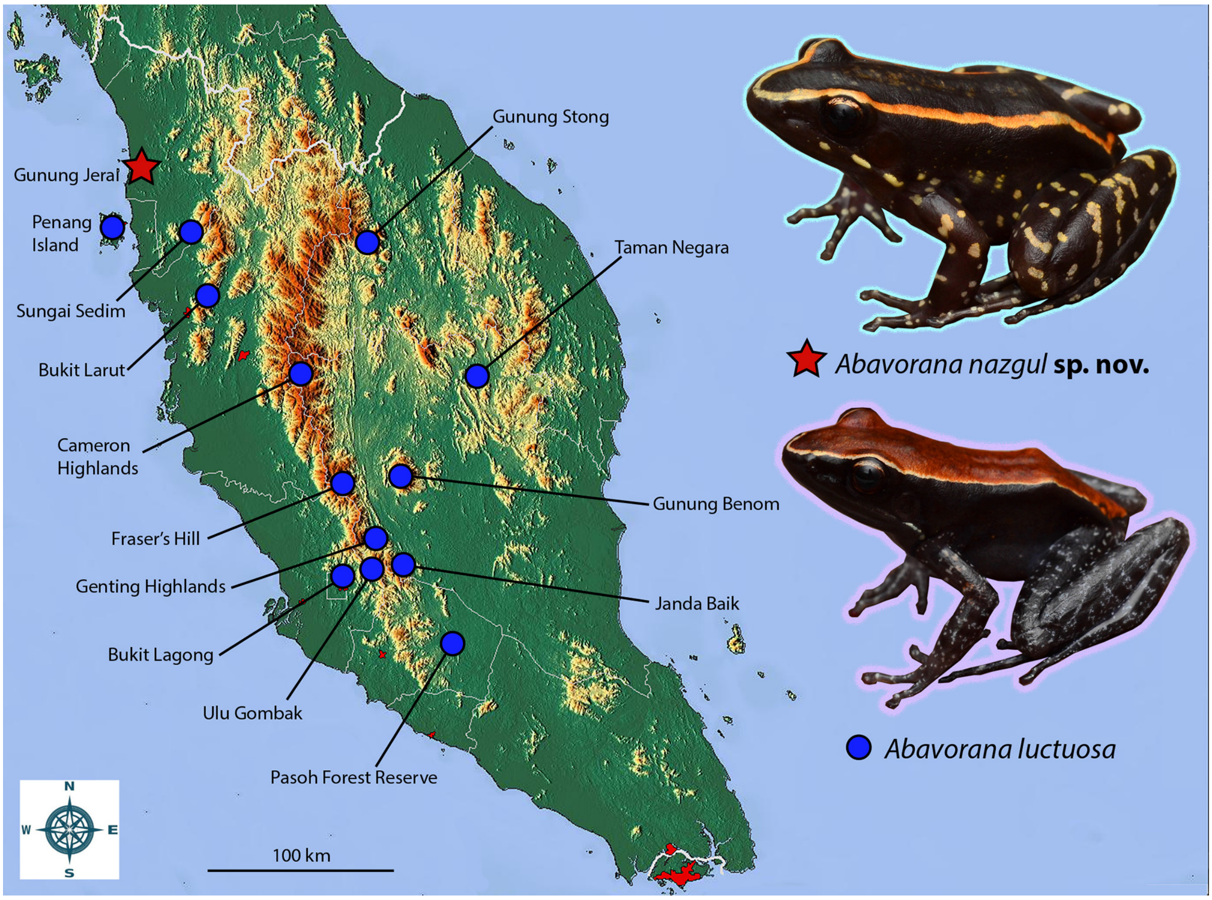

FIGURE 6. Distribution of *Abavorana* in Peninsular Malaysia. Red star = type locality of *A. nazgul* sp. nov. at Gunung Jerai, Kedah, blue circle = reported localities of *A. luctuosa*.

FIGURE 7. Streamside microhabitat of *Abavorana nazgul* **sp. nov.** at Gunung Jerai, Kedah.

The specific distinction of *Abavorana nazgul* **sp. nov.** is most likely related to the geological history of Gunung Jerai and its resultant influence of the biogeography of its flora and fauna. Geologically, Gunung Jerai has been isolated from other mountain systems in Peninsular Malaysia for its entire existence and has existed as a land-bridge island numerous times in the past when sea-levels rose and fell with alternating interglacial cycles (Bradford 1972; WWF Malaysia 1977). This isolated coastal massif that rises to 1200 m in elevation is bordered by the Straits of Malacca on the west and surrounded on the other sides by notably flat plains which do not exceed 15 m in elevation. The nearest mountains to the east lie some 32 km inland or 35 km southwest on Penang Island (WWF Malaysia 1977). Over time, the *Abavorana* population on Gunung Jerai has evolved into a distinct highland species, *A. nazgul* **sp. nov**. This makes it the second species of herpetofauna endemic to Gunung Jerai after *Cnemaspis harimau* (Chan *et al*. 2010a). Previously another frog, *Odorrana monjerai* was thought to be endemic to Gunung Jerai but has been found at Bukit Hijau, Kedah (Chan *et al*. 2010b).

The discovery of *A. nazgul* **sp. nov.** also echos Grismer *et al*. (2016) in noting that the majority the many new species recently discovered are actually lineages that are easily diagnosed on the basis of morphology and colour pattern and have come from areas that have been widely surveyed for well over a century. A similar scenario is observed here, as surveys into the herpetofauna of Gunung Jerai have been carried out since the early 1900s (Robinson & Kloss 1916; Sukumaran 2005; Matsui & Jaafar 2006; Shahrul *et al.* 2006; Chan *et al*. 2010a). It has taken a hundred years since the first survey at the site for *A. nazgul* **sp. nov.** to be formally recognised as a distinct species. Its elusive nature kept it hidden and even when it was found, as it was understandably thought to be a colour morph of *A. luctuosa* (Sukumaran 2005). This study also demonstrates that, despite the type locality of *A. luctuosa* being Sarawak, East Malaysia (Frost 2017), the *A. luctuosa* populations from Borneo are paraphyletic and there are more species currently masquerading under this specific nomen. This is in accord with Inger (1966) and Grandison (1972) who suggested *A. luctuosa* is a species complex in need of reappraisal. Such findings highlight the importance and need for the thorough examination of specimens in collections and the use of modern molecular tools for more detailed analyses into species relationships and taxonomy. It also emphasizes the importance and need for scientific collecting and cataloguing of specimens for comparative studies. This must be encouraged as a sound taxonomy is the basis for understanding biodiversity which in turn can direct the implementation of sustainable management programs in order to conserve the biodiversity, especially in unique, fragile habitats like the mountains.

Acknowledgements

We wish to thank Yusof Omar, A.R. Nor Amira and M. Fatim Syakirah for assistance in the field. We thank Alan Resetar of the FMNH for the loaning of material under their care for examination. We thank Dr. Jack W. Sites Jr. for allowing us to use the facilities at his lab for parts of the molecular analyses. Research by LLG was supported in part by a grant from the College of Arts and Sciences, La Sierra University, Riverside, California and from a National Geographic Society Explorers Grant (9277-15), while research by Shahrul Anuar was supported by a Universiti Sains Malaysia Grant (811331). We are also grateful to the Department of Wildlife and National Parks, Peninsular Malaysia for issuing us a research permit [JPHL&TN(IP): 100-6/1/14(39)] to conduct research.

References

Berry, P.Y. (1975) *The amphibian fauna of Peninsular Malaysia*. Tropical Press, Kuala Lumper, 127 pp.

Bradford, E.F. (1972) *The Geology and Mineral Resources of the Gunong Jerai Area, Kedah*. Geological Survey Headquarters, Ipoh, 242 pp.

Camargo, A., De Sa, R.O. & Heyer, W.R. (2006) Phylogenetic analyses of mtDNA sequences reveal three cryptic lineages in the widespread neotropical frog *Leptodactylus fuscus* (Schneider, 1799) (Anura, Leptodactylidae). *Biological Journal of the Linnean Society*, 87 (2), 325–341.
https://doi.org/10.1111/j.1095-8312.2006.00581.x

Chan, K.O., Azman, M.S., Azlin, N. & Pan, K.A. (2009) Additions to the herpetofauna of Pasoh Forest Reserve, Negeri Sembilan, Peninsular Malaysia. *Tropical Life Sciences Research*, 20 (1), 71–80.

Chan, K.O., Brown, R.M., Lim, K.K.P., Ahmad, N. & Grismer, L.L. (2014a) A new species of frog (Amphibia: Anura: Ranidae) of the *Hylarana signata* complex from Peninsular Malaysia. *Herpetologica*, 70 (2), 228–240.

Chan, K.O., Grismer, L.L., Anuar, S., Quah, E.S.H., Muin, M.A., Savage, A.E., Grismer, J.L., Norhayati, A., Remegio, A.C. & Greer, L.F. (2010a) A new endemic Rock Gecko *Cnemaspis* Strauch 1887 (Squamata: Gekkonidae) from Gunung Jerai, Kedah, northwestern Peninsular Malaysia. *Zootaxa*, 2576, 59–68.

Chan, K.O., Belabut, D. & Ahmad, N. (2010b) A revised checklist of the amphibians of Peninsular Malaysia. *Russian Journal of Herpetology*, 17, 202–206.

Chan, K.O., Wood, P.L., Jr., Anuar, S., Muin, M.A., Quah, E.S.H., Sumarli, A.X. & Grismer, L.L. (2014b) A new species of upland Stream Toad of the genus *Ansonia* Stoliczka, 1870 (Anura: Bufonidae) from northeasten Peninsular Malaysia. *Zootaxa*, 3764 (4), 427–440.

Davis, H.R., Grismer, L.L., Klabacka, R.L., Muin, M.A., Quah, E.S.H., Anuar, S., Wood, P.L. Jr. & Sites, J.W. Jr. (2016) The phylogenetic relationships of a new Stream Toad of the genus *Ansonia* Stoliczka, 1870 (Anura: Bufonidae) from a montane region in Peninsular Malaysia. *Zootaxa*, 4103 (2), 137–153.
https://doi.org/10.11646/zootaxa.4103.2.4

De Queiroz, K. (2005) A Unified Concept of Species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences*, 56, 196–215.

Dubois, A. (1992) Notes sur la classification des Ranidae (Amphibiens anoures). *Bulletin Mensuel de la Société Linnéenne de Lyon*, 61, 305–352.
https://doi.org/10.3406/linly.1992.11011

Flower, S.S. (1896) Notes on a second collection of batrachians made in the Malay Peninsula 1895–96, with a list of the species recorded from that region. *Proceedings of the Zoological Society of London*, 1896, 856–914.

Frost, D.R. (2017) Amphibian Species of the World: an Online Reference. Version 6.0. Electronic Database. American Museum of Natural History, New York, USA. Available from: http://research.amnh.org/herpetology/amphibia/index.html (accessed 21 June 2017)

Grandison, A.G.C. (1972) The Gunong Benom Expedition 1967. 5. Reptiles and amphibians of Gunong Benom with a description of a new species of *Macrocalamus*. *Bulletin of the British Museum of Natural History (Zoology)*, 23, 45–101.

Grismer, L.L., Chan, K.O., Grismer, J.L., Wood, P.L. Jr. & Norhayati, A. (2010) A checklist of the herpetofauna of the Banjaran Bintang, Peninsular Malaysia. *Russian Journal of Herpetology*, 17, 147–160.

Grismer, L.L. & Quah, E.S.H. (2015) The Rediscovery of *Sphenomorphus malayanus* Doria, 1888 (Squamata: Scincidae) from the Titiwangsa Mountain Range of Peninsular Malaysia and its re-description as *S. senja* sp. nov. *Zootaxa*, 3931 (1), 63–70.
https://doi.org/10.11646/zootaxa.3931.1.4

Grismer, L.L, Quah, E.S.H., Wood, P.L. Jr., Anuar, S., Muin, M.A., Davis, H.R., Murdoch, M.L., Grismer, J.L., Cota, M. & Cobos, A.J. (2016) Dragons in the mist: three new species of *Pseudocalotes* Fitzinger (Squamata: Agamidae) from the sky island archipelago of Peninsular Malaysia. *Zootaxa*, 4136 (3), 461–490.
https://doi.org/10.11646/zootaxa.4136.3.3

Grismer, L.L., Shahrul, A., Muin, M.A., Quah, E.S.H. & Wood, P.L. Jr. (2013a) Phylogenetic relationships and description of a new upland species of Bent-toed Gecko (*Cyrtodactylus* Gray, 1827) of the *C. sworderi* complex from northeastern Peninsular Malaysia. *Zootaxa*, 3616 (3), 239–252.
http://dx.doi.org/10.11646/zootaxa.3616.3.2

Grismer, L.L., Wood, P.L. Jr., Quah, E.S.H., Shahrul, A., Muin, M.A. Sumontha, M., Norhayati, A., Bauer, A.M., Wangkulangkul, S., Grismer, J.L. & Pauwels, O.S.G. (2012) A phylogeny and taxonomy of the Thai-Malay Peninsula Bent-toed Geckos of the *Cyrtodactylus pulchellus* complex (Squamata: Gekkonidae): combined morphological and molecular analyses with descriptions of seven new species. *Zootaxa*, 3520, 1–55.

Grismer, L.L., Wood, P.L. Jr., Anuar, S., Muin, M.A., Quah, E.S.H., McGuire, J.A., Brown, R.M., Ngo, V.T. & Pham, H.T. (2013b) Integrative taxonomy uncovers high levels of cryptic species diversity in *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) and the description of a new species from Peninsular Malaysia. *Zoological Journal of the Linnaean Society*, 169, 849–880.

Grismer, L.L., Wood, P.L. Jr., Anuar, S., Quah, E.S.H., Muin, M.A., Maketab, M., Chan, K.O., Sumarli, A.X., Loredo, A.I. & Heinz, H.M. (2014a) The phylogenetic relationship of three new species of the *Cyrtodactylus pulchellus* complex (Squamata: Gekkonidae) from poorly explored regions in northeastern Peninsular Malaysia. *Zootaxa*, 3764 (4), 427–440.

Grismer, L.L., Wood, P.L. Jr., Anuar, S., Quah, E.S.H., Muin, M.A., Chan, K.O., Sumarli, A.X. & Loredo, A.I. (2015b) Repeated evolution of sympatric, paleoendemic species in closely related, co-distributed lineages of *Hemiphyllodactylus* Bleeker, 1860 (Squamata: Gekkonidae) across a sky-island archipelago in Peninsular Malaysia. *Zoological Journal of the Linnean Society*, 174, 859–876.

Grismer, L.L, Wood, P.L. Jr., Lee, C.H., Quah, E.S.H., Anuar, S., Ngadi, E. & Sites, J.W. Jr. (2015a) An integrative taxonomic review of the genus *Bronchocela* (Kuhl, 1820) from Peninsular Malaysia with descriptions of new montane and insular endemics. *Zootaxa*, 3948 (1), 1–23.

Grismer, L.L., Wood, P.L. Jr., Shahrul, A., Riyanto, A., Norhayati, A., Muin, M.A, Sumontha, M., Grismer, J.L., Chan, K.O., Quah, E.S.H. & Pauwels, O.S.G. (2014b) Systematics and natural history of Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia. *Zootaxa*, 3880 (1), 1–147.

Huelsenbeck, J.P. & Ronquist, F. (2001) MrBayes: Bayesian Inference of Phylogenetic Trees. *Bioinformatics (Oxford)*, 17,

754–755.
https://doi.org/10.1093/bioinformatics/17.8.754

Inger, R.F. (1966) The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana: Zoology*, 52, 1–402.

Inger, R.F. & Stuebing, R.B. (2005) *A Field Guide to the Frogs of Borneo. 2nd Edition*. Natural History Publications (Borneo) Sdn Bhd. Kota Kinabalu, Sabah, viii + 201 pp.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentlies, P. & Drummond, A. (2012) Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28 (12), 1647–1649.
https://doi.org/10.1093/bioinformatics/bts199

Leong, T.M. & Lim, K.K.P. (2003b) Herpetofaunal records from Fraser's Hill, Peninsular Malaysia with larval descriptions of *Limnonectes nitidus* and *Theloderma asperum* (Amphibia: Ranidae and Rhacophoridae). *The Raffles Bulletin of Zoology*, 51, 123–136.

Lim, K.K.P., Leong, T.M. & Lim, B.L. (2002) Herpetofaunal records from Cameron Highlands, peninsular Malaysia. *Journal of Wildlife and Parks*, 20, 49–57.

Loredo, A.I., Wood, P.L. Jr., Quah, E.S.H., Anuar, S., Greer, L.F. & Grismer, L.L. (2013) A phylogenetic based taxonomy of *Asthenodipsas vertebralis* (Boulenger, 1900), the description of a new species from Peninsular Malaysia, and the resurrection of a species from Sumatra. *Zootaxa*, 3664 (4), 505–524.

Maddison, D.R. & Maddison, W.P. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.04. Available from: http://mesquiteproject.org (accessed 25 July 2017)

Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P. & Kosuch, J. (2002) *Amphibians and Reptiles of Mount Kinabalu (NorthBorneo)*. A.R.G. Ganter Verlag Kommanditgesellschaft, Ruggel, 424 pp.

Manthey, U. & Grossmann, W. (1997) *Amphibien & Reptilien Südostasiens*. Natur und Tier Verlag, Münster, 512 pp.

Matsui, M., Belabut, D.M. & Ahmad, N. (2014) Two new species of fanged frogs from Peninsular Malaysia (Anura: Dicroglossidae). *Zootaxa*, 3881 (1), 75–93.
https://doi.org/10.11646/zootaxa.3881.1.6

Matsui, M., Belabut, D.M., Norhayati, A. & Yong, H.S. (2009) A new species of *Leptolalax* (Amphibia, Anura, Megophryidae) from Peninsular Malaysia. *Zoological Science*, 26, 243–247.
https://doi.org/10.2108/zsj.26.243

Matsui, M. & Jaafar, I. (2006) A new cascade frog of subgenus *Odorrana* from Peninsular Malaysia. *Zoological Science*, 23 (7), 647–651.
https://doi.org/10.2108/zsj.23.647

Minh, Q., Nguyen, M.A.T. & von Haeseler, A. (2013) Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30, 1188–1195.
https://doi.org/10.1093/molbev/mst024

Nylander, J., Olsson, U., Alström, P. & Sanmartín, I. & Baker, A. (2008) Accounting for Phylogenetic Uncertainty in Biogeography: A Bayesian Approach to Dispersal-Vicariance Analysis of the Thrushes (Aves: *Turdus*). *Systematic Biology*, 57, 257–268.
https://doi.org/10.1080/10635150802044003

Oliver, L.A., Prendini, E., Kraus, F. & Raxworthy, C.J. (2015) Systematics and biogeography of the *Hylarana* frog (Anura: Ranidae) radiation across tropical Australasia, Southeast Asia, and Africa. *Molecular Phylogenetics and Evolution*, 90, 176–192.
https://doi.org/10.1016/j.ympev.2015.05.001

Peters, W.C.H. (1871) Über neue Reptilien aus Ostafrica und Sarawak (Borneo), vorzüglich aus der Sammlung des Hrn. Marquis J. Doria zu Genua. *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin*, 1871, 566–581.

Robinson, H.C. & Kloss, C.B. (1916) The Natural History of Kedah Peak. *Journal of the Federated Malay States Museums*, 7 (2), 219–244.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian Phylogenetic Inference under Mixed Models. *Bioinformatics (Oxford)*, 19, 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180

Shahrul Anuar MS., Mark Rayan, D., Nurul 'Ain, E., Nor Zalipah, M., Mohd Yusof, O. & Ganesan, M. (2006) Brief notes on the reptilian fauna of Gunung Jerai. *In*: Shaharuddin, M.I., Wan Yusoff, W.A., Md. Som, J., Yusoff, M. & Latiff, A. (Eds.), *Hutan Simpan Gunung Jerai, Kedah: Pengurusan, persekitaran fizikal dan kepelbagaian biologi*. Forestry Department of Peninsular Malaysia, Kuala Lumpur, pp. 427–432.

Sukumaran, J. (2005) *Anuran Assemblages of Gunung Jerai, Kedah, Peninsular Malaysia*. Unpublished M.Sc. Thesis. Faculty of Science, University of Malaya, Kuala Lumpur, 102 pp.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, 28, 2731–2739.
https://doi.org/10.1093/molbev/msr121

Tolkien, J.R.R. (1954) *The Lord of the Rings: The Fellowship of the Ring*. George Allen & Unwin, 398 pp.

Trifinopoulos, J., Nguyen, L.T., von Haeseler, A. & Minh, B.Q. (2016) W-iq-tree: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44, 232–235. [W232–W235]
https://doi.org/10.1093/nar/gkw256

Wiens, J.J. & Penkrot, T.A. (2002) Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology*, 51, 69–91.
https://doi.org/10.1080/106351502753475880

Wilcox, T.P., Zwickl, D.J., Heath, T.A. & Hillis, D.M. (2002) Phylogenetic Relationships of the Dwarf Boas and a Comparison of Bayesian and Bootstrap Measures of Phylogenetic Support. *Molecular Phylogenetics and Evolution*, 25, 361–371.
https://doi.org/10.1016/S1055-7903(02)00244-0

Wood, P.L. Jr., Grismer, L.L., Norhayati, A. & Senawi, J. (2008) Two new species of torrent-dwelling toads *Ansonia* Stoliczka, 1870 (Anura: Bufonidae) from Peninsular Malaysia. *Herpetologica*, 64 (3), 321–340.
https://doi.org/10.1655/07-065.1

Wood, P.L. Jr., Grismer, J.L., Grismer, L.L., Norhayati, A., Chan, K.O. & Bauer, A.M. (2009) Two new montane species of *Acanthosaura* Gray, 1831 (Squamata: Agamidae) from Peninsular Malaysia. *Zootaxa*, 2012, 28–46.

WWF Malaysia (1977) *Gunung Jerai State Park, Kedah: Its Natural Resources and its Future Role*. World Wildlife Fund Malaysia, Kuala Lumpur, 34 + xxxi leaves.

Zug, G.R. (2010) Speciation and dispersal in a low diversity taxon: the Slender Geckos *Hemiphyllodactylus* (Reptilia, Gekkonidae). *Proceedings of the California Academy of Sciences, Fourth Series*, 63 (1), 1–70.
https://doi.org/10.5479/si.00810282.631

APPENDIX. Material examined.

The following preserved specimens were examined.
Abavorana luctuosa. Malaysia—Kedah: Sungai Sedim, LSUHC 9731; Kelantan: Gunung Stong, LSUHC 11087; Pahang: Fraser's Hill, USMHC 2191–2192, Genting Highlands, USMHC 1662; Penang: Penang Hill, USMHC 1651–1652, USMHC 1720–1724, USMHC 2310.