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Cryptic speciation within *Asthenodipsas vertebralis* (Boulenger, 1900) (Squamata: Pareatidae), the description of a new species from Peninsular Malaysia, and the resurrection of *A. tropidonotus* (Lidth de Jude, 1923) from Sumatra: an integrative taxonomic analysis

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Abstract

A review of the taxonomic status of the Asian Slug Snake, *Asthenodipsas vertebralis* (Boulenger, 1900) based on an integrative taxonomic approach using molecular, morphological, color pattern, and ecological data indicate it is composed of three well supported monophyletic lineages: (1) Pulau Tioman and Fraser's Hill, Pahang and Bukit Larut, Perak; Peninsular Malaysia; (2) its sister lineage from Northern Sumatra; and (3) the remaining basal lineage from Peninsular Malaysia. Furthermore, we consider the high sequence divergence (6.3%–10.2%) between these lineages (especially in areas of sympatry) and discrete differences in their morphology, color pattern, and microhabitat preference as evidence they are not conspecific. As such, we resurrect the name *A. tropidonotus* (Lidth de Jude, 1923) for the Sumatra populations, restrict the name *A. vertebralis* to the populations from Pulau Tioman, Genting Highlands, Fraser's Hill, Gunung Benom, and Bukit Larut that contain terrestrial, banded adults; and consider *A. lasgalenensis* **sp. nov.** to be restricted to the populations from Fraser's Hill, Cameron Highlands, and Bukit Larut that contain arboreal, unbanded adults.

Key words: Malaysia, Bukit Larut, Fraser's Hill, Pulau Tioman, Cameron Highlands, Genting Highlands, Sumatra, *Asthenodipsas*, integrative taxonomy, new species, cryptic species

Introduction

The family Pareatidae, Asian Slug Snakes, has had a turbulent taxonomic history (David & Vogel 1996; Iskandar & Colijn 2002; Rao & Yang 1972) with the most recent taxonomy (Grossmann & Tillack 2003; Guo *et al.* 2011) generally settling on the recognition of three genera; *Pareas* Wagler, *Aplopeltura* Duméril, and *Asthenodipsas* Peters given the likelihood that *Pareas* is paraphyletic (Guo *et al.* 2011). Grossmann & Tillack (2003) synonymized *P. tropidonotus* (Lidth de Jude) with *P. vertebralis* (Boulenger) and placed them both in the resurrected genus *Asthenodipsas* along with *A. laevis* (Boie) and *A. malaccanus*. *Asthenodipsas vertebralis* is a nocturnal, montane species with a fragmented distribution extending from central Peninsular Malaysia to Sumatra. Within Peninsular Malaysia, *A. vertebralis* is known only from the upper regions of Bukit Larut, Perak; Gunung Benom, Cameron Highlands, Fraser's Hill, (Grossmann & Tillack 2003); Pulau Tioman of the Seribu Archipelago (Grismer 2011; Grismer *et al.* 2006); and Genting Highlands, Pahang (Sly 1976; Fig. 1). This species is generally restricted to elevations above 980 m in hill dipterocarp and lower montane cloud forests (Boulenger

1900; J. Grismer *et al.* 2004; Grismer, 2011; Lim 1967; Manthey & Grossmann 1997) where it is most often found on vegetation 1–3 m above the ground coiled on leaves branches or foraging for slugs and snails.

The typical adult color pattern reported for *Asthenodipsas vertebralis* consists of a solid uniform dark grey to very dark brown dorsum with a pale underbelly and whitish labials while hatchlings, juveniles, and subadults have an orangish to reddish brown ground color overlain with hourglass-shaped darker bands and spots with whitish labials and a whitish venter (Figs. 2,3). The notion of adult *A. vertebralis* being unbanded has been perpetuated by numerous color illustrations (i.e. Cox *et al.* 1998; Grismer 2011; Das 2011; Manthey & Grossmann 1997) and the redescription of this species by Grossmann and Tillack (2003) based on adult specimens from Cameron Highlands, Pahang. However, Grossmann and Tillack (2003:183) noted an exception the to unbanded adult pattern with in a banded adult male (ZMB 52072; 730 mm total length[TL]) from Fraser's Hill, Pahang that had an intensely yellow vertebral row of scales that became discontinuous and faded towards the tail; the anterior portion of the head had yellow spots; the supralabials were bright yellow with partly incomplete dark margins; irregularly shaped dark spots occurred on the lower side of the head, the outer row of dorsals, and ventrals; and the subcaudals were dark brown with dirty yellow margins. From their color figure 7, we can see this specimen also had dorsal bands. We have collected similarly patterned individuals from Fraser's Hill (LSUHC 10669, adult TL 595 mm [Fig. 7] and LSUHC 10920, subadult TL 478 mm) and Grismer (2011:170) noted a similarly colored adult from Pulau Tioman (LSUHC 5167; TL 758 mm; Fig. 5). Additionally, we have examined specimens and/or color photos of similarly patterned adults from Bukit Larut (LSUHC 9138; TL 640 mm), Cameron Highlands (LSUDPC 6230–33), and Gunung Benom (BM 1967.2277; TL 617 mm; Fig. 5).

In this study, we used an integrative taxonomic approach (Padial 2010) to (1) assess the taxonomy and relationships of the sampled populations, (2) test the hypothesis of conspecificity between unbanded and banded adults (especially in areas of sympatry at Bukit Larut and Fraser's Hill), and (3) to delimit species boundaries if necessary. Specimens of *Asthenodipsas vertebralis* from five populations across its range in Northern Sumatra and Peninsular Malaysia (Fig. 1) were used to construct a molecular phylogeny based on 1,073 base pairs (bp) of the mitochondrial gene cytochrome *b* (*cyt b*). This phylogeny was compared with morphological analyses of scalation and color pattern along with observations on microhabitat preference between the pattern types. The resulting taxonomy was based only on specimens whose color pattern or sequence data we could observe firsthand so as not to potentially mismatch scalation data from Grossmann and Tillack (2003) with an erroneously inferred color pattern.

Materials and methods

Molecular analysis. Sequence data were obtained for a 1,073 bp fragment from the cytochrome *b* gene (*cyt b*) from 29 individuals composing the ingroup and five individuals from *Aplopeltura boa*, *Pareas carinatus* and *Asthenodipsas laevis* composing the outgroup (Guo *et al.* 2011). Two ingroup *cyt b* sequences from Guo *et al.* (2011) were obtained from GeneBank. New sequences used in this study are deposited in GenBank (Table 1).

Mitochondrial DNA was isolated from liver tissue stored in 95% ethanol and extracted using the animal tissue protocol provided by the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). *Cyt b* was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 2.5 µl genomic DNA (concentration 10–30 µg of DNA), 2.5 µl light strand primer (concentration 4ppm) HI4910 5'–GACCTGTGATMTGAAAACC AYC–3' (Burbrink 2000), 2.5 µl heavy strand primer (concentration 4ppm) THRSN2 5'–CTTTGGTTTACAAGA ACAATGCT–3' (Burbrink 2000), 7.5 µl of Qiagen Taq PCR Core Kit (Valencia, CA, USA) which contains 5 units/ µl Taq DNA Polymerase, PCR Buffer 15 mM MgCl₂, CoraLoad PCR Buffer 15 mM MgCl₂, Q–Solution 5x solution, dNTP Mix 10 mM each dNTP, MgCl₂ and 10.0 µl nuclease free H₂O. PCR reactions were completed using an Eppendorf Mastercycler gradient thermocycler with the following reaction conditions: initial denaturation at 94°C for 2 min, second denaturation at 94°C for 35 s, annealing at 46°C for 35 s followed by an extension cycle at 72°C for 95 s +4 s per cycle for 32 cycles. PCR products were visualized using gel electrophoresis using a 1.0% agarose gel. PCR products that had a distinct band with the correct molecular weight based on the standardized ladder were purified using AMPure magnetic bead solution (Agentcourt Bioscience, Beverly, MA, USA) and sequenced through the Davis Sequencing, Inc. Facility (Davis, CA, USA). Sequences were analyzed 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 Geneious™ version v5.4 (Drummond *et al.* 2011). Sequences were aligned

by eye and to ensure the correct amino acid reading frame MacClade v4.08 (Maddison and Maddison, 2003) was used to check for premature stop codons.

Phylogenetic trees were constructed using Bayesian Inference (BI), Maximum Likelihood (ML), and Maximum Parsimony (MP). For the MP analysis bootstrap estimates were run for ten random sequence replicates using the heuristic Tree Bisection and Reconnection (TBR) branch swapping algorithm for 1000 replicates in PAUP* (Swofford, 2002). The resulting trees were summarized using the majority ruled consensus approach and bootstrap support values > 70 were considered well supported (Felsenstien 1985).

TABLE 1. Samples used in the molecular analyses with GenBank accession numbers. LSUHC = La Sierra University Herpetological Collection, Riverside, California, USA.

LSUHC Voucher	Species	Locality	GeneBank Accession Nos.
	<i>Aplopeltura boa</i>	Peninsular Malaysia	JF827673
7248	<i>Aplopeltura boa</i>	East Malaysia, Sabah, Sepilok	KC916746
6471	<i>Asthenodipsas carinatus</i>	Cambodia, Pursat Province, O'Som	KC916747
10604	<i>A. carinatus</i>	Peninsular Malaysia, Kedah, Sungai Sedim	KC916748
10346	<i>A. laevis</i>	Peninsular Malaysia, Penang, Pulau Pinang	KC916749
	<i>A. tropidonotus</i>	Indonesia, Sumatra,	AY425808
10669	<i>A. vertebralis</i>	Peninsular Malaysia, Pahang, Fraser's Hill	KC916750
10920	<i>A. vertebralis</i>	Peninsular Malaysia, Pahang, Fraser's Hill	KC916751
5167	<i>A. vertebralis</i>	Peninsular Malaysia, Pahang, Pulau Tioman	KC916752
9873	<i>A. vertebralis</i>	Peninsular Malaysia, Perak, Bukit Larut	KC916753
9138	<i>A. vertebralis</i>	Peninsular Malaysia, Perak, Bukit Larut	KC916754
9098	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Fraser's Hill	KC916755
9099	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Fraser's Hill	KC916756
9050	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916757
8869	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916758
9150	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916759
9152	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916760
10266	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916761
10273	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916762
10272	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916763
10654	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916764
10797	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916765
10798	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916766
10799	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Perak, Bukit Larut	KC916767
	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	AY425807
6593	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916768
7228	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916769
7239	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916770
7240	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916771
10259	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916772
10260	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916773
10261	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916774
10262	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916775
10668	<i>A. lasgalenensis</i> sp. nov.	Peninsular Malaysia, Pahang, Cameron Highlands	KC916776

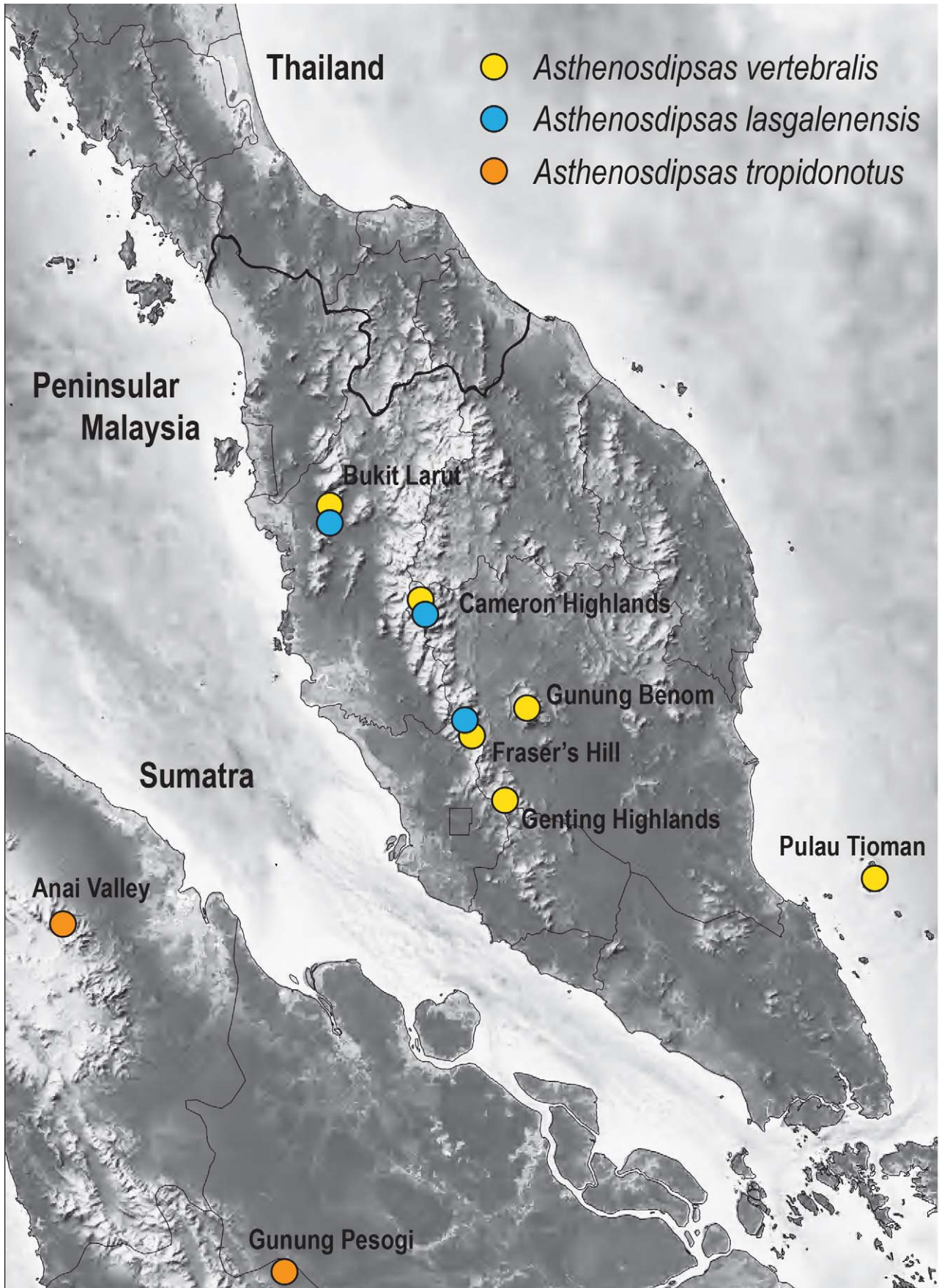


FIGURE 1. Distribution map of *Asthenodipsas vertebralis* (yellow circles), *A. lasgalenensis* **sp. nov.** (blue circles), and *A. tropidonotus* (orange circles) in Peninsular Malaysia and Northern Sumatra.

Bayesian Inference (BI) and Maximum Likelihood (ML) data were split into three partitions corresponding to codon positions. A partitioned ML analysis was conducted by RAxML HPC v7.2.3 (Stamatakis, 2006) using the best fit model of sequence evolution GTR+I+Gamma, selected by ModelTest v3.7 (Posada & Crandall, 1998) under the Akaike information criterion. The GTR+I+Gamma model was applied to all partitions due to computer programming limitations within RAxML HPC v7.2.3 (Stamatakis, 2006). A 200 replicate search was implemented for the ML inference with a random starting tree. Gaps were treated as missing data and node confidences were assessed using 1000 bootstrap pseudoreplicates under the rapid hill-climbing algorithm (Stamatakis et al. 2008). Bootstrap replicates with a value > 70 were considered well supported.

A partitioned Bayesian analysis was implemented in MrBayes v3.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck 2003) following the default priors using the following models of evolution selected by ModelTest v3.7 (Posada & Crandall, 1998); 1st position GTR+Gamma and GTR+I +Gamma for the 2nd and 3rd positions. Two simultaneous runs were performed with eight chains per run, seven hot and one cold. The analysis was run for 10,000,000 generations and sampled every 1000 generations from the Markov Chain Monte Carlo (MCMC). The analysis was halted after the average standard deviation split frequency fell below 0.01. The program Are We There Yet? (AWTY) (Nylander *et al.* 2008) was employed to plot the log likelihood scores against the number of generations to assess convergence and to determine the appropriate number of burn-in trees. The first 25% of the trees were discarded as a burn-in. A consensus tree was computed from the two parallel runs using TreeAnnotator v1.6.1 (Drummond & Rambaut 2007). Nodes that had Bayesian posterior probabilities (BPP) 0.95 or greater were considered significantly supported. Nodal support values for all analyses are reported in the order of BI/ML/MP. Inter- and intrapopulational sequences divergences (p-distances) were estimated for *Asthenodipsas vertebralis* using MEGA v5.05 (Tamura *et al.* 2011) under the default conditions (Table 2).

Morphological analysis. We examined 27 specimens of *Asthenodipsas vertebralis* from every locality from which it has been reported. Scale nomenclature and coding follows Grossmann and Tillack (2003) for purposes of comparison. Paired characters were presented as right/left (Table 3). The following measurements were made with dial calipers in millimeters: width of head (WH) behind the orbitals; head length (HL) from tip of snout to posterior margin of head, and head depth (HD), the maximum height of head from the occiput to the throat behind the orbitals; snout-vent length (SVL), tip of snout to the vent; and tail length (TL), vent to tip of tail. All scale counts were recorded in left/right order using a Leica WILD M10 stereomicroscope: dorsal scales (Do) were counted two head lengths behind head, at mid-body, and one head length in front of vent; ventral scales (Ven) were counted beginning immediately posterior to the chin shield to vent; vertebral scale size (VeS) was categorized as slightly enlarged (-), enlarged (+), and greatly enlarged (++) as compared to the outgroup *Aplopeltura boa*; paired subcaudal scales (SubC) were counted from the anal plate to the terminal tip of the tail; number of postocular scales (PoO) directly in contact with eye was recorded; temporal scales (T) were counted in the anterior, secondary, and tertiary rows; supralabial scales (SupL) were counted from the rostral scale to rectis of the mouth and those in contact with eye were recorded in brackets; infralabial scales (Infl) were counted from mental scale to rectis of the mouth and those in contact with anterior chin shields were recorded in brackets; the presence of a single anterior inframaxillary (SaIM) or chin shield was noted by + (present) or - (absence) and marked (D) if divided and pairs of inframaxillaries or chin shields (pIM) were counted from saIM to the first ventral scale; bands (B) in contact with the ventral scales were counted from the nape to the anal plate. Scalation data on the Sumatran specimens (RMNH 4902A,B) were taken from Grossmann and Tillack (2003). Sexual dimorphism in the numbers of ventral and subcaudal scales is absent in *Asthenodipsas* (Grossmann & Tillack 2003).

TABLE 2. Uncorrected p-distances for the major clades of *A. vertebralis* calculated with MEGA v5.02 (Tamura *et al.* 2012). Genetic distances in bold are within clades and distances in regular text are between major clades of the *A. vertebralis* groups.

	<i>A. vertebralis</i> (clades B–D)	Cameron Highlands (clade G)	Bukit Larut (clade F)	Fraser's Hill (clade E)	Sumatra (clade A)
<i>A. vertebralis</i> (clades B–D)	0.003				
Cameron Highlands	0.084	0.008			
Bukit Larut	0.078	0.009	0.000		
Fraser's hill	0.084	0.028	0.019	0.000	
Sumatra	0.063	0.102	0.099	0.100	–

TABLE 3. Measurements and scale counts of *Asthenodipsas vertebralis* and *A. lasgalenensis* sp. nov. (type material in bold). See specimens and Methods for abbreviations. M=male; F=female.

Species	Catalog Number	Sex	SVL	TaL	Do	VeS	Ven	SubC	PoO	T	SupL	InfL	SalM	pIM	B
<i>vertebralis</i>	BMNH	F	380	80	15/15/15	++	195	65	2/2	2+1/2+2	7/7(3+4/3+4)	7/7(1)	+	3	
holotype	1946.1.20.14														
<i>vertebralis</i>	BMNH	F	503	114	15/15/15	++	202	66	1/1	2+2/2+2	7/7(3+4/3+4)	6/6(1)	+	3	65
	1967.2277														
<i>vertebralis</i>	LUSHC	F	481	103	15/15/15	++	204	83	1/1	2+2/2+2	7/7(3+4/3+4)	6/6(1)	+	3	50/52
	8366														
<i>vertebralis</i>	LSUHC	F	191	42	14/15/15	++	196	65	1/1	2+2+2/2+2+1	7/7(2/2)	7/7(1)	+	3	54/56
	9100														
<i>vertebralis</i>	LSUHC	F	483	112	15/15/15	++	200	77	??	2+2+2/?	7/7(3+4/3+4)	7/6(1)	+	3	64/57
	10669														
<i>vertebralis</i>	LSUHC	F	454	114	15/15/14	++	215	77	1/1	2+2+1/2+2+2	7/7(3+4/3+4)	7/6(1)	+	3	63/63
	10920														
<i>vertebralis</i>	LSUHC	M	610	148	15/15/13	++	205	70	1/1	2+2+2/2+2+1	7/7(2/2)	6/7(1)	+	3	61/62
	5167														
<i>vertebralis</i>	LSUHC	F	300	68	14/14/14	++	201	65	1/2	2+1+2/2+2+2	7/7(2/2)	6/6(1)	+	3	63/63
	9873														
<i>tropidonotus</i>	RMNH	M	533	132	15/15/15	++	199	73	1/1	2+1/2+2	6/6(3+4/+4)	6/6(1)	-	3	
	4902 A														
<i>tropidonotus</i>	RMNH	M	549	144	15/15/15	++	204	76	1/1	2+2/2+2	7/7(3+4/3-5)	6/7(1)	+	3	
	4902 B														
<i>lasgalenensis</i>	LSUHC	M	412	117	15/15/15	++	189	64	2/2	2+2+2/2+2+2	7/8(2/2)	7/7(1)	D+	3	0
holotype	8869														
<i>lasgalenensis</i>	LSUHC	M	584	145	15/15/15	++	182	67	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	0
paratype	9098														
<i>lasgalenensis</i>	LSUHC	/	415	59	15/15/14	++	185	36+	2/1	2+2+2/2+2+2	7/7(2/2)	8/7(1)	+	3	0
paratype	6593														
<i>lasgalenensis</i>	LSUHC	F	427	86	15/15/15	++	180	60	2/2	2+2+2/2+2+2	7/7(1/2)	8/8(1)	+	3	0
paratype	9150														
<i>lasgalenensis</i>	LSUHC	F	342	51	15/15/15	++	182	59	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	0
	10997														
<i>lasgalenensis</i>	LSUHC	F	464	114	15/15/15	++	177	59	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	0
	9152														

.....continued on the next page

TABLE 3. (Continued)

Species	Catalog Number	Sex	SVL	TaL	Do	VcS	Ven	SubC	PoO	T	SupL	InfL	SaIM	pIM	B
<i>lasgalenensis</i>	LSUHC 10726	F	472	94	15/15/15	++	175	60	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	0
<i>lasgalenensis</i>	LSUHC 10654	M	520	128	15/15/15	++	188	71	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	0
<i>lasgalenensis</i>	LSUHC 10668	M	420	91	15/15/15	++	170	70	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	0
<i>lasgalenensis</i>	LSUHC 10272	F	529	140	15/15/15	++	184	72	2/2	2+2+2/2+2+2	7/7(1/1)	7/8(1)	D+	3	0
<i>lasgalenensis</i>	LSUHC 7239	F	340	66	15/15/15	++	182	58	1/2	2+2+1/2+1+2	7/7(2/2)	7/7(1)	+	3	0
<i>lasgalenensis</i>	LSUHC 7228	F	208	43	15/15/15	++	177	54	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	53/49
<i>lasgalenensis</i>	LSUHC 10260	M	250	66	15/15/15	++	175	72	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	-	3	47/47
<i>lasgalenensis</i>	LSUHC 7240	F	224	50	15/15/15	++	176	59	1/1	2+2+1/2+2+1	7/7(2/2)	7/7(1)	+	3	42/44
<i>lasgalenensis</i>	LSUHC 10261	F	290	59	15/14/15	++	190	56	1/1	2+2+2/1+2+2	7/7(2/2)	7/7(1)	+	3	0
<i>lasgalenensis</i>	LSUHC 9099	F	182	42	15/15/15	++	182	63	2/2	2+2+2/2+2+2	7/8(2/2)	7/7(1)	+	3	40/43
<i>lasgalenensis</i>	LSUHC 10259	M	200	48	15/15/15	++	188	64	2/2	2+3+2/2+2+2	6/7(2/2)	7/6(2)	+	3	44/49
<i>lasgalenensis</i>	LSUHC 10262	F	380	82	15/15/15	++	180	60	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	D+	3	0
<i>lasgalenensis</i>	LSUHC 9151	F	174	36	14/15/15	++	177	58	2/2	2+2+2/2+2+2	7/7(2/2)	7/8(1)	D+	3	45/43
<i>lasgalenensis</i>	LSUHC 10266	F	375	99	15/15/15	++	181	68	2/2	2+2+2/2+2+2	7/7(1/1)	7/8(1)	+	3	0
<i>lasgalenensis</i>	LSUHC 10798	F	150	35	15/15/15	++	178	61	2/2	2+2+2/2+2+2	7/7(3/3+4)	7/8(1)	+	3	50/50
<i>lasgalenensis</i>	LSUHC 10799	F	215	57	15/15/15	++	180	70	2/2	2+2+2/2+2+2	7/7(3+4/3+4)	7/7(1)	+	3	46/47
<i>lasgalenensis</i>	LSUHC 10797	F	162	35	15/15/14	++	178	60	2/2	2+2+2/2+2+2	7/7(3+4/4)	7/7(1)	+	3	43/45
<i>lasgalenensis</i>	LSUHC 9050	F	427	86	15/15/15	++	173	59	2/2	2+2+2/2+2+2	7/7(2/2)	7/7(1)	+	3	47/48

Some of the morphological and color pattern data were analyzed using a Student's *t*-test on Microsoft Excel to test for significance of differences between mean scale counts between the banded and unbanded populations as well as the mean number of bands between banded juveniles and banded adults.

Results

The final alignment of Cyt *b* was composed of 1073 bp with 513 parsimony informative sites and 92 variable parsimony uninformative sites. The phylogeny (Fig. 4) indicates that the specimen from Sumatra (AY425808), Pualu Tioman (LSUHC 5167), two specimens from Fraser's Hill (LSUHC 10669, 10920), and two specimens from Bukit Larut (LSUHC 9138, 9873) form a strongly supported (1.0/100/100) monophyletic group (clades A–D) that is the sister lineage to a reasonably well supported (-97/80) monophyletic group containing all other *Asthenodipsas vertebralis* from Peninsular Malaysia (clades E–G). These lineages bear a notable 7.8–10.2% sequence divergence between them (Table 1). Individuals from clades A–D are banded subadults or adults (Table 2; Figs. 3,5,6) and this group is hereinafter referred to as the banded lineage. All other individuals from Peninsular Malaysia (clades E–G) are unbanded adults or banded juveniles or hatchlings (hatchling and juvenile TL < 460 mm *fide* Grossmann and Tillack [2003]; Figs. 2,3) and this group is hereinafter referred to as the unbanded lineage. Within the banded lineage, the specimen from Sumatra (clade A) is basal (Fig. 4) and bears a genetic distance of 6.3% from the other clade members (Table 1), while there is only a 0.3% sequence divergence between the specimens from Pulau Tioman, Bukit Larut, and Fraser's Hill (clades B–D).

There is only minimal genetic substructuring among individuals in the unbanded lineage (Fig. 4) with the populations from Fraser's Hill, Bukit Larut, and Cameron Highlands forming monophyletic groups (1.0/100/100, -/91/77, and 99/77/70, respectively). The Fraser's Hill population (clade E) is basal to the Bukit Larut and Cameron Highlands populations (clades F and G) although this relationship is only weakly supported. Sequence divergence between clades E–G is low, ranging from 0.9–2.8%.

Discrete differences in numbers of ventral scales was found between the banded and unbanded lineages (195–215 vs. 167–190, respectively). A Student's *t*-test also found significant differences in band numbers ($p=1.24 \times 10^{-7}$) with the banded adults from Peninsular Malaysia (clades B–D) having a significantly lower mean value than the banded hatchlings and juveniles from the unbanded lineage (46.8 vs. 62.0, respectively; Table 2). Mean values for the numbers of subcaudals were also found to be significantly different ($p=0.00283$, 0.04, respectively) with the Malaysian portion of the banded lineage (clades B–D) being lower (64.5 vs. 72.3, respectively; Table 2). The banded adult color pattern of specimens from the banded lineage differs discretely from the unicolor unbanded adult pattern of specimens in the unbanded lineage (Figs. 2,3,5). Although the color pattern of adult specimens from the banded lineage loosely resembles the juvenile color pattern of specimens from the unbanded lineage, the former has significantly fewer bands in juveniles (Table 2) and the labials, chin shields and ventral scales are yellow to orange and opposed to white.

All LSUHC specimens from the unbanded ($n=24$) and banded ($n=6$) lineages used in the genetic and morphological analyses were collected by us. All members of the unbanded lineage were found from 1–5 m above the ground in vegetation either coiled on branches or at the base of leaves (usually the juveniles) or were observed foraging through the vegetation (usually the adults). All specimens from the banded lineage were found moving across the ground or on the road. The only exceptions were LSUHC 5167 from Pulau Tioman which was found moving through vegetation 1 m above the ground and BM 1967.277 from Gunung Benom which was reported to have been on "the branch of a tree" (Grandison 1972). Noteworthy here is that these banded individuals are not known to be in sympatry with any portion of the unbanded lineage. Together, these data suggest the unbanded and banded lineages may be partitioning their habitat in regions of microsympatry.

Taxonomy

The Sumatran population, originally described as *Asthenodipsas tropidonotus* (Lidth de Jeude 1923), is composed of banded adults (Fig. 6). Grossmann and Tillack (2003), however, synonymized this species with *A. vertebralis* on the basis of morphology. Conversely, the molecular data indicate the Sumatran population is distinct from *A.*

vertebralis from Peninsular Malaysia and is part of a strongly supported lineage that includes a sister lineage of banded adult specimens from Pulau Tioman, Fraser's Hill, and Bukit Larut (clades B–D). The Sumatran population is separated from clades B–D by a notable sequence divergence of 6.3% and from unbanded populations of *A. vertebralis* (clades E–G) by a larger divergence of 9.9–10.2% (Table 1). Additionally, the Sumatran population is discretely diagnosable from the unbanded lineage in having 199–204 ventral scales as opposed to 167–190. Therefore, we no longer consider *A. tropidonotus* a junior synonym of *A. vertebralis* and resurrect it to its previous species status. It is diagnosable by the unique combination of having a maximum SVL of 549 mm in males (females unknown); 15/15/15 dorsal scale rows; 199–204 ventral scales; 73–76 subcaudal scales; a single postocular; 2+1–2 temporals; six or seven supralabials and infralabials; the presence of a single anterior inframaxillary; and having dorsal bands as adults (Table 3; Fig. 6).

The phylogenetic and morphological analyses (Fig. 4; Tables 2,3,4) show strong support for the monophyly and discrete diagnosability of the banded specimens from Bukit Larut, Fraser's Hill, and Pulau Tioman in clades B–D from the unbanded lineage. In the absence of morphological diagnostic differences between these populations and no noteworthy genetic differentiation (0.3% sequence divergence between them even though they are separated by 280–450 km and two mountain ranges, Fig. 1), the conspecificity of these populations is inferred. From the remainder of *A. vertebralis* (the unbanded lineage, clades E–G), with which this portion of the banded lineage is currently considered conspecific, it bears a notable sequence divergence of 7.8–8.4%. Furthermore, the molecular analysis indicates there is no genetic exchange between the banded and unbanded lineages at Bukit Larut or Fraser's Hill where they are nearly syntopic. The sequence divergence between the banded and unbanded Bukit Larut specimens is 7.8% and the divergence between unbanded and banded Fraser's Hill specimens is 8.4%. Additionally, the color pattern analysis shows that the unbanded and banded lineages are statistically diagnosable from one another on the basis of mean band number and discretely diagnosable from one another on the basis of adult coloration (Table 3,4). Furthermore, the morphological analysis indicates that the banded and unbanded lineages of Peninsular Malaysia are discretely diagnosable on the basis of numbers of ventral scales (167–190 vs. 195–215, respectively) and the banded lineage has a significantly lower number of subcaudal scales (64.5 vs. 72.3; Table 3).

The description of the holotype of *Asthenodipsas vertebralis* (referred to as a subadult by Grossmann and Tillack, 2003; TL 460 mm) by Boulenger (1900:308) notes that it is “Reddish brown above, with small dark brown spots and ill-defined dark crossbands; an interrupted yellow vertebral line, formed by a small spot on each median scale; labials and chin-shields yellowish, edged with dark brown, belly yellowish, with some brown spots on the sides.” All other subadults and juveniles from the unbanded lineage examined here and by Grossmann and Tillack (2003) have white labials and a pale venter as opposed to these regions being yellow (Table 5) in all age classes of specimens in clades B–D of the banded lineage. Furthermore, we examined 24 specimens of *A. vertebralis* from the unbanded lineage and found that the shift from the banded juvenile color pattern with a prominent vertebral stripe to the unbanded adult color pattern lacking a vertebral stripe happens between a TL of 316 mm (LSUHC 10260; banded with vertebral stripe) and 349 mm (LSUHC 10261; unbanded and no vertebral stripe; Table 5). Based on these data, the banded holotype with the vertebral stripe from Bukit Larut with a TL of 460 mm is 111 mm (or 32%) larger than the smallest unbanded specimen lacking a vertebral stripe (LSUHC 10261; TL 349 mm) and as such, we infer here, that the holotype bears an adult color pattern and thus is a member of the banded lineage and not the unbanded lineage. Additionally, we examined an unbanded specimen lacking a vertebral stripe from the type locality of Bukit Larut (LSUHC 10266) which had nearly the same TL as the holotype (474 mm). Furthermore, the holotype has 195 ventral scales (Grossmann and Tillack 2003) which is well outside the range of that reported for the unbanded lineage (167–190) and is commensurate with that of the banded lineage (196–215).

Given the genetic, morphological, color pattern, and ecological data presented above, we consider the banded lineage (clades B–D) and the unbanded lineage (clades E–G) to constitute separate species. As such, we restrict the name *A. vertebralis* to the peninsular populations composed of banded adults (clades B–D) being that we infer the holotype from Bukit Larut is a member of this clade and describe the populations containing unbanded adults (the unbanded lineage, clades E–G) as the new species:

TABLE 4. Diagnostic morphological characters of the species of *Asthenodipsas*. See Materials and Methods. for abbreviations. M=male; F=female.

	Max SVL	Do	Ven	SubC	PoO	T
<i>vertebralis</i>	454F, 610M	14–15/14–15/13–15	195–215	65–77	1 or 2	2+1–2 +1–2
<i>tropidonotus</i>	549M	15/15/15	199–204	73–76	1	2+1–2
<i>lasgalenensis</i>	598M 571F	14–15/15/ 14–15	167–190	54–77	1 or 2	1–2+1–3+1– 2

TABLE 4. (Continued)

	InfL	SupL	SaIM	B	Labials/venter	Vertebral stripe	Dorsal banding
<i>vertebralis</i>	6 or 7	7	+	52–65	Yellow	Throughout life	Throughout life
<i>tropidonotus</i>	6 or 7	6 or 7	+	/	Light colored	Throughout life	Throughout life
<i>lasgalenensis</i>	6–8	6–8	+,D+	42–56	White	Hatchlings and juveniles only	Hatchlings and juveniles only

***Asthenodipsas lasgalenensis* sp. nov.**

Mirkwood Forest Slug Snake

Figures 2,3

Pareas vertebralis Smedley 1931:122; Tweedie 1953:34 (in part), 1957:35 (in part); Sly 1976: 156; Tweedie 1987:36 (in part); Rao and Yang 1972:144; Lim *et al.* 2002:55; Manthey and Grossmann 1967:378; Cox *et al.* 1998:79; Leong and Lim 2003:133; Das & Yakkob 2007:74.

Asthenodipsas vertebralis Grossman and Tillack 2003:177; Iskandar and Colijn 2002; (in part); Das 2010:160 (in part); Grismer *et al.* 2010:155 (in part); Grismer 2011:170 (in part).

Holotype. Adult male, LSUHC 8869 collected by L. Lee Grismer, P. L. Wood Jr., J. L. Grismer, and C. K. Onn on 2 March 2008 from Bukit Larut, Perak, Malaysia (4° 44.596' N, 100° 45.537' E; 1184 m).

Paratypes. Adult female (LSUHC 9050) bears the same data as the holotype. Adult male (LSUHC 9098) collected by L. Lee Grismer, P. L. Wood Jr., J. L. Grismer, and C. K. Onn on 6 June 2008 on Pine Tree Trail at Fraser's Hill, Pahang, West Malaysia (3° 43.234' N, 101° 45.478' E; 1203 m). Adult female (LSUHC 6954) collected by L. Lee Grismer and C. K. Onn on trail 11 at Tanah Rata, Cameron Highlands, Pahang, Malaysia (4°31.275'N, 101°23,193'E; 2050 m). Adult female (LSUHC 9150) collected by Norhayati Ahmad and L. Lee Grismer on Bishop's Trail at Fraser's Hill, Pahang, Malaysia (3° 42.590' N, 101° 44.236' E; 1239 m).

Additional specimens examined. See Table 5 and appendix.

Diagnosis. *Asthenodipsas lasgalenensis* sp. nov. is distinguished from all other species of the Pareasidae by the unique combination of having of a maximum TL 771 (Smedley 1931); 15/15/14–15 dorsal scale rows/167–190 ventrals; 54–77 subcaudal scales; one or two postorbitals; 1–2+1–3+1–2 temporals; 6–8 supralabials and infralabials; whitish ventral scales bearing small dark lateral spots; dorsum of adults unicolor dark brown; dorsum of hatchlings and juveniles bearing an orangish to light gray ground color overlain with 42–56 irregularly shaped rhomboidal darker bands beginning posterior to dark nuchal bar and extending the length of body and tail and onto lateral spots; edges of ventral scales but not encircling body; a light vertebral stripe; whitish labials usually edged in darker color; dark brown to black head; dark red to red-orange eyes. These character states are summarized across all species in Table 3.

Description of holotype. Adult male SVL 412 mm and Tal 117 mm; rostral as wide as high; head somewhat bulbous in shape, longer than wide; nasals undivided; internasals shorter than prefrontals; prefrontals contact eye; frontal hexagonal, slightly longer than wide; loreals absent; supraoculars subpentagonal, half the length and same width as frontal; preoculars longer than wide; upper and lower postocular, lower postocular extending to below orbit; no suboculars; supralabials 7/7 with 3rd and 4th contacting orbit and 7th elongate; temporals 2+2+2/2+2+2, left side has one small scale between postoculars and first pair of temporals; mental triangular wider than long; anterior inframaxillary rectangular, in contact with infralabials 1–5; inframaxillaries slightly rounded, elongated ovals in three pairs following the anterior inframaxillary; infralabials 8/8 with the 1st pair in medial contact.



FIGURE 2. Upper. Adult male *Asthenodipsas lasgalenensis* **sp. nov.** from Bukit Larut, Perak (holotype LSUHC 8869). Lower. Adult female *A. lasgalenensis* **sp. nov.** from Cameron Highlands, Pahang (paratype LSUHC 6954).



FIGURE 3. Coloration of a hatchling *Asthenodipsas vertebralis* from Fraser's Hill, Pahang (upper left LSUHC 9100) and a subadult female from Bukit Larut, Perak lower right LSUHC 9837. Coloration of hatchling *A. lasgalenensis* from Bukit Larut, Perak (LSUHC 10798, upper right and LSUHC 10797, lower left).

Body long, thin, laterally compressed, bearing a prominent keel-shaped vertebral region; dorsals smooth, 15/15/15 in number, vertebrales greatly enlarged; 189 ventrals; 64 divided subcaudals; anal scute entire; tail tapering to a point.

Coloration in life (Fig. 2). Head, body and tail unicolor dark brown; labials white, edged in dark brown; belly white, edged in dark brown and bearing scattered, dark lateral blotches extending into midventral region; subcaudal region gray laterally white midventrally; iris orange.

Variation. The paratypes approximate the holotype in all aspects of coloration except that LSUHC 6593 and 9150 have fewer dark lateral ventral blotches.

Juvenile coloration (Fig. 3). Juveniles LSUHC 7228, 7240, 9099, 9151, 10259–60, 10789, 10799, 10797, 10997 (see Table 2 for scalation and appendix for locality data) that are not part of the type series bear a coloration and pattern of having dark brown on the top of the head; an orangish to light gray ground color overlain with 42–56 irregular hourglass-shaped darker bands beginning posterior to the dark nuchal bar and extending the length of the body and tail and onto lateral edges of ventral scales but not encircling body; a light vertebral stripe; whitish labials and ventral scales usually edged in darker color; dark brown to black head; and red-orange eyes.

Distribution. *Asthenodipsas lasgalenensis* **sp. nov.** is known only from Genting Highlands, Fraser's Hill, Cameron Highlands, Pahang and Bukit Larut, Perak (Fig. 1). It is likely *A. lasgalenensis* **sp. nov.** and *A. vertebralis* range throughout the montane cloud forests of northeastern Peninsular Malaysia as well as throughout similar habitats in southern Thailand south of the Isthmus of Kra.

Natural History. The localities from which *Asthenodipsas lasgalenensis* **sp. nov.** was found are montane cloud forests above 800 m in elevation. All specimens were found at least 1 m above the ground at night foraging or resting in vegetation.

Etymology. The specific epithet *lasgalenensis* is derived from the name *Eryn Lasgalen* which means in the "Wood of Greenleaves" in the fictional Sindarian language from J.R.R Tolkien's *The Lord of the Rings* (1955). It was the name used by the Wood Elves for the Mirkwood Forest after its cleansing following the War of the Ring.

This name was chosen because Tolkien's (1955) description of this forest showed great similarity to the cloudy, upland forests within which this species is found.

Comparisons. *Asthenodipsas lasgalenensis* **sp. nov.** is differentiated from all other species of *Asthenodipsas* on the basis of phylogenetics (Fig. 4; Table 2), morphology, color pattern (Tables 3,4; Figs. 2–5,7), and perhaps microhabitat preference. It is discretely diagnosable from *A. vertebralis* (a species to which it was previously ascribed) and *A. tropidonotus* based on having 167–190 ventral scales as opposed to having 195–215 and 199–204 ventral scales, respectively. It is further separated from *A. vertebralis* in having a significantly lower mean number (\bar{x} =46.8; 40–56) of trapezoidal-shaped dorsal bands as opposed to a higher mean number (\bar{x} =62.0; 57–64) and a significant difference in the mean number of subcaudal scales (\bar{x} =64.5; 54–77 vs. \bar{x} =72.3; 65–77). It is discretely diagnosable from *A. vertebralis* in having yellow to orangish labials and ventrals as opposed to whitish labials and ventrals; a yellowish vertebral stripe throughout life as opposed to losing the light vertebral stripe between 316 mm and 349 mm TL; and a dorsal banding pattern throughout life as opposed to transforming from a dorsal banded pattern to a unicolor pattern between 316 mm and 349 mm TL. Furthermore, the top of the head in hatchling and juvenile *A. lasgalenensis* **sp. nov.** is dark brown as opposed to orange. Additionally, *A. lasgalenensis* **sp. nov.** appears to be terrestrial when sympatric with *A. vertebralis* as opposed to being arboreal.

TABLE 5. Correlation between the presence of banding and a vertebral stripe with total length (TL) in *Asthenodipsas lasgalenensis* **sp. nov.** Asterisked species could not be included in the genetic analysis. ** Tail broken.

Locality	LSUHC cat. No.	vertebral stripe	color pattern	SVL mm	Tal mm	TL mm
Bukit Larut	10798	present	banded	150	35	185
Bukit Larut	10797	present	banded	162	35	197
Bukit Larut	9151*	present	banded	174	36	210
Fraser's Hill	9099	present	banded	182	42	224
Cameron Highlands	10259	present	banded	200	48	248
Cameron Highlands	7728	present	banded	208	43	251
Bukit Larut	10799	present	banded	215	57	272
Cameron Highlands	7240	present	banded	224	50	274
Cameron Highlands	10260	present	banded	250	66	316
Cameron Highlands	10261	absent	unbanded	290	59	349
Genting Highlands	10997*	present	banded	342	51	393
Cameron Highlands	7239	absent	unbanded	340	66	406
Cameron Highlands	10262	absent	unbanded	380	82	462
Bukit Larut	10266	absent	unbanded	375	99	474
Cameron Highlands	6593	absent	unbanded	415	59	474
Cameron Highlands	10668	absent	unbanded	420	91	511
Bukit Larut	9150	absent	unbanded	427	86	513
Bukit Larut	8869	absent	unbanded	412	117	529
Cameron Highlands	10726*	absent	unbanded	472	94	566
Bukit Larut	9050	absent	unbanded	473	100	573
Bukit Larut	9152	absent	unbanded	464	114	578
Bukit Larut	10654	absent	unbanded	520	128	648
Bukit Larut	10272	absent	unbanded	529	140	669
Fraser's Hill	9098	absent	unbanded	584	145	729

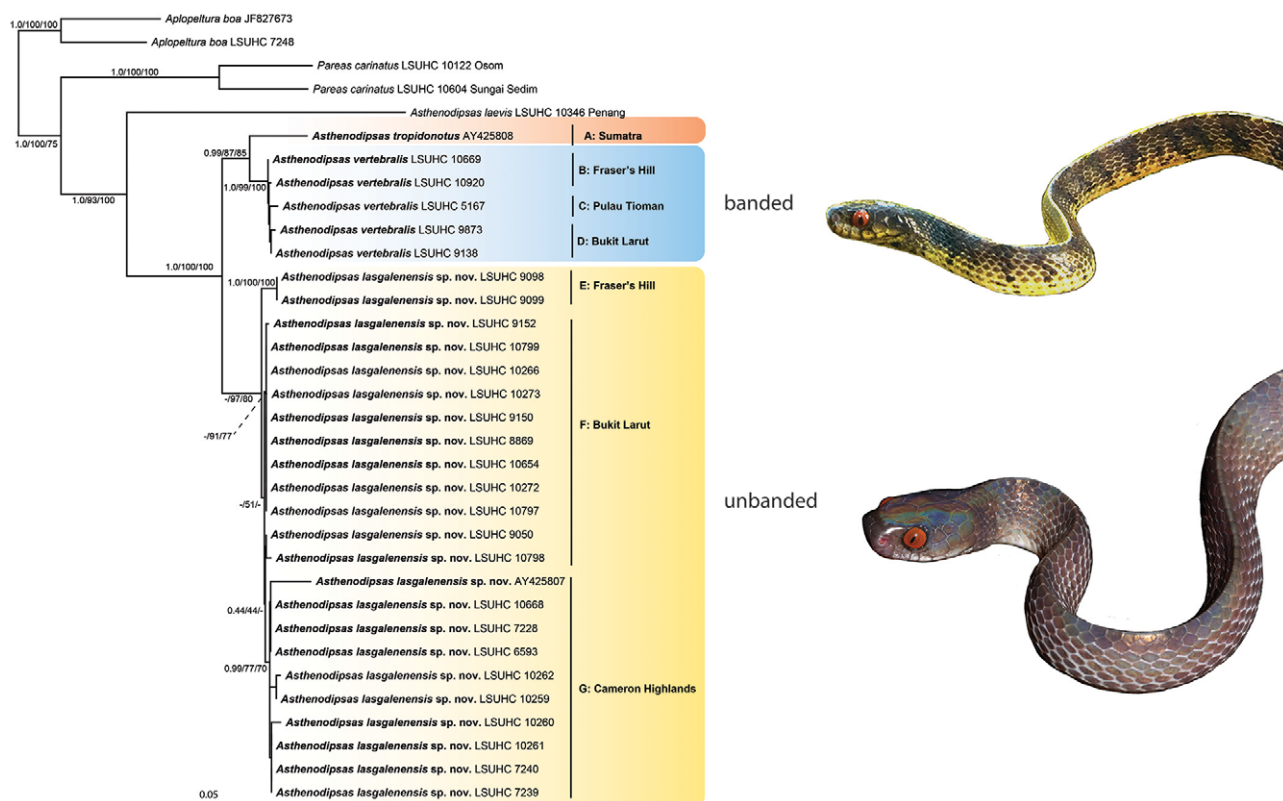


FIGURE 4. Bayesian Inference tree based on 1,073 bp of *cyt b* showing the relationships between Pareatidae and the placement of *Asthenodipsas lasgalenensis* sp. nov. Bayesian posterior probabilities (BPP) and ML and MP bootstrap support values, respectively (BPP/ML/MP), at the nodes.

Discussion

Using an integrative taxonomic approach to establish a phylogenetic based taxonomy revealed that the general morphological similarity between *Asthenodipsas lasgalenensis* sp. nov., *A. tropidonotus*, and *A. vertebralis* coupled with their high genetic dissimilarity indicated this group is a species complex composed of at least three species. This approach revealed further that *A. vertebralis* from Peninsular Malaysia is more closely related to *A. tropidonotus* from Sumatra than to *A. lasgalenensis* sp. nov. from Peninsular Malaysia. Additionally, the fact that *A. lasgalenensis* sp. nov. is microsympatric with *A. vertebralis* at Bukit Larut, Fraser's Hill, and Cameron Highlands with no molecular, morphological, or color pattern evidence of gene flow between them as well as possible habitat partitioning, serves as strong evidence that these are independent, non-reticulating lineages on their own evolutionary trajectories (i.e. different species).

An interesting divergence pattern in *Asthenodipsas lasgalenensis* sp. nov. that is beginning to emerge in the analyses of other upland species from Peninsular Malaysia (i.e. Grismer *et al.* 2012a) is that the sequence divergence between the populations from Cameron Highlands (clade G) and Fraser's Hill (clade E) is 2.8% while the divergence between Cameron Highlands and Bukit Larut (clade F) is only 0.9% indicating that the Cameron Highlands and Fraser's Hill populations are not each other's closest relatives even though they occur along the same mountain range (Fig. 1).

Although we only used mtDNA, we can still hypothesize how glacioeustatic driven climatic processes of the last 2.4 million years may have contributed to the current distribution and relationships of these populations. The overall low sequence divergence (Table 2) between the allopatric populations of *Asthenodipsas lasgalenensis* sp. nov. and *A. vertebralis* (note their extremely short branch lengths, Fig. 4) suggests that their separation is a recent event. During the last 2.4 million years the Sundaic Region has been one of the most dynamically evolving landscapes in Southeast Asia (Bird *et al.* 2005; Cannon *et al.* 2009; Hall 1998, 2001, 2002; Outlaw & Voelker 2008; Reddy 2008; Woodruff 2003, 2010). The areal portions of this region only represent approximately 50% of the Sundaic



FIGURE 5. *Asthenodipsas vertebralis*. Upper left; adult female (LSUHC 10920) from Fraser's Hill, Pahang. Upper right: adult male (LSUHC 9138) collected by L. Lee Grismer and Chan Kin Onn on 16 November 2008, specimen lost in transit. Middle left: adult male (LSUHC 5167) from Pulau Tioman, Pahang. Middle right: adult specimen of unknown sex (LSUDPC 6233) from Cameron Highlands, photograph provided by Gernot Vogel. Lower left and right: dorsal and ventral views, respectively, of BM 1967.2277 from Gunung Benom, Pahang.



FIGURE 6. *Asthenodipsas tropidonotus* from West Sumatra from (upper) Anai Valley, City Padang, Panjang and (lower) from Gunung Pesogi near Danau Ranau, Lampung (lower). Photographs provided by Gernot Vogel.

landmass—the remaining 50% (the Sunda Plains) lying beneath the South China Sea—and this geographic configuration has persisted for only about 2% of the last 2.4 million years (Woodruff 2010). The cyclical, fluctuating changes in sea levels and complete submergence of the Sunda Plains coupled with concomitant changes in climate, have had a dramatic impact on the diversity and patterns of distribution of the Sundaic flora and fauna—patterns which cannot be surmised from current geography alone. One area of Southeast Asia where the effects of these sea level changes are most pronounced is along the Thai-Malay Peninsula. The long, rocky spine of this unique physiographic feature is sculpted by a series of isolated, imbricating mountain ranges whose upland habitats have provided refugia from the warmer, intervening lowland regions during Pleistocene interglacial episodes (Cannon *et al.* 2009; Woodruff 2010) when higher sea levels and temperatures transformed the Thai-Malay

Peninsula into an archipelago of habitat-island mountain tops. The genetic signatures of such isolation events should be recovered in the fauna that they impacted and would manifest themselves in divergences between sympatric species in the same mountain ranges (Bell *et al.* 2010, 2011; Grismer *et al.* 2012a). The low genetic divergence between the disjunct, upland, populations of *A. lasgalenensis* **sp. nov.** and *A. vertebralis* suggests that gene flow occurred during the last glacial maximum (~20 years before present) when current upland forests would have migrated downslope following a 3–6° C drop in temperature (Cannon *et al.* 2009; Woodruff 2010), allowing previously isolated populations to come back into contact.

The results of this study add to a growing body of data on the hidden diversity in Peninsular Malaysia and Singapore (see Grismer 2011) and underscore the superiority of an integrative taxonomic approach for uncovering cryptic species and delimiting species boundaries as opposed to a traditional analysis based solely on morphology (see Grismer *et al.* in prep. for an extended discussion). This is especially true for common, widely distributed taxa on the Thai-Malay Peninsula, which upon close examination, more often than not prove to be complexes of multiple species (Grismer *et al.*, 2008, 2010, 2011, 2012a, b; Johnson *et al.* 2012). The conservation implications of discovering cryptic species buried in the synonymy of unstudied species complexes is obvious.



FIGURE 7. Microhabitat of *Asthenodipsas vertebralis* at Brinchong Trail, Cameron Highlands.

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APPENDIX

The following preserved specimens were examined.

Aplopeltura boa. Malaysia—Sabah: Sepilok, LSUHC 7248.

Pareas carinatus. Cambodia—Pursat: O'som LSUHC 10122. Malaysia—Kedah: Sungai Sedim LSUHC10604.

Asthenodipsas laevis. Malaysia—Pulau Pinang: Penang Hill LSUHC 10346.

Asthenodipsas vertebralis. Malaysia—Perak: Bukit Larut LSUHC 8366, 9873; Pahang: Pualu Tioman LSUHC 5167; Fraser's Hill LSUHC 9100, 10669, 10920. Genting Highlands LSUHC 10997.

Asthenodipsas lasgalenensis **sp. nov.** Malaysia—Perak: Bukit Larut LSUHC 8869, 9150, 9151, 10266, 10272, 10797, 10798, 10799. Pahang: Cameron Highlands LSUHC 6593, 7228, 7239, 7240, 10259, 10260, 10261, 10262, 10726; Fraser's Hill LSUHC 9098, 9099, 9100.