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A new species of pitviper of the genus *Popeia* (Squamata: Viperidae) from Pulau Tioman, Pahang, West Malaysia

L. LEE GRISMER¹, JESSE L. GRISMER^{1,2} & JIMMY A. MCGUIRE³

¹Department of Biology, La Sierra University, Riverside California 92515-8247 USA.
E-mail: lgrismer@lasierra.edu
²Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA.
E-mail: jgrism1@lus.edu
³Museum of Vertebrate Zoology, 3101 Valley Life Science Building, University of California, Berkeley, California 94720-3160, USA.

Abstract

We describe a new species of pitviper *Popeia buniana* from Pulau Tioman, Pahang State, West Malaysia based on it having unique aspects of scalation, body proportions, and color pattern. Its long, thin body is in contrast with the shorter, more robust bodies of other arboreal pitvipers, suggesting it may be an active forager rather than an ambush feeder. Its close relationship to *P. barati* and *P. sabahi* of Sumatra and Borneo, respectively, rather than with species of the adjacent Malay Peninsula is in accord with biogeographic patterns of other flora and fauna endemic to the islands of the Outer Arc of the Seribuat Archipelago.

Key words: Arboreal, *Popeia*, *P. buniana*, *P. barati*, *P. fucata*, *P. nebularis*, *P. popeiorum*, Malaysia, Morphometrics, New species, Pulau Tioman, Seribuat Archipelago

Introduction

Pitvipers of the genus *Trimeresurus sensu lato* are nocturnal, forest-dwelling species that inhabit a wide variety of environments ranging from secondary lowland forests to primary cloud forests (Malkmus *et al.* 2002). It is the largest group of Asian pitvipers and its 40 or so species collectively range from northern India in the west, eastward through the majority of East Asia to Taiwan and the Ryukyu Archipelago, Japan; and southward through the Philippines, Thailand, West Malaysia, Borneo, and the other major islands of the Sunda Shelf (Sumatra, Java, Sulawesi and some smaller islands extending east to Timor; Gumprecht *et al.* 2004; Malkmus *et al.* 2002; Manthey & Grossmann 1997; Vogel 2006).

Based on a combined molecular and morphological phylogeny, Malhotra and Thorpe (2004) demonstrated that the monophyletic *Trimeresurus sensu lato* contained five major clades to which they assigned seven genera. To one of these clades, the *Trimeresurus popeiorum* complex, they assigned the name *Popeia*. Based on morphology, Vogel *et al.* (2004) proposed that *Popeia* was a complex of five species: *P. barati* from Sumatra; *P. fucata*, ranging from southern Burma and peninsular Thailand south through West Malaysia including Pulau Tioman; *P. nebularis* from Cameron Highlands, West Malaysia; *P. popeiorum*, occurring in India, Myanmar, northern and western Thailand, and Laos; and *P. sabahi* from Borneo. Based on morphology and a mitochondrial DNA phylogeny, Sanders et al. (2006) recognized essentially the same lineages as Vogel *et al.* (2004) but proposed a more "conservative" taxonomy. They considered *Popeia* to be composed of three species; *P. popeiorum* and *P. nebularis* which were essentially the same lineages as those recognized by Vogel et al. (2004), but considered *P. sabahi* to comprise all the lineages from southern Thailand (south of *P. popeiorum*), West Malaysia, Sumatra, Borneo, and Pulau Tioman (Fig. 1).



FIGURE 1. The phylogenetic relationships of the southern clade of Sanders et al. (2006) using the taxonomy of Vogel *et al.* (2004). Sanders et al. (2006) consider the entire clade to be *Popeia* sabahi.

These two classifications differed in their phylogenetic placement of the Pulau Tioman population of *Popeia*. By including the Pulau Tioman population in *P. fucata*, Vogel *et al.* (2004) tentatively aligned its phylogenetic relationships with populations of *Popeia* from the Malay Peninsula. Sanders *et al.* (2006), however, demonstrated that the Pulau Tioman population and those from western Sumatra (*P. barati* of Vogel *et al.* 2004) and Borneo (*P. sabahi* of Vogel et al. 2004), formed an unresolved trichotomy, thus rendering *P. fucata sensu* Vogel *et al.* (2004) polyphyletic (Fig. 1). Although Vogel *et al.* (2004) noted that the color pattern of the Pulau Tioman specimen was unique, their sample size was too limited

(n=1) to make an unequivocal decision as to its species status. Sanders *et al.* (2006) noted that the Tioman population had a corrected pairwise sequence divergence (ND4 and cytb) of 2.0% from the west Sumatran population (*P. barati*); 2.6% from a west Malaysian population from Fraser's Hill (*P. fucata*); and 1.7% from a Bornean population from northern Sabah (*P. sabahi*). However, their genetic analysis of the Tioman population was also based on only a single specimen.

During a series of herpetological surveys on Pulau Tioman between July 2002 and March 2004, two additional adult males were collected. An examination of the four specimens now in hand confirms this population has the diagnostic character states of *Popeia* Malhotra & Thrope, 2004 along with a number of unique features that differentiate it from all other species of *Popeia* regardless of whose taxonomy one follows. Furthermore, this population should not be recognized as *P. fucata* of the Malay Peninsula (*sensu* Vogel *et al.* 2004) because it is most closely related to Sumatran and Bornean populations (Sanders *et al.* 2006). Therefore, we use a general lineage species concept (de Queiroz 1998) herein and describe the Pulau Tioman population as a new species.

Material and methods

We choose to follow the taxonomy of Vogel *et al.* (2004) in our study of the Pulau Tioman population. Although there is general concordance between the lineages delineated by Vogel *et al.* (2004) and Sanders *et al.* (2006), it is our opinion that according species status to the diagnosable, allopatric populations within the more inclusive clade that Sanders *et al.* (2006) recognize as *Popeia sabahi* is not only the best way to represent a portion of this group's evolutionary history in a classificatory sense, but facilitates more finely grained, population comparisons. We do recognize that *P. fucata* (*sensu* Vogel *et al.* 2004) is polyphyletic (Sanders *et al.* 2006) but, because it is beyond the scope of this paper to address this issue, we do use *P. fucata* specimens as our peninsular Malaysian sample. We are aware that this is tantamount to treating *P. fucata* as a lineage but in this case, it is a logistical practicality that does not alter the species status of the Pulau Tioman population. The taxonomy of *P. fucata* is being addressed elsewhere (Grismer & Grismer, in prep.).

Measurements and scale counts were obtained from preserved specimens of *Popeia* throughout the Sunda Region including four specimens from Pulau Tioman (Appendix). Many specimens pertinent to this study were on loan to, or reserved for, others during our investigation so we have relied on data from Vogel *et al.* (2004) and their extensive, raw, unpublished data set which they generously made available. Measurements and terminology follow Vogel *et al.* (2004). All measurements were taken with dial calipers to the nearest 0.1 mm. Measurements included: Snout-vent length (SVL); tail length (Tal); total length (TL); head width (HW), measured from the widest part of the head posterior to eye; head length (HL), measured from the posterior margin of the mandible to the tip of the rostrum; distance between nostrils (DBN), taken with the caliper tips inserted into the

zootaxa (1305) zootaxa (1305) nostrils; distance from the anterior edge of the eye to the posterior edge of the pit cavity (DETP); distance from anterior margin of eye to the posterior margin of the nostril (DE TN); distance from the anterior edge of the eye to the rostral scale (DETR); the horizontal eye diameter (HED); the vertical eye diameter (VED); distance of the lower eye margin to bottom edge of the third supralabial (DEL); width of the internasal scale (WINN); length of the supraocular (LSupOc); width of the supraocular (WSupOc); length of the third supralabial (L3SL); height of third supralabial (H3SL); and length of fourth supralabial (L4SL). Several of these measurements were expressed as the morphometric ratios (Table 2).

Scale counts taken were supralabials; infralabials; ventral scales; subcaudal scales; number of dorsal scale rows at midbody (NMSR); number of dorsal scale rows one head length behind the head (NASR); number of dorsal scale rows one head length anterior to the vent (NPSR); number of scales between the internasals (NInN); number of scales bordering the supraocular (CSupOc); number of canthal scales between the intranasal scale and the supraocular (Can); number of intersupraoculars forming the shortest line between the supraoculars (Cep); number of head scales on a vertical line from the rostral scale to the limit of the neck (HeSC); number of scales between the third supralabial and subocular (C3SL); number of scales between the fourth supralabial and subocular (C4SL); and number of scales between the fourth and fifth supralabial and the subocular (C45SL). Color pattern characters include presence or absence of dark bands on body (DBB); presence of a line of white, vertebral spots (VS); the percentage of coverage of the scale of the first dorsal scale row by the ventrolateral stripe (VLS/1DSR); presence or absence of a postorbital stripe (POS); color of the postorbital stripe (CPOS), presence or absence of a ventrolateral stripe (VLS); color of the ventrolateral stripe (CVLS); and color of the iris (CI) which is difficult to assess in preserved specimens.

The means of all scale counts and ratios were compared between sexes and between the Pulau Tioman population and all other species using a two-sample Student *t*-Test assuming equal or unequal variances with a Bonferroni-corrected *p* value set at 0.05 (i.e. p<0.008). Those that showed significant differences between males and females were scored for males only because the Pulau Tioman sample consisted of just one female. The data from each sex was combined for those characters that showed no significant, sexually dimorphic differences. All analyses were run on Microsoft Office 2005 using Excel 5.0.

Museum acronyms are BMNH (British Museum of Natural History, now the Natural History Museum, London), FMNH (Field Museun of Natural History, Chicago, Illinois), LSUHC (La Sierra University Herpetological Collection, Riverside, California), LSUDPC (La Sierra University Digital Photo Collection), and ZRC (Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore).

	buniana	barati	fucata
Ventral scales (m+f)	170–174	142–158	156–171
	<i>n</i> =4	<i>n</i> =19	<i>n</i> =59
	<i>x</i> =171.8; <i>sd</i> =2.06	<i>x</i> =148.8; <i>sd</i> =0.82	<i>x</i> =163.7; <i>sd</i> =0.44
Subcaudal scales	76–78 (m)	62–73 (m)	69–84 (m)
	<i>n</i> =3	<i>n</i> =12	<i>n</i> =40
	<i>x</i> =77.3; <i>sd</i> =1.62	<i>x</i> =69.4; <i>sd</i> =2.53	<i>x</i> =75.9; <i>sd</i> =3.51
	61 (f)	55–59 (f)	59–73 (f)
	/	<i>n</i> =6	<i>n</i> =18
	/	<i>x</i> =57.2; <i>sd</i> =1.62	<i>x</i> =63.8; <i>sd</i> =3.6
HL/SVL	0.44–0.47 (m)	0.52–0.58 (m)	0.46–0.59 (m)
	<i>n</i> =3	<i>n</i> =10	<i>n</i> =38
	x=0.46; sd=0.023	<i>x</i> =0.56; <i>sd</i> =0.045	<i>x</i> =0.51; <i>sd</i> =0.031
	0.55 (f)	0.54–0.64 (f)	0.51-0.63 (f)
	<i>n</i> =1	<i>n</i> =5	<i>n</i> =13
	/	<i>x</i> =0.059; <i>sd</i> =0.004	<i>x</i> =0.057; <i>sd</i> =0.004
DETP/DETN (m+f)	0.22-0.33	0.55-0.62	0.51-0.66
	n=4	<i>n</i> =17	<i>n</i> =55
	x=0.28; sd=0.027	<i>x</i> =0.59; <i>sd</i> =0.005	<i>x</i> =0.58; <i>sd</i> =0.005
WInN/WSupOc (m+f)	0.90-1.2	1.36–2.12	1.10-2.00
	<i>n</i> =4	<i>n</i> =17	<i>n</i> =54
	x=1.08; sd=0.06	<i>x</i> =1.64; <i>sd</i> =0.19	<i>x</i> =1.52; <i>sd</i> =0.22
Tal/TL	0.22–0.23 (m)	0.19–0.23 (m)	0.18–0.24 (m)
	<i>n</i> =3	<i>n</i> =4	<i>n</i> =41
	x=0.22; sd=0.006	<i>x</i> =0.21; <i>sd</i> =0.012	<i>x</i> =0.22; <i>sd</i> =0.010
	0.22 (f)	0.16–0.18 (f)	0.16–0.19 (f)
	<i>n</i> =1	<i>n</i> =3	<i>n</i> =18
	/	<i>x</i> =0.17; <i>sd</i> =0.01	<i>x</i> =0.17; <i>sd</i> =0.01
DETR/HL	0.27-0.29 (m)	/	0.32–0.40 (m)
	<i>n</i> =3	/	<i>n</i> =2
	x=0.20; sd=0.07	/	<i>x</i> =0.36; <i>sd</i> =0.06
	0.27 (f)	/	0.36–0.40 (f)
	<i>n</i> =1	/	<i>n</i> =6
	/	/	<i>x</i> =0.38; <i>sd</i> =0.02
			to be continued.

TABLE 1. Diagnostic character states separating *Popeia buniana* from other species of *Popeia*. See Materials and Methods for character abbreviations. m=male, f=female, *x=mean*, *sd=standard deviation*, *n=sample size*.

(1305) (con)

	buniana	barati	fucata
DETR/HW	0.41–0.44 (m) /		0.56–0.59 (m)
	<i>n</i> =3	/	n=2
	x=0.42; sd=0.02	/	<i>x</i> =0.58; <i>sd</i> =0.02
	0.40 (f)	/	0.46–0.68 (f)
	n=1	/	<i>n</i> =6
	/	/	<i>x</i> =0.59; <i>sd</i> =0.08
CI	turquoise w/	orange or	yellowish green,
	maroon center (m)	yellow (m and f)	gold, or copper
	gold (f)		(m and f)
POS	present (m)	absent (m)	present (m)
	absent (f)	absent (f)	absent (f)
Color of VLS	bicolor (m)	white/bicolor (m)	bicolor (m)
	white (f)	absent (f)	white (f)
VLS/1DSR	<50%	<50%	<50%
TABLE 1 (continued).	nebularis	popeiorum	sabahi
Ventral scales (m+f)	147_153	149_173	147_157
ventral seales (III+1)	n=8	n=32	n=14
	x=150.9; $sd=0.79$	x=161.9: $sd=0.71$	x=151.8; $sd=0.75$
Subcaudal scales	61–65 (m)	59–75 (m)	69–76 (m)
	n=2	<i>n</i> =19	n=7
	x=63.0; $sd=2.83$	x=68.1; $sd=4.22$	x=71.6: <i>sd</i> =2.74
	50–60 (f)	56–64 (f)	59–65 (f)
	<i>n</i> =5	<i>n</i> =11	<i>n</i> =5
	<i>x</i> =63.8; <i>sd</i> =3.81	x=59.8; sd=3.00	<i>x</i> =62.2; <i>sd</i> =2.71
HL/SVL	0.58–0.61 (m)	0.47–0.56 (m)	0.5–0.58 (m)
	<i>n</i> =3	<i>n</i> =12	<i>n</i> =4
	x=0.59; $sd=0.017$	x=0.52; sd=0.038	x=0.53; sd=0.035

to be continued.

0.51–0.70 (f)

0.52-0.61

x=0.060; *sd*=0.002

x=0.57; *sd*=0.012

n=3

n=8

0.51–0.62 (f)

0.52-0.62

n=26

x=0.056; *sd*=0.004

x=0.57; *sd*=0.005

n=7

0.62–0.69 (f)

0.52-0.60

x=0.065; *sd*=0.003

x=0.55; *sd*=0.011

n=5

n=8

DETP/DETN (m+f)

(continued).			
	nebularis	popeiorum	sabahi
WInN/WSupOc (m+f)	1.24–1.59	1.11–1.95	1.44–1.94
	<i>n</i> =8	<i>n</i> =27	<i>n</i> =8
	<i>x</i> =1.36; <i>sd</i> =0.13	<i>x</i> =1.37; <i>sd</i> =0.23	<i>x</i> =1.60; <i>sd</i> =0.19
Tal/TL	0.19 (m)	0.18–0.21 (m)	0.19–0.24 (m)
	<i>n</i> =2	<i>n</i> =17	<i>n</i> =7
	<i>x</i> =0.19; <i>sd</i> =0.002	<i>x</i> =0.19; <i>sd</i> =0.01	<i>x</i> =0.21; <i>sd</i> =0.02
	0.17 (f)	0.15–0.17 (f)	0.17–0.18 (f)
	<i>n</i> =5	<i>n</i> =11	<i>n</i> =3
	<i>x</i> =0.17; <i>sd</i> =0.003	<i>x</i> =0.16; <i>sd</i> =0.01	x=0.18; sd=0.003
DETR/HL	0.34 (m)	/	/
	/	/	/
	/	/	/
	0.45 (f)	/	0.36–0.52 (f)
	/	/	<i>n</i> =8
	/	/	<i>x</i> =0.43; <i>sd</i> =0.06
DETR/HW	0.62 (m)	/	/
	<i>n</i> =1	/	/
	/	/	/
	0.63 (f)	/	0.55–0.79 (f)
	n=1	/	<i>n</i> =8
	/	/	<i>x</i> =0.65; <i>sd</i> =1.00
CI	pale green	deep red	deep red or
	(m and f)	(m and f)	orange (m and f)
POS	absent (m)	bicolor (m)	absent (m)
	absent (f)	white/absent (f)	absent (f)
Color of VLS	white/blue (m)	bicolor (m)	bicolor (m)
	absent (f)	white	white/yellow (f)
VLS/1DSR	<50%	100%	<50%

ZOOTAXA
(1305)

TABLE 2. Mensural and meristic characters of the type series of *Popeia buniana*. See Materials and Methods for abbreviations.

malemalemalemalemalefemaleBupralabials99ParatypeParatypesupralabials13111310HeSc32313034Can3231304Cep12111214CasL0000C4SL1122C4SL1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals78767861Tal157179161127SVL542604576596TL69978373723HW15.42.0.21.7.12.3.1HED3.83.22.33.1HED3.13.22.63.2DEN5.46.76.56.9DETN5.46.76.56.9DETN5.47.13.13.4DETN5.43.13.55.8DBP2.94.13.43.1UFIN1.41.93.55.8DETN5.47.13.43.1UFIN1.41.93.55.8DBP2.94.13.43.1UFIN1.4 <td< th=""><th></th><th>ZRC 2.6176</th><th>ZRC 2.6177</th><th>ZRC 2.3439</th><th>BMNH 2007</th></td<>		ZRC 2.6176	ZRC 2.6177	ZRC 2.3439	BMNH 2007
HolotypeParatypeParatypeParatypesupralabials990infralabials13111310HeSc32313034Can3334Cep12111214C3SL0000C4SL112C4SL111C4SL212C4SL211CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861TL69978373723HW15420.217.122.3HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DETN5.46.76.56.9DETN5.46.76.55.8DBP2.94.13.43.1WINN1.41.93.55.8DBP2.94.13.43.1WINN1.41.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.9 <td></td> <td>male</td> <td>male</td> <td>male</td> <td>female</td>		male	male	male	female
supralabials 9 9 9 10 infralabials 13 11 13 10 HeSc 32 31 30 34 Can 3 3 3 4 Cep 12 11 12 14 C3SL 0 0 0 0 C4SL 1 1 1 2 C4SSL 2 1 2 2 NINN 1 1 1 1 CSupOc 9 8 10 9 NMSR 20 20 19 21 NASR 25 24 27 23 NPSR 14 14 15 16 ventrals 170 174 173 170 subcaudals 78 76 78 61 Tal 157 179 161 127 SVL 542 604 576		Holotype	Paratype	Paratype	Paratype
infralabials13111310HeSc32313034Can3334Cep12111214C3SL0000C4SL1112C4SSL2122NINN1111CSupOc98109NMSR201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861TL699783737723HW15.420.217.122.3HED3.83.22.33.1DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSUL3.15.64.25.7	supralabials	9	9	9	10
HeSc32313034Can3334Can11214Cap12111214C3SL0000C4SL1122C4SSL2122NIN1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WinN1.41.91.51.5LSupOc3.55.14.95.1WsupOc1.21.81.41.6LSL3.15.64.25.7	infralabials	13	11	13	10
Can3334Cep12111214C3SL0000C4SL1112C4SSL2122NINN1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861TL699783737723HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	HeSc	32	31	30	34
Cep12111214C3SL0000C4SL1112C4SL2122NIN1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSUL3.15.64.25.7	Can	3	3	3	4
C3SL0000C4SL1112C4SL2122NINN1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	Сер	12	11	12	14
C4SL1112C45SL2122NINN1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	C3SL	0	0	0	0
C45SL2122NINN1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WsupOc1.21.81.41.6LSUL3.15.64.25.7	C4SL	1	1	1	2
NInN1111CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WsupOc1.21.81.41.6LSuL3.15.64.25.7	C45SL	2	1	2	2
CSupOc98109NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSUL3.15.64.25.7	NInN	1	1	1	1
NMSR20201921NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSupOc3.15.64.25.7	CSupOc	9	8	10	9
NASR25242723NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WinN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSUL3.15.64.25.7	NMSR	20	20	19	21
NPSR14141516ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETR8.69.58.710.4DEP2.94.13.43.1DETR5.46.76.56.9DETR3.13.93.55.8DBP2.94.13.43.1UINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSUL3.15.64.25.7	NASR	25	24	27	23
ventrals170174173170subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSupL3.15.64.25.7	NPSR	14	14	15	16
subcaudals78767861Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSUL3.15.64.25.7	ventrals	170	174	173	170
Tal157179161127SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6LSUS3.15.64.25.7	subcaudals	78	76	78	61
SVL542604576596TL699783737723HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	Tal	157	179	161	127
TL699783737723HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	SVL	542	604	576	596
HW15.420.217.122.3HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	TL	699	783	737	723
HL24.629.725.333.1HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	HW	15.4	20.2	17.1	22.3
HED3.83.22.33.1VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	HL	24.6	29.7	25.3	33.1
VED3.13.22.63.2DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	HED	3.8	3.2	2.3	3.1
DBN2.94.13.13.4DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WInN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	VED	3.1	3.2	2.6	3.2
DEPT1.31.4522.25DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WINN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	DBN	2.9	4.1	3.1	3.4
DETN5.46.76.56.9DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WInN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	DEPT	1.3	1.45	2	2.25
DETR8.69.58.710.4DEL3.13.93.55.8DBP2.94.13.43.1WInN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	DETN	5.4	6.7	6.5	6.9
DEL3.13.93.55.8DBP2.94.13.43.1WInN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	DETR	8.6	9.5	8.7	10.4
DBP2.94.13.43.1WInN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	DEL	3.1	3.9	3.5	5.8
WInN1.41.91.51.5LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	DBP	2.9	4.1	3.4	3.1
LSupOc3.55.14.95.1WSupOc1.21.81.41.6L3SL3.15.64.25.7	WInN	1.4	1.9	1.5	1.5
WSupOc1.21.81.41.6L3SL3.15.64.25.7	LSupOc	3.5	5.1	4.9	5.1
L3SL 3.1 5.6 4.2 5.7	WSupOc	1.2	1.8	1.4	1.6
	L3SL	3.1	5.6	4.2	5.7

to be continued.

	ZRC 2.6176	ZRC 2.6177	ZRC 2.3439	BMNH 2007
	male	male	male	female
	Holotype	Paratype	Paratype	Paratype
H3SL	3.2	4.1	3.3	5.2
L4SL	3.4	3.1	4.3	3.1
Tal/TL	0.22	0.23	0.22	0.18
WInN/WSupOc	1.2	1.1	1.1	0.9
VED/DEL	1.1	0.8	0.7	0.5
LSupOc/WSupOc	2.9	2.8	3.5	3.2
HW/HL	0.6	0.7	0.7	0.7
DBP/HL	0.4	0.3	0.3	0.3
DBN/HL	0.1	0.1	0.1	0.1
DETP/DETN	0.6	0.4	0.5	0.5
DEPT/HW	0.2	0.1	0.2	0.2
DETR/HW	0.4	0.4	0.4	0.4
DEPT/HL	0.1	0.1	0.1	0.1
DETR/HL	0.3	0.3	0.3	0.3
BC	36	50	48	47
BC/SVL	0.06	0.08	0.08	0.07
DBB	present	present	present	0
POST	present	present	present	0
CPOST	maroon	maroon	maroon	0
VLS	present	present	present	0

TABLE 2 (contiuned).

Systematics

Popeia buniana sp. n. Figures 2, 4

Suggested common name. The Fairy Pitviper

Holotype. ZRC 2.6176, adult male (Fig. 2) from Tekek-Juara Trail at 2° 49'.18.0"N x 104° 10'28.5"E at 295 m, Pulau Tioman, Pahang State, West Malaysia. Collected by J. A. McGuire and J. L. Grismer on 21 July 2002.

Paratypes. ZRC 2.6177, adult male collected on the Tekek-Juara trail at 292 m in elevation, Pulau Tioman by L. L. Grismer, J. L. Grismer, P. L. Wood, and T. M. Youmans on 15 March 2004. ZRC 2.3493, adult male from 400 m in elevation on Gunung Kajang, Pulau Tioman collected on 26 June 1996. BMNH field number 2007 (specimen

zootaxa (1305) zooTAXA uncatalogued), adult female collected at 810 m on Gunung Kajang at Gua Tenguk Air byM. Day, August 1988.



FIGURE 2. Upper: Holotype of *Popeia buniana*, ZRC 2.6176, adult male 542 mm SVL from the Tekek-Juara Trail. Lower: Adult female: LSUDPC 1135 from Gua Tengkok Air. Collected, released, and photographed by P. Hein.

Diagnosis. *Popeia buniana* is significantly different (p<0.008) from all other species of the *popeiorum* complex by having more ventral scales (170–174, x=171.8; sd=2.06); the facial pit being closer to the eye (DETP/DETN: 0.22–0.33, x=0.28, sd=0.027); and having a relatively thinner internasal scale (WInN/WsupOc: 0.9–1.2, x=1.08, sd=0.06). Male *P. buniana* differ from male *P. barati*, *P. popeiorum*, and *P. sabahi* in having significantly fewer subcaudal scales (76–78, x=77.3, sd=1.62). Male *P. buniana* have a significantly shorter head (HL/SVL; 0.44–0.47, x=0.46, sd=0.023) than that of male *P. barati* or *P. nebularis* and they have a significantly longer tail (Tal/TL: 0.22–0.23, x=0.22, sd=0.006) than that of male *P. nebularis* and *P. popeiorum*. Male *P. buniana* differ from

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male *P. barati, P. nebularis,* and *P. sabahi* in having a postorbital stripe as opposed to lacking a stripe; from *P. fucata* in lacking white, vertebral spots as opposed to having spots; and from *P. nebularis* in having a bicolored, ventrolateral stripe as opposed to having a white or blue stripe. Female *P. buniana* differ from female *P. barati* and *P. nebularis* in having a white, ventrolateral stripe as opposed to not having stripes. *Popeia buniana* differs from *P. popeiorum* in that the ventrolateral stripe covers 50% of the scale in the first dorsal scale row as opposed to covering 100% of the scale.

Description of holotype. Adult male; body long and thin; head triangular and elongate; snout elongate and pointed; distance between nostrils 2.9 mm, DBN/HL 0.11; distance between pits 6 mm; DBP/HL 0.25; head length 24 mm; head width 15 mm; HW/ HL 0.57, head 10.5 mm wider than neck; SVL 542 mm; Tal 157 mm; 22 dorsal scales one head length behind head; 21 dorsal scales at midbody; 14 dorsal scales one head length anterior to vent; 3 preventral scales (the second and third divided); 170 ventral scales; 78 subcaudal scales.

In dorsal view, rostral large and triangular, followed posteriorly by a large, circular, azygous scale bordered laterally by internasals; azygous scale followed posteriorly by a second, triangularly shaped scale; internasals rectangular, twice as wide as high, bordered posterolaterally by canthals; canthals small, triangular, more rounded distally, twice as high as wide; followed posteriorly by 3 (L) 3 (R) scales; canthals followed posteriorly by supraocular; supraocular three times as high as wide, surrounded by 9 (L) 8 (R) head scales; 13 intersupraoculars along a line between middle of supraoculars; and 32 scales along a line from rostral scale to limit of neck.



FIGURE 3. Map showing location of Pulau Tioman, Pahang State, West Malaysia.

ZOOTAXA

(1305)

In lateral view, nares visible; rostral bordered laterally by nasal; nasal bordered ventrally by first supralabial, nasal and first supralabial not fused; supralabials 9 (L) 9 (R); infralabials 12 (L) 12 (R); nasal bordered posteriorly by loreal; loreal bordered ventrally and posteriorly by second supralabial; second supralabial rectangularly shaped, twice as high as wide, upper portion bordered posteriorly by upper and lower preocular; upper and lower preocular thin and rectangularly shaped, three times wide as high; upper preocular bordered ventrally by lower preocular; lower preocular bordered ventrally by second supralabial; upper and lower preocular; lower preocular bordered ventrally by second supralabial; upper and lower preocular; lower preocular bordered ventrally by eye; eight scales surround eye including preoculars; eye followed posteriorly by upper and lower postocular; upper postocular small and square; lower postocular long, rectangularly shaped, three times as high as wide.



FIGURE 4. Left: Male *Popeia fucata* (LSUHC 5098, SVL 585 mm) from Genting Highlands, Pahang, West Malaysia. Right: Male paratype *P. buniana* (ZRC 6118, SVL 604 mm) from the Tekek-Juara trail, Pulau Tioman, Pahang, West Malaysia. Note the longer *P. buniana* is much more gracile in body stature.

Mental triangular, equally high as wide, followed posterolaterally by first infralabial; first supralabials contact at midline, four times as wide as high; eight rows of divided gular scales between first ventral scale and first infralabial; genials and chinshields absent.

Color in life. The ground color in life is a pale turquoise with 81 transverse, zigzagging, maroon bands 4.6 mm apart on the body and 39 brownish bands on the tail.

The center of the iris is copper and the outer edges are turquoise. A postorbital, maroon stripe extends 8.7 mm from the posterior margin of the eye to 6 mm anterior to the posterior margin of the mandible. A ventrolateral, white stripe runs the entire length of the body to the tip of the tail and is bordered ventrally by a reddish stripe that runs the entire length of the body before fading into the venter coloration at the base of the tail. The tail is banded in two shades of brown with the ground color being the lighter of the two.

Paratypes. BMNH 2007 (female) differs from the holotype in having 10 supralabials on each side as opposed to nine. It differs further in having six rows of divided, gular scales as opposed to eight, having 61 subcaudal scales as opposed to 78, 11 (L) 10 (R) scales surrounding the eye as opposed to eight (L and R), seven scales contacting the supraocular (L and R) as opposed to 9 (L) 8 (R), 11 intersupraoculars as opposed to 13, three scales between the canthal and the supraocular, in having 10 infralabials on the left side as opposed to 12, and having 34 scales forming a straight line from the rostral scale to the limit of the neck as opposed to 32. In aspects of coloration, it lacks almost all traces of transverse banding and is nearly uniform green and it lacks a postorbital stripe and ventrolateral stripes. Being that the male paratypes are colored like the holotype suggests that coloration in this species is sexually dimorphic. Morphometric differences are presented in Table 3.

ZRC. 2.3493 (male) differs from the holotype in having six rows of divided gular scales as opposed to eight, 173 ventral scales as opposed to 170, the second supralabial contacts the nasal scale as opposed to no nasal scale contact, 10 scales contact the supraocular on the right as opposed to eight, there are three scales between the canthal and the supraocular as opposed to two, and there are 30 scales in a straight line from the rostral scale to the limit of the neck as opposed to 32.

ZRC 2.6177 (male) differs from the holotype in having five rows of divided gular scales as opposed to eight, 174 ventral scales as opposed to 170, 11 infralabials as opposed to 13, 76 subcaudals as opposed to 78, 24 scale rows one head length behind the head, 18 scale rows at midbody as opposed to 21, eight (L) nine (R) scales surrounding the supraocular, 11 intersupraoculars as opposed to 12, and 31 scales in a straight line from the rostral scale to the limit of the neck as opposed to 32. The dorsal surface of the tail is nearly a uniform reddish-brown as opposed to being banded.

Distribution. *Popeia buniana* is only known from Pulau Tioman (Fig. 3), a small island located 38 km off the southeast coast of Pahang State, West Malaysia. The addition of *P. buniana* to the herpetofauna of Pulau Tioman raises the number of endemic species of reptiles and amphibians on Pulau Tioman to 12 (Grismer 2006).

TABLE 3. Student *t*-test data for the significantly different character means between *Popeia* buniana and all other species of *Popeia*. Mean values for *P. buniana* are listed on the top left for each species-character combination.

	barati	fucata	nebularis
Ventral scales	171.8 vs. 148.8	171.8 vs. 163.71	171.8 vs. 150.8
	<i>t</i> =17.41; <i>p</i> =1.02E-7	<i>t</i> =7.18; <i>p</i> =0.002	<i>t</i> =16.08 <i>p</i> =8.74E-7
DETP/DETN	0.28 vs. 0.59	0.28 vs. 0.58	0.28 vs. 0.55
	<i>t</i> =17.41; <i>p</i> =1.02E-7	<i>t</i> =-11.38; <i>p</i> =0.001	<i>t</i> =-9.41; <i>p</i> =0.0007
WInN/WSupOc	1.08 vs. 1.64	1.08 vs. 1.52	1.08 vs. 1.36
	<i>t</i> =-7.21; <i>p</i> =0.0001	<i>t</i> =-6.39; <i>p</i> =0.003	<i>t</i> =-3.60; <i>p</i> =0.004
Subcaudal scales	77.3 vs. 69.4	/	/
	<i>t</i> =8.20; <i>p</i> =7.75E-05	/	/
HL/SVL	0.46 vs. 0.56	/	0.46 vs. 0.59
	<i>t</i> =-4.81; <i>p</i> =0.003	/	<i>t</i> =-7.34; <i>p</i> =0.005
Tal/TL	/	/	0.22 vs. 0.19
	/	/	<i>t</i> =8.71; <i>p</i> =0.003

	popeiorum	sabahi
Ventral scales	171.8 vs. 161.2	171.8 vs. 151.8
	<i>t</i> =8.44; <i>p</i> =0.0002	<i>t</i> =15.66; <i>p</i> =1.04E-6
DETP/DETN	0.28 vs. 0.57	0.28 vs. 0.57
	<i>t</i> =-10.93; <i>p</i> =0.002	<i>t</i> =-10.00; <i>p</i> =0.0006
WInN/WSupOc	1.08 vs. 1.37	1.08 vs. 1.60
	<i>t</i> =-3.87; <i>p</i> =0.008	<i>t</i> =-5.52; <i>p</i> =0.0004
Subcaudal scales	77.3 vs. 68.1	77.3 vs. 71.6
	<i>t</i> =7.95; <i>p</i> =2.36E-06	<i>t</i> =5.74; <i>p</i> =0.0006
HL/SVL	/	/
	/	/
Tal/TL	0.22 vs. 0.19	/
	<i>t</i> =7.27; <i>p</i> =0.002	/

Life History. Our understanding of the life history of *Popeia buniana* is limited to observations made when specimens were collected. The holotype was collected on the Tekek-Juara trial at 2230 hours at 295 m in elevation where the lowland dipterocarp forest transitions to hill dipterocarp forest (Latiff *et al.* 1999). It was found 10 m above the ground on the end of a tree branch approximately 20 mm in diameter, which was adjacent to the trunk of another tree approximately 0.5 m in diameter. We speculate that the snake was tracking small lizards that might be running along this section of the adjacent tree.

BMNH 2007 was collected near Gua Tengkok Air, below the summit of Gunung Kajang at 815 m in elevation in hill dipterocarp forest in low vegetation approximately 1 m above the ground (Day 1990). ZRC 2.3493 was collected at 400 m in elevation on Gunung Kajang in low vegetation (Lim & Lim 1999). Specimen ZRC 2.6177 was collected on the Tekek-Juara trial at 2130 hours at approximately 240 m in elevation 2 m above the ground crawling thought the lower branches of a small tree approximately 50 mm in diameter. During July of 2002 an adult female (Fig. 2; LSUDPC 1132, 1135) was collected (and later released) approximately 200 m below the summit of Gunung Kajang in primary hill dipterocarp forest (P. Hein pers comm., 2002) at the end of a tree branch approximately 25 mm in diameter while crossing to the end of another branch approximately 20 mm in diameter, 8 m above the ground. Vogel (2006:129) figures a female *P. buniana* in a bush eating a *Rana hosii*.

Etymology. The specific epithet is derived from the Malay word "bunian", which is a small, feminine, mischievous, elf or fairy-like spirit believed to inhabit the forests. Our respected friend and guide Mr. Muhamad Ishak Mat Sohor, indicated that the bunian of Pulau Tioman lived in the Tengkok Air Cave near the summit of Gunung Kajang, one of our campsites and collecting localities for this new pitviper. We were cautioned to show respect to the bunian so she would not become angry with our taking of specimens from "her" forest. Therefore, in deference to this belief, we honor the bunian with the feminine patronym *buniana*, a noun in apposition meaning "Fairy Pitviper".

Discussion

Even with the small sample size of three or four *Popeia bunaina*, at least 10 characters clearly differentiate this species from all other *Popeia* in various aspects of squamation, body proportions, and color pattern (Tables 1 and 2). With a larger sample size and more females, it is likely that *P. buniana* will be found to differ even further than is presented here. For example, females, like the males, probably have relatively longer tails as suggested by the Tal/TL ratio of 0.22 of BMNH 2007, which falls far outside the range for that ratio of all other species (Table 1). Similarly, the data suggest that female *P. buniana* have smaller heads than female *P. nebularis* (HL/SVL 0.55 vs. 0.62–0.69, respectively; Table 1). In males, the means of two other characters, DETR/HL and DETR/HW, are considerably lower than those of *P. fucata* and *P. nebularis*. However, with a sample size of only two male *P. fucata*, one male *P. nebularis*, and three male *P. buniana*, the *p* values greatly exceeded 0.008 even though the ranges (for *P. fucata*) did not overlap (Table 1). We had no specimens of *P. barati*, *P. popeiorum*, or *P. sabahi* to examine for these characters.

Sanders *et al.* (2006) clearly demonstrate that *Popeia buniana* forms a clade with insular *P. barati* and *P. sabahi* of Sumatra and Borneo, respectively, rather than with geographically more proximate populations of *Popeia* from peninsular Malaysia (Fig. 3)

zootaxa (1305) zootaxa (1305) as implied by the taxonomy of Vogel *et al.* (2004; Fig. 1). This biogeographical pattern of being more closely related to species hundreds of kilometers away on other islands of the Sunda Shelf rather than to populations from the Malay Peninsula, just 28 km to the west, occurs in other species as well. Reptiles, such as *Gonocephalus chamaeleontinus, Cnemaspis limi, Calamaria ingeri,* and *Gongylosoma mukutense,* occurring on the Outer Arc of the Seribuat Archipelago (Grismer *et al.* 2006), are most closely related to Bornean, Sumatran, or Javan species (Grismer *et al.* 2003; 2004). This biogeographical pattern is not restricted to reptiles but has been reported in mosses (Tan & Mohamad 1999), decapods (Yeo & Ng 1999; Yeo *et al.* 1999), a balitorid loach (Kottelat 1990), freshwater gobies (Ng *et al.* 1999), and mouse deer (Adura 1998). These montane relicts are remnants of lineages that once ranged continuously along a mountainous arc that extended eastward across the lowlands of the exposed Sunda Shelf from Sumatra through the Riau Archipelago, the Outer Arc of the Seribuat Archipelago, through the Anambas and the Natunas archipelagos and on to Borneo, prior to the latest rise in sea level (Inger & Voris 2001; Voris 2000).

Greene (1997) noted that arboreal, active foragers have long, thin bodies and tails and use lateral undulation to counter gravity by spreading their body weight over the branches and foliage in an S-shape. Ambush feeders on the other hand, have short, squat bodies with short prehensile tails that anchor the body to the vegetation and reduce the chances of falling while the forepart of the body is extended. Although inherently difficult to accurately quantify, especially with a small sample size, we believe the thin-bodied morphology of *Popeia buniana*, as suggested by its high numbers of subcaudal and ventral scales (Table 1) and general appearance (Fig. 4), suggest it may be an active forager. Anecdotal observations made during the collection of specimens support this hypothesis. The holotype was observed at the end of a branch approximately 10 m above the ground with its body in a stretched, S-shaped-position, common to other active foragers and ZRC 2.6177 and LSUDPC 1135 were observed stretched out while moving through vegetation 2–8 m above the ground.

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Appendix

Popeia fucata

MALAYSIA: Pahang, Cameron Highlands ZRC 2.5164, 2.887, Fraser's Hill, ZRC 2.2890, Genting Highlands, LSUHC 5098, Gunung Tahan ZRC 2.2883; Pulau Penang, ZRC 2.2876, 2.2879; Perak, Bukit Larut, ZRC 2.2880; Selangor, ZRC 2.2892. Unknown locality: FMNH 69994.

Popeia sabahi

MALAYSIA: Sabah, Mount Kinabalu, ZRC 2.2893–94, 2.2896, 2.2899; Sipitang District, FMNH 233155, 240511–12, 243942.