

Popeia inornata, A NEW SPECIES OF PITVIPER FROM WEST MALAYSIA (SQUAMATA: VIPERIDAE: CROTALINAE)*

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We describe a new species of green pitviper from Southeast Asia. This species is a member of the genus *Popeia* (formerly known as the *Trimeresurus popeiorum* complex), and is distinguished from congeners by a combination of morphological and molecular characters. These include the absence of a red lateral stripe in adult males, low ventral scale counts and green eye coloration in males and females, and five fixed nucleotide differences in a 720 base pair fragment of the mitochondrial cytochrome *b* gene. The new species is known only from the Cameron Highlands range in West Malaysia, where it was found between 1200 – 2000 m above sea level in or near undisturbed evergreen rainforest.

Keywords: Reptilia, Squamata, Serpentes, Viperidae, Crotalinae, *Popeia inornata* species nov., *Trimeresurus popeiorum*, Cameron Highlands, Pahang, Malaysia, Southeast Asia.

1. INTRODUCTION

The numerous “green pitvipers” in the Asian *Trimeresurus* complex show striking morphological similarity, as well as considerable geographic variation and sexual dimorphism. This has long confounded taxonomic resolution of the group (Stejneger, 1927; Pope and Pope, 1933; Regenass and Kramer, 1981) and continues to impede field identification. However, the recent application of molecular and multivariate morphological methods has resolved the status and relationships of many of the green *Trimeresurus* species, and in many cases has revealed previously undetected, cryptic species (Malhotra and Thorpe, 2000; Giannasi et al., 2001; Malhotra and Thorpe, in press a, b).

The genus *Popeia* Malhotra and Thorpe, 2004 (a genus of feminine gender [Article 30.2.4; ICZN, 2000] formerly referred to as the *Trimeresurus popeiorum* species complex) has a wide geographic distribution in Southeast Asia and occurs almost exclusively at moderate and high altitudes in undisturbed rainforests. Regenass and Kramer (1981) split the complex into three subspecies, but the geographic range of these has proved to be largely inaccurate (Sanders, Malhotra, and Thorpe, unpublished): *Trimeresurus popeiorum popeiorum* Smith, 1937 (terra typica restricta [Taylor and Elbel, 1958]: Khasi Hills, India) was recognised on the South-east Asian mainland, a new subspecies *T. popeiorum sabbahi* was described to accommodate the Borneo population, and another new subspecies, *T. popeiorum barati*, was described from the Barisan range in western Sumatra (Regenass and Kramer, 1981).

This scheme is inconsistent with a recent analysis of the taxonomy of the genus *Popeia* based on analysis of DNA sequences from four mitochondrial genes, multivariate morphometrics and information on ecology, carried out using museum specimens and newly collected material spanning the geographic range of the genus (Sanders, Malhotra, and Thorpe, unpublished). Consequently, a taxonomic reorganisation of *Popeia* has been proposed (Sanders, Malhotra, and Thorpe, unpublished).

Two well-differentiated clades of *Popeia*, corresponding mainly to the northern and southern parts of

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the range, were indicated in the phylogeny. The southern clade includes lineages in southern Thailand, southern peninsular Malaysia, Pulau Tioman, Sumatra, and Borneo, while the northern clade includes populations in northern and western Thailand, Myanmar, and Laos and in the Cameron Highlands of West Malaysia. Sanders, Malhotra, and Thorpe (unpublished) proposed a conservative arrangement of the southern clade populations as a single equatorial species. The majority of northern clade populations can be clearly assigned to the nominate form of *Popeia popeiorum* by morphological similarity, but the population from the Cameron Highlands is morphologically and ecologically divergent from all other northern clade populations. Moreover, it is also distantly allopatric from these, and categorical patterns of morphological variation indicate that intergradation with parapatric southern clade populations is unlikely (Sanders, Malhotra, and Thorpe, unpublished). Here we provide the formal description of this new species.

2. MATERIAL AND METHODS

Snakes were wild-caught in Thailand, Malaysia, and Indonesia; these provided blood samples, morphometric data (under anaesthesia), and ecological information. Blood and tissue samples were also obtained from museum and private collections when reliable locality information was available. A total of 32 specimens of *Popeia* were sampled from Myanmar, Thailand, Laos, peninsular Malaysia, Borneo, and Sumatra. Blood samples were taken from the caudal vein with a hypodermic syringe, placed in 1 ml 0.1 M EDTA, and stored in SDS-Tris buffer (2% SDS, 100 mM Tris); liver and muscle tissue was preserved in 80% ethanol. In addition to field-collected specimens, we examined material in the holdings of various museums. Museum abbreviations follow standard usage (Leviton et al., 1985), except the following: LSUHC (La Sierra University Herpetology Collection, Riverside, California, USA), PCGV (personal collection of Gernot Vogel), PH (Perhelitan, Kuala Lumpur, Malaysia), QSMI (Queen Saovabha Memorial Institute, Bangkok, Thailand), ZRC (Raffles Museum of Biodiversity Research, The National University of Singapore, Singapore). AFS/KLS indicate wild-caught specimens examined under anaesthesia. Specimens used in morphometric and molecular analyses are listed in Appendix I. A total of 14 live and preserved specimens from the Cameron Highlands were available for descriptive morphology studies; information on selected morphological characters of five additional individuals from

that population was obtained from published (Chan-ard et al., 1999:199 – 200) and unpublished photographs.

In the description that follows, terminology for most scales follows Klauber (1972), with modifications and additions according to Gutberlet and Campbell (2001). Interoculars were counted in a vertical line from below the pupil of the eye to the mouth, including one subocular and one supralabial. Canthals are the scales along the lateral edge of the dorsal surface of the head, and are situated between the internasals and the supraoculars. Canthals are counted in a single row, and the small scales adjacent to the supraoculars are also included in the canthal series, even when these scales are excluded from the canthus rostralis proper by the most dorsal preocular. Intersupraoculars are counted in a straight line between the two supraoculars, which are not included in the series. Gulars are counted in a straight line between the chinshields and the first scale on the underside of the head which is wider than long (i.e., the first preventral, or ventral if no preventrals are present). In some specimens, dorsal scale rows were counted one head length behind the occiput, at midbody, and one head length anterior to the vent. In others, the complete scale reduction formula was noted. The first ventral is considered to be the first scale on the underside of the head that is bordered on both sides by the first row of dorsals (Dowling, 1951). The last ventral is the scale anterior to the anal plate. Slashes are used to denote paired structures on the left/right sides of the body.

In color descriptions, the capitalized colors and color codes (the latter in parentheses) are those of Smithe (1975). Geographical coordinates and most altitudes were determined using a hand-held GPS system (Garmin GPS 12).

2.1. Multivariate Morphometrics

In order to obtain information on diagnostic characteristics of the new species, specimens of the genus *Popeia* were grouped according to the species defined by Sanders, Malhotra, and Thorpe (unpublished). Males and females were treated separately in all analyses to avoid bias caused by sexual dimorphism. Stepwise discriminant function analyses were carried out between the Cameron Highlands specimens and, separately, specimens referable to *P. popeiorum* and the southern clade species. Characters measured were first screened by two-way analysis of variance (ANOVA) with sex and locality as the factors, and only characters that were significantly different between locality were included in the analysis. A list and definitions of characters measured can be found in Appendix II.

2.2. Mitochondrial DNA Sequence Analysis and Fixed Nucleotide Differences

Whole genomic DNA was extracted from blood and tissues using standard proteinase K protocols (Sambrook and Russell, 2001). Cytochrome *b* sequences were obtained as described in de Queiroz et al. (2002). Unincorporated nucleotides and primers were removed from PCR products and single stranded product was then sequenced using dye-labelled terminators (ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit, Applied Biosystems, Foster City, CA, USA) and run on ABI Prism model 377 and 3100 automated DNA sequencers (Applied Biosystems). Fixed nucleotide differences between mtDNA lineages were systematically compared using MEGA version 2.1 (Kumar et al., 2001).

3. RESULTS

3.1. Multivariate Morphometrics

Both scalation and color pattern characters contributed to the discrimination of the new species in the DFA, although in both sexes more characters were identified to distinguish the new species from *P. popeiorum* than from the southern clade species. Characters that are important in the DFA are listed in Table 1 with their mean values and ranges.

3.2. Mitochondrial DNA Sequence Analysis and Fixed Nucleotide Differences

Partial nucleotide sequences of the mitochondrial cytochrome *b* gene were determined for eleven individuals of the new species, including both sexes, the holotype, and two paratypes. For comparison, cytochrome *b* sequences were determined for eleven representatives of the northern clade (exclusive of the new species), and for 13 snakes representing the southern clade. Five fixed nucleotide differences were identified in a 720 bp fragment of the cytochrome *b* gene, corresponding to positions 30, 174, 273, 378 and 423 in a published sequence for *T. popeiorum* (DDBJ/EMBL/GenBank Nucleotide Sequence Database accession number AF171888, now referable to the new species described herein). In *P. popeiorum* s. str. and the southern clade species the bases at these positions are C, T, T, A, C, respectively, while they are T, C, C, G, T in the new species. Accession numbers for these sequences are given in Appendix I.

3.3. Systematic Account

Popeia inornata species nov. (Figs. 1 – 8)

Trimeresurus popeorum — Lim (1982:21, title page, and Fig. 22) [partim].

Trimeresurus popeiorum ssp. — Chan-ard et al. (1999:199 – 200).

Holotype. ZMB (Institut für systematische Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany) 66281, adult male, Cameron Highlands, Pahang, Malaysia, collected by indigenous collectors, July 2002 (Figs. 1 – 3).

Paratypes. [*N* = 8] BMNH (The Natural History Museum, London, United Kingdom) 2003.1, adult female, road to Gunung Brinchang, Cameron Highlands, Pahang, Malaysia (04°30.682' N, 101°24.596' E, 1763 m above sea level), collected by Wolfgang Grossmann and Christian Schäfer, February 1997. CAS-SU (California Academy of Sciences, San Francisco, CA, USA) 8863,

TABLE 1. Mean Values and Ranges of Morphological Characters Important in Multivariate Discrimination Between the New Species and Other Members of *Popeia*

Males			
Character	<i>P. popeiorum</i> (<i>n</i> = 15)	<i>P. inornata</i> (<i>n</i> = 2)	Southern clade species (<i>n</i> = 33)
VSC	162.9 (158 – 171)	153.0 (150 – 156)	158.5 (141 – 172)
SUPLAB	10.2 (9 – 11)	9.0 (9 – 9)	9.8 (9 – 11.5)
BTWSUPOC1	9.3 (8 – 12)	9.0 (8 – 10)	9.2 (8 – 12)
BTWSUPOC2	13.6 (10 – 17)	12.0 (11 – 13)	13.0 (11 – 16)
NASPIT	1.5 (0 – 2)	1.0 (1 – 1)	1.3 (0 – 2)
VS21to19	99.4 (83.5 – 110)	86.5 (77.5 – 95.5)	75.0 (8.5 – 107.5)
STRIPE	2.0 (2 – 2)	0.7 (0.5 – 1.0)	1.6 (0 – 2)
OCSTRIPE	1.5 (0 – 2)	0	0.1 (0 – 2)
LIPCOL	1.0 (0 – 2)	0	0.6 (0 – 2)
Females			
Character	<i>P. popeiorum</i> (<i>n</i> = 9)	<i>P. inornata</i> (<i>n</i> = 7)	Southern clade species (<i>n</i> = 24)
VSC	164.2 (159 – 171)	151.1 (149 – 153)	156.8 (144 – 173)
BTWSUPOC2	14.8 (11 – 16)	11.7 (10 – 13)	13.1 (11 – 16)
NASPIT	1.8 (1 – 2)	1.2 (1 – 2)	0.8 (0 – 2)
LAB4	1.1 (1 – 2)	0.9 (0 – 1)	1.1 (1 – 2)
LAB5	1.4 (1 – 2)	1.1 (1 – 1.5)	1.3 (1 – 2)
VS19to17	110.3 (108.5 – 115.5)	97.6 (94.5 – 100)	102.7 (83.5 – 117)
LIPCOL	0.9 (0 – 3)	0	0.8 (0 – 2)
SCR1	0.1 (0.1 – 0.4)	0.1 (0 – 0.2)	0.1 (0 – 0.9)

Note. For character abbreviations see Appendix II. Bold entries indicate the taxon or taxa for which that character is helpful in discriminating from the new species. Sample sizes are given in parentheses.



Fig. 1. Adult male holotype of *Popeia inornata* in life. Photograph by A. Gumprecht.

adult female, “Tana Rata, Cameron Highlands, Pahang, Malaya” [= Tanah Rata, Cameron Highlands, Pahang, Malaysia], collected by A. W. C. T. Herre, 28 October 1940. SMF (Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany) 82934, adult female, Bala’s Holiday Chalets, Tanah Rata, Cameron Highlands, Pahang, Malaysia, 1642 m above sea level, collected by Christian Schäfer and Wolfgang Grossmann, 1 February 1997. SMF 82935, female neonate, captive-born, parents from Cameron Highlands, Pahang, Malaysia. SMF 83002, six-month-old male sibling of SMF 82935. ZRC (Raffles Museum of Biodiversity Research, National University of Singapore, Singapore) 2.2884, adult female, Cameron Highlands, Pahang, Malaysia, 4500 ft [~1370 m] above sea level, collected by G. H. Sworder, 16 June 1927. ZRC 2.2886, adult female, Tanah Rata, Cameron Highlands, Pahang, Malaysia, collected by K. B. Williamson, 1930. ZRC 2.5164, adult

female, Parit Falls, Cameron Highlands, Pahang, Malaysia, collected by T. M. Leong, 30 July 2001.

Diagnosis. The new species is distinguished from other species of the *Trimeresurus* (*sensu lato*) complex, with the exception of other members of the genus *Popeia* and some members of the genus *Cryptelytrops* Cope, 1860, by a long calyculate hemipenis without papillae (as described in Malhotra and Thorpe, 2004). *Popeia inornata* is distinguished from members of *Cryptelytrops* by full separation of the first supralabial and nasal scales. It is distinguished from other members *Popeia* by the absence of a red or orange lateral stripe in adult males. Both sexes of *P. inornata* are separated from *P. popeiorum* s. str. by low ventral scale counts (no higher than 156, compared to no lower than 158), and from both *P. popeiorum* and the southern clade species by green eye coloration, with the exception of West Malaysian representatives of the southern clade, from which *P. inornata* can be distinguished by low ventral scale counts alone (149 – 156 vs. 157 – 172). With respect to the classification of Regeness and Kramer (1981), *P. inornata* is distinguished from the Borneo population (*T. p. sabahi sensu* Regeness and Kramer, 1981) by the absence of a red or orange lateral stripe in adult males and by green eye coloration in both sexes. It differs from snakes from the Barisan range of western Sumatra (*T. p. barati sensu* Regeness and Kramer, 1981) in having a longer and less compact head, a coloration of interstitial skin and dorsal scale bases that forms black bands with narrow light blue interspaces (vs. no dark bands on uniformly bluish gray to blue interstitial skin), and lower and upper margins of supralabials and infralabials, respectively, that are distinctly blue in life (vs. bluish white to lighter blue). *Popeia inornata* is further distinguished from west Sumatran specimens by the dorsal coloration of the tail which in life is a well-defined and solid brick red with light margins on red dorsal scales (vs. a light brown to golden hue which is less clearly demarcated laterally). While Regeness and Kramer (1981) distinguished *T. p. barati* on the basis of lower midbody dorsal scale counts (17 – 19 vs. 21 in the rest of their *T. popeiorum* group), an additional specimen examined by Sanders, Malhotra, and Thorpe (unpublished) from west Sumatra has 21 scale rows. Additional morphological characters that can be used in combination to diagnose the new species are listed in Table 1; diagnostic molecular characters are given above.

Popeia inornata is not known to share its geographic range with any other green pitviper species. It is easily distinguished from juvenile and adult male *Tropidolaemus wagleri* (Boie, 1827) by the distinct red and



Fig. 2. Dorsal view of the head of the holotype of *Popeia inornata*, prior to shedding. Photograph by A. Gumprecht.

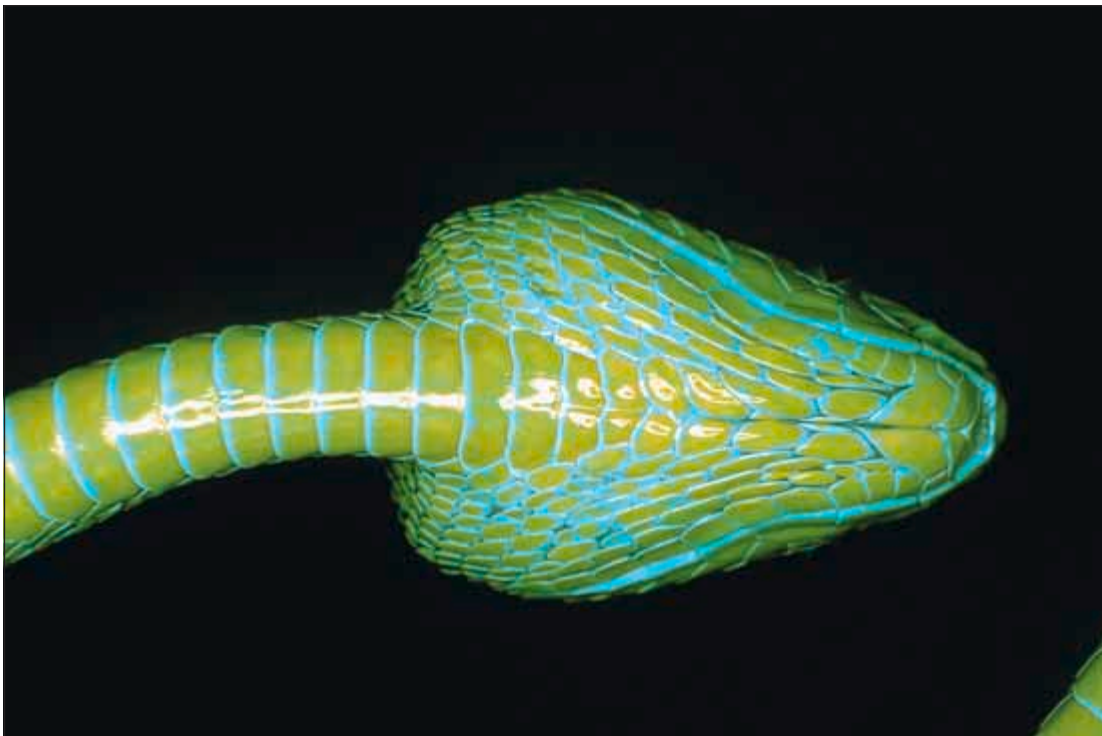


Fig. 3. Ventral view of the head of the holotype of *Popeia inornata*. Photograph by A. Gumprecht.



Fig. 4. Adult female *Popeia inornata*. Note the lack of sexual dimorphism in adult snakes of the new species (compare to Fig. 1). Photograph by A. Gumprecht.



Fig. 5. Adult female *Popeia inornata*, showing the blue lip coloration and lower side of head. Photograph by A. Gumprecht.



Fig. 6. Juvenile male *Popeia inornata* (paratype SMF 83002, 3 months old). Compare to Fig. 1 for ontogenetic changes in the color pattern of males (juvenile red and white lateral stripe, banded tail, and white lips). Photograph by A. Gumprecht.



Fig. 7. Ventral view of a subadult female *Popeia inornata*, showing absence of a red lateral stripe (present in juvenile males: Fig. 6), presence of a distinct white lateral stripe (reduced or absent in adults of either sex: Figs. 1, 4), and blue lips (white in juveniles of either sex:

white pre- and postocular stripe, red and white dorsal bands or spots, and keeled scales on the lower side of the head possessed by the latter species. Adult females of *T. wagleri* are even more distinct from *P. inornata* due to their highly divergent, largely black and yellow coloration and relatively massive girth. The new species can be distinguished from *Parias hageni* (Lidth de Jeude, 1886) by the dorsal coloration and pattern of the tail, which in *Pa. hageni* is green with a few irregular reddish-brown spots, and solid reddish-brown only in about the distal half of the tail (vs. laterally well-defined and solid brick red from about the anal region to the tip in *P. inornata*).

Description of the holotype. A medium-sized, slender arboreal pitviper with long prehensile tail; head triangular in dorsal aspect and very distinct from slender neck; eye medium-sized, pupil vertically elliptical in

light; rostral trapezoidal, dorsal margin about half as wide as ventral margin, more than twice as wide as high; nostril completely enclosed in nasal scale; nasal scale elliptical, completely divided above naris on left side, fused above naris on right side, indistinctly divided below naris on both sides, nasal in broad contact with but discrete from first supralabial; loreal single, bordered dorsally by first canthal, about as wide as high; prominent loreal pit, upper margin of pit located below level of shortest straight distance between eye and naris; prefoveals, postfoveals and subfoveals absent; prelacunal fused to second supralabial on both sides; interoculars 3/3; preoculars 3/3; upper preocular longer than high, contributing to canthus; middle preocular formed by supralacunal, longer than upper preocular; lower preocular formed by sublacunal, about as long as, but posteriorly wider than middle preocular, entering orbit but



Fig. 8. Adult male *Popeia inornata* photographed *in situ* in montane rainforest at night (Gunung Brinchang, Cameron Highlands, Pahang, Malaysia; 1600 m above sea level). Photograph by W. Grossmann.

stopping just short of contacting the eye; suboculars 1/1, long and narrow, each partially segmented, in contact with third supralabials, but separated by one scale from fourth and fifth supralabials, extending up to form approximately half of posterior orbit; postoculars 2/2, lower postocular on both sides separated from postero-dorsal extension of subocular by one tiny apical scale which does not contact the eye; supralabials 9/9; infralabials 12/12, first pair of infralabials in broad contact with each other medially; mental approximately triangular, wider than long; chinshields longer than wide, contacting first 3/4 infralabials; gulars between chinshields and first scale on underside of head that is wider than long 4/4, first pair of gulars separated medially by two small scales; 3 prefrontals; 2 internasals, relatively small, separated from each other by a scale less than half the size of an internasal, one tiny apical scale where rostral, right nasal, right internasal and scale separating internasals meet; distinct canthus rostralis, canthals 3/3, anterior canthal distinctly larger, approximately 2–2.5 times longer than wide, smaller than internasal, posterior canthals small, of same size as adjacent intercanthals; intercanthals 6, immediately posterior to internasals; intercan-

thals 7, between posterior ends of anterior canthals; intercanthals 10, between posterior canthals; minimum number of intersupraoculars 10, number of intersupraoculars between posterior edges of supraoculars 13; dorsal head scales, from level of posterior of supraoculars forward, small and smooth to very weakly keeled, keels becoming more distinct on posterior head scales; supraoculars relatively small, about twice as long as wide, distinctly wider than adjacent intersupraoculars; dorsal scale rows 23–21–15; ventrals 149; anal entire; subcaudals 65/66 (one undivided scale followed by 14/15 divided, one undivided, 40/40 divided, two undivided, and 7/7 divided subcaudals); tail spine slightly compressed laterally, as long as adjacent 2.5 subcaudals, tip blunt; dorsals extending onto tail spine only slightly farther than subcaudals; dorsal scales small and elongate, those of middorsum at midbody about twice as long as wide, becoming wider posteriorly such that length only slightly exceeds width; dorsal body scales moderately keeled vertebrally, slightly keeled laterally, keels extend to terminus of scale; paraventrals smooth, similar in size and shape to adjacent dorsals; parasubcaudals and most other dorsal scales on tail smooth.

Measurements of the holotype (in millimetres, head measurements taken from the right side of the head). Snout-vent length 669, length of prehensile tail 183, head length 35.4, head width between outer edges of supraoculars 17.9, head width at widest point 20.85, length of supraocular scale 5.38, width of supraocular scale 2.54, distance from posterior edge of pit to anterior edge of naris 7.56, eye-pit-distance 2.24, eye-naris-distance 8.40, eye diameter 5.07. Further explanation of how these measurements were taken can be found in Appendix II.

Full dorsal scale row reduction formula. See Table 2.

Color in life. Dorsal head scales Shamrock Green (162B), some scales in posterolateral parts of head with Jet Black (89) anterior margins; interstitial skin on head Jet Black (89); laterally, scales gradually lighter towards supralabials, from grayish Peacock Green (162C) to dark Lime Green (159); interior of pit light Rose Pink (108D); eye Olive-Green (46) with lighter green margins; interstitial skin and/or scale margins between supralabials and adjacent scales Sky Blue (168C) to Light Sky Blue (168D); lower margins of supralabials, upper margins of infralabials, lower margin of rostral and suture of third and fourth supralabials Sky Blue (168C) to Venetian Blue (168B); neck grayish Parrot Green (60) to Peacock Green (162C), several dorsal scales with Jet Black (89) bases; dorsal scales of body Parrot Green (260) to Peacock Green (162C) vertebraally, laterally gradually lighter to Lime Green (159, 59); body with dark bands on interstitial skin formed by Jet Black (89) areas of interstitial skin and dorsal scale bases, interrupted by Robin's Egg Blue (93) interspaces; black bands wider anteriorly, usually extending over about two dorsal scales, separated by narrow blue interspaces extending over less than one dorsal scale; posteriorly, black bands reduced, usually covering less than one dorsal scale, separated by blue interspaces that extend over the length of about two dorsal scales; black interstitial bands not extending onto paraventrals; lateral stripe from Light Sky Blue (168D) finely dusted with Plumbeous (78) pigment to Robin's Egg Blue, indistinct on anterior body, more distinct posteriorly, covering upper 1/3 to 1/2 of paraventrals and lower margin of dorsals of second rows, becoming indistinct again at level of cloaca, then continuing on parasubcaudals and outer margins of subcaudals to merge with ventral tail color-

ation at about level of subcaudals 3/5; scales on lower side of head from Lime Green (159) and other yellowish green tones on the mental and infralabials to Buff-Yellow (53) in the gular region; most scales on lower side of head with Sky Blue (168C) to Light Sky Blue (168D) margins; coloration of ventral side of body continuous with that of head, ventral scales being colored in a complex mixture of yellowish and light green tones giving an overall impression ranging from greenish Olive-Yellow (52) to greenish Spectrum Yellow (55); all ventrals with light blue posterior margins, on posterior body distinctly subdivided into Sky Blue (168C) basally and Light Sky Blue (168D) distally; color of ventral side of tail base continuous with that of posterior body but less yellowish, scale margins heavily pigmented with Sky Blue (168C) to Pratt's Payne's Gray (88); subcaudals generally with lighter (greenish) base and centre, darker (bluish to grayish) inner and light (Light Sky Blue [168D] to whitish) outer margin; from about subcaudal 37 posteriorly increasingly reddish pigmentation of scale bases and centres; dorsum of tail reddish, from Deep Vinaceous (4) on tail base gradually changing to Ferruginous (41) on tip; area with reddish coloration overall well-defined and solid, starting vertebraally at level of anal plate, gradually extending laterally, separated from subcaudals up to about level of subcaudal 20, then fully extending onto parasubcaudals, to also encroach upon subcaudals near tail tip; posterior margins of reddish dorsals on tail base with Medium Plumbeous (87) and whitish margins, the gray becoming reduced posteriorly, where whitish margins remain; reddish dorsals on tail base finely dusted with black pigment, which is also reduced distally.

Color of preserved holotype. After five months of preservation in 70% ethanol, the coloration of the holotype has changed very little, the only noticeable changes involving certain shades of green: Dorsum of head Bunting Green (150) anteriorly, posteriorly darker to almost Leaf Green (146); lateral head scales Bunting Green (150), lighter anteriorly and on supralabials; dorsal scales of body Bunting Green (150) vertebraally to light Yellowish Olive-Green (50) laterally; ventral side of head and anterior body Opaline Green (162D); posteriorly, ventrals greenish Olive-Yellow (52) with light posterior margins as above.

Variation in paratypes. In both sexes, the number of ventral scales varies between 150 and 154; the num-

TABLE 2. Full Dorsal Scale Row Reduction Formula

31	$\frac{8+9(7)}{9+10(8)}$	29	$\frac{6+7(8)}{7+8(8)}$	27	$\frac{11+12(10)}{5+6(10)}$	25	$\frac{5+6(12)}{5+6(15)}$	23	$\frac{5+6(24)}{5+6(21)}$	21	$\frac{4+5(95)}{5+6(96)}$	19	$\frac{4+5(100)}{4+5(100)}$	17	$\frac{4+5(108)}{4+5(107)}$	15
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ber of subcaudals ranges from 51 – 70, all of which are divided. Rostral up to four times wider ventrally than dorsally, 1.3 times to more than 2 times wider than high; nasal undivided or incompletely divided above or below naris; supralabials 9 – 10; suboculars 1/1, frequently partially divided in up to three parts (posterior end of left subocular discrete as separate scale in SMF 82935, indistinctly separated in BMNH 2003.1); interoculars 2 – 3; postoculars 2 – 5; infralabials 11 – 13; chinshields contacting first 3 – 4 infralabials; gulars 3 – 6, pairs of gulars frequently separated by up to 4 small median scales, gulars in SMF 82935 followed by 2/3 scales wider than long resembling divided prefrontals; regular prefrontals 0 – 3; minimum number of intersupraoculars 8 – 12, maximum 12 – 13; canthals 4 – 5 (BMNH 2003.1, SMF 82934 and SMF 82935 with small first canthal of regular intercanthal size separating large second canthal from internasal, followed by two, two and three small canthals, respectively, separating large canthal from supraocular); intercanthals 5 immediately posterior to internasals, 7 – 10 between posterior canthals; loreals 1 – 2, bordered dorsally by first or second canthal; internasals 0 – 2, in contact or separated medially by one small scale (in BMNH 2003.1, internasal suture separated from rostral by one tiny apical scale); dorsal scale rows 21 – 23/20 – 21/13 – 15, most dorsal body scales of the juvenile paratypes smooth or (especially anteriorly and ventrally) very weakly keeled, some paraventrals in BMNH 2003.1 very weakly keeled.

Adult females closely resemble the holotype in details of color pattern (see also Figs. 4 – 5). While sexual dimorphism is not marked in either scalation or coloration in adult *P. inornata*, the juvenile paratypes exhibit sexual dimorphism in color pattern, and demonstrate that ontogenetic changes in coloration occur. In summary, the sexual dimorphism consists of the juvenile male paratype (SMF 83002) having a red stripe below a white lateral stripe (Fig. 6); and the ontogenetic color change comprises the absence of the red ventrolateral stripe in adult males (Figs. 1, 8); the presence of a distinct white to chamois lateral stripe in young snakes of both sexes (Figs. 6 – 7) which is indistinct, reduced, bluish or absent in adults (Figs. 1, 4, 8); a change in lip coloration from white in juveniles of both sexes (Fig. 6) to blue in subadults and adults (Figs. 5 – 6); and a dorsal tail pattern of light and dark grayish olive bands in juveniles of both sexes (Fig. 6) which changes to a well-defined, solid, rufous, brick red, or ferruginous tail coloration in adults.

Details of the coloration of the female neonate follow (SMF 82935, after six months of preservation in 70% ethanol): Head and body Greenish Olive (49) verte-

brally to Citrine (51) laterally; head laterally gradually lighter (to Olive-Yellow [52]) towards supralabials); pre- or postocular stripes absent; upper margins of infralabials and mental, and lower margins of supralabials and rostral white; light lateral stripe first discernible behind and at level of angle of jaw, as an area of Olive-Yellow (52) dorsals becoming lighter towards ventrals, then starting as distinct stripe at level of third/fourth ventrals, first involving upper half of dorsals in paraventral and lower half of those in second row; lateral stripe then Chamois (123D) in lower margin to lower half of second row and upper half of paraventral row; lower half of scales in paraventral row gradually darker, to Olive-Yellow (52) in basal and ventral parts of scales; lateral stripe interrupted in anal region, then followed by light lateral stripe on tail up to level of subcaudals 5 – 6, here, lower quarter of parasubcaudals and outer edges of subcaudals are Cream Color (54); head ventrally from Olive-Yellow (52, infralabials, gulars) to Buff Yellow (53, median parts of chinshields, first infralabials); ventrals anteriorly Olive-Yellow (52) to Sulphur Yellow (57), posterior margins lighter; ventral color gradually brighter posteriorly and towards outer margins of ventrals, from Olive-Yellow (52) medially to Bunting Green (150) on outer margins, and with light posterior margins (light greenish yellow, close to Spectrum Yellow [55] but with green hue); subcaudals like ventrals, but some with dark outer edge from dorsal tail pattern, dark pigment on outer edges of subcaudals increasing on tail tip; dorsal scales on tail finely dusted with black pigment, arranged in alternating darker and lighter areas covering about one scale in width, lighter areas Olive (30), darker areas Dark Brownish Olive (129); only posteriorly, this dark dorsal tail coloration extends onto a few outer margins of subcaudals.

The juvenile male paratype (SMF 83002) differs from the female neonate mainly in having a lateral stripe which is white (rather than chamois) on the lower margin to lower half of the second row and upper half of the paraventral row, and a clearly demarcated red ventrolateral stripe (light Crimson [108] in life) covering the lower half of scales in the paraventral row. In life, the venter of the juvenile male was Pistachio (161), the dorsum from Peacock Green (162C) to Opaline Green (162D), and the dorsum of the tail had Mahogany Red (132B) bands and Light Russet Vinaceous (221D) interspaces.

Variation in all examined specimens ($N = 19$). Females of *P. inornata* appear to reach a larger overall size (maximum recorded 836 mm SVL compared to 669 mm for males) and have relatively shorter tails. In both sexes, ventral scale counts vary between 149 and 156,

and subcaudal scale counts between 51 and 68. The holotype had four undivided subcaudal scales, but subcaudals were divided in all other specimens. There are a minimum of 7 and a maximum of 13 intersupraoculars. There may be 0–1 scales between the fourth supralabial and the subocular, and 1–2 scales between the fifth supralabial and the subocular scale. Infralabials range from 11–13 (mode 12) with the exception of one male having 9/11 infralabials. There are 4–6 intercanthals immediately posterior to internasals, and 6–10 between posterior canthals. Dorsal head scales are smooth to very weakly keeled, and many of those posterior to the intersupraoculars may have black anterior margins. A range from smooth to fairly strongly keeled dorsal scales has been noted on the body. Variation in other characters lies in the range of that reported for the type series.

Etymology. The specific epithet *inornata* is an adjective in the feminine singular gender. The scientific name of the new species alludes to the fact that adult males of *P. inornata* lack ornamentation by a distinctive orange to brick red ventrolateral stripe, which is typically present in adult males of sexually dimorphic members of the genus *Popeia*, and that both sexes show reduction of the white lateral stripe.

4. DISCUSSION

4.1. Systematics. *Popeia inornata* is strongly differentiated both morphologically and genetically, and distantly allopatric from any of the three subspecies of *T. popeiorum* recognized by Regenass and Kramer (1981). In their analysis of the taxonomy of the genus *Popeia*, Sanders, Malhotra, and Thorpe (unpublished) demonstrate that the divisions revealed by the analysis of DNA sequences from four mitochondrial genes, multivariate morphometrics and information on ecology are inconsistent with the current subspecific taxonomy of this genus. As a consequence of these findings, Sanders, Malhotra, and Thorpe (unpublished) propose a taxonomic reorganisation of *P. popeiorum* into three species as indicated herein. In either scheme, *P. inornata* is clearly distinguishable.

4.2. Distribution, habitat, and natural history. *Popeia inornata* is known only from the Cameron Highlands in West Malaysia. This mountain range comprises an area of 649 km² and extends from 600 to 2032 m above sea level, although most of it is situated between 1200–1800 m. Natural vegetation consists of dipterocarp forests in lower elevations, lower montane forests dominated by oaks and laurels, and upper montane forests characterized by *Rhododendron* and rich epiphyte

vegetation, notably *Nepenthes* spp. The climate in the Cameron Highlands is mild and wet: recorded mean daily maximum temperatures at 1448 m above sea level range from 21.7–23.3°C and mean daily minima from 12.8–14.4°C with absolute maxima/minima of 25.0–26.7°C/2.2–8.3°C (Müller, 1996). Rainfall peaks in October and November as well as April; January–February and June–July are the months with lowest precipitation. Specimens of *P. inornata* were observed or collected in the months of both January–February, June–July, October, and November, in undisturbed lower montane wet forest, selectively logged forest, secondary forest, bamboo stands, and adjacent agricultural and succession zones. Altitude records for the new species range from approximately 1200–1982 m above sea level, with the majority of observations made at elevations between 1500–1800 m. Most specimens (two juveniles, two adult females and one adult male) were found along the edge or crossing the road near a strawberry farm, around the Gunung Brinchang junction, and on the road to Gunung Brinchang. Road collection localities were bordered by transitional vegetation connecting deforested agricultural lands in lower parts with primary forest remnants on steeper slopes, by primary forest, and in one case by a tea estate. Specimens were observed active on or along the road during dry weather in the evening (20:50–21:30 [W. Grossmann, in litt. 24.IX.2003]). R. Malkmus, C. Schäfer, and K.-D. Schulz (personal communication) observed various specimens of *P. inornata* along the banks of a stream near Tanah Ratah at night, one of the paratypes (ZRC 2.5164) was collected near a small stream, and an adult male of 577 mm SVL and 81 g body mass was found at 22:05 perched on a log of 15 cm diameter in selectively logged forest near Tanah Rata (J. A. McGuire, personal communication). Occasionally, *P. inornata* may also enter human settlements: Schäfer and Grossmann found a juvenile female in the roof of the main building of Bala's Holiday Chalets, Tanah Rata (1526 m above sea level) during daytime on a cloudy day with occasional rain-showers (W. Grossmann, in litt. 24.IX.2003). *Popeia inornata* is mostly nocturnal and at least semiarboreal, but is often encountered active on the ground, presumably in search of prey. According to indigenous people, snakes of this species are usually found in primary forest curled up on top of ferns about 40 cm above the ground. No specific records on the natural diet of this species are available. Both adults and juveniles have accepted laboratory mice as food in captivity. The new species is viviparous as evinced by a female giving birth to one live and one fully developed stillborn juvenile on 22 July 2003. The juveniles measured 206 mm (female) and

~190 mm (male), and a roadkilled juvenile female found in July 1993 measured 230 mm total length.

4.3. Venom and snakebite. Nothing is known about the biochemical and biological activities of the venom of *P. inornata*. Although venom samples from this species may have been studied, the species identity of green pitvipers used in earlier toxinological publications (e.g., Tan et al., 1989) is difficult to evaluate in the absence of voucher specimens or genetic samples. The same applies to many clinical reports. Nevertheless, due to the high elevation habitat excluding many of the medically most significant venomous snake species of peninsular Malaysia, *P. inornata* might be the most important source of snakebite in the Cameron Highlands.

4.4. Conservation status. Less than a dozen pitvipers are among approximately 200 snake species previously identified as threatened or endangered worldwide, but recent estimations suggest that at least 80 species (more than half of all crotaline species) may be vulnerable to extinction (Greene and Campbell, 1992). Of special concern are taxa with small and/or highly fragmented ranges, narrow habitat preferences, and/or substantial human persecution. Habitat conversion is the greatest overall threat to pitviper populations, and loss of natural habitat due to agriculture, tea plantations, golf courses and real estate development has been substantial especially in the western parts of the Cameron Highlands since their discovery in 1885. *Popeia inornata* is regarded by indigenous people as the commonest of all venomous snakes in the Cameron Highlands. However, it is unclear whether this statement is based on observations made in undisturbed primary montane forest habitat, or suggests that viable populations exist in secondary habitats. The impact that habitat destruction and fragmentation in the form of logging of primary forests and the isolation of forest remnants have on populations of this endemic species is thus unknown. Another factor affecting populations of *P. inornata* with unknown magnitude is road mortality. Road traffic in the Cameron Highlands appears substantial, especially in the first hours after sunset, when many nocturnal snakes exhibit high activity, and a considerable proportion of all observed *P. inornata* were encountered dead on the road. Given the scarcity of basic natural history data, additional studies on these pitvipers should be encouraged to elucidate their ecology and to allow a detailed assessment of their conservation status.

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APPENDIX I

Specimens Used in Morphometric and Molecular Analyses

Locality information is followed by catalogue or field reference numbers, sex (f, female; m, male; ?, undetermined), and accession numbers for nucleotide sequences where appropriate. Specimens marked with an asterisk were not used in the morphological analysis.

Popeia popeiorum sensu Sanders, Malhotra, and Thorpe (unpublished): INDIA: West Bengal: Darjeeling: BMNH 72.4.17.377, m. Meghalaya: Khasi Hills: BMNH 72.4.17.137, m. MYANMAR: Bago Division: Bago Yoma (18°52'59.8" N, 95°52'44.9" E, 420 m): CAS 205847, f, AY371816. Kayin and/or Kayah State: Carin Gebirge: NMW 23923:1, m; NMW 23923:2, m. Mon State: Kyaikhtyo Township: Kyaikhtyo Wildlife Sanctuary: Sawaun Taung Chaung Camp (17°26'28.7" N, 97°05'23.1" E): CAS 216609, m, AY371805; Kyait Hto Township: Kyaikhtyo Wildlife Sanctuary: Tributary of Moe Baw Chaung: CAS 222195, m, AY371806. Taninthayi Division: Kissaraing, Mergui: BMNH 1940.3.9.43, m. THAILAND: Uthai Thani, W. Thailand: RMNH 16715, f. Chiang Mai Province: AFS96.17, f, AF171902; Pa Meang, North of Chiang Mai, N. Siam: BMNH 1937.2.1.24, f; BMNH 1937.2.1.25, m; Doi Suthep: FMNH 178655, f; Doi Suthep Fisheries Station: FMNH 178658, m; Mae Solat: FMNH 178656, m; Doi Pra Kao: FMNH 178659, m; N Chiangmai [Chiang Mai], Siam: NMW 27947:1, m; Doi Inthanon: AFS02.14*, f, AY371809. Lampang Province: AFS96.3, m, AF171906. Phang Nga Province: AFS02.05*, f, AY371807. Phetburi Province: AFS98.16, f, AY059572; AFS98.34, m, AY371800. LAOS: Lao Mountains, Cochin China: BMNH 62.7.28.1, f; BMNH 62.7.28.4, m. Kasi District: Vientiane Municipality: FMNH 258949, f, AY371799. Phongsaly Province: Phou Dendin NBCA: FMNH 258950, f, AY059571.

Popeia southern clade species, sensu Sanders, Malhotra, and Thorpe (unpublished): THAILAND: Nakhon Si Thammarat Province: AFS97B.13, m, AY371796; AFS98.1, m, AY371804; AFS96.18, ?, AF171904; AFS96.19, ?, AF171904; PSGV 34, m; PSGV 223, m. Krabi Province: QSMI (unnumbered), f; QSMI (unnumbered), m; QSMI 13.1, m; QSMI 13.2, m; QSMI 17, m; QSMI 7, m; QSMI 50.1, f; QSMI 50.2, f; QSMI 50.3, f. MALAYSIA (WEST): Belum: ZRC 2.5361, m. Bukit Fraser: AFS02.07*, ?, AY371817; KLS00.001, f, AY059570; PH (unnumbered), m; KLS01.61*, m, AY371821; ZRC 2.2889, m; ZRC 2.2891, m; ZRC 2.2892,

f. Pulau Penang: KLS01.103, m. Pulau Tioman: BMNH (MLD 2007), f; ZRC 2.3493, m; Pulau Tioman: Tekek-Juara trail: LSUHC 4809, m. Ulu Trengganu: Gunung Lawit: East Ridge: BMNH 1974.4995, m, BMNH 1974.4997, f, Summit Ridge: BMNH 1974.4999, f, BMNH 1974.5000, m. Pahang: Gunung Benom: Nr. Camp IV: BMNH 1967.2289, f. MALAYSIA (EAST): Sabah: Kinabalu: KLS01.104, f; KLS01.114, m, AY371802; KLS01.116, f, AY371803; KLS01.117, m; KLS01.122, f; KLS01.121, f, AY371815; KLS01.106*, ?, AY371798; NMBA 21026, m; NMBA 21026, m; Pendalaman Div.: Sipitang Dist.: Mendolong: FMNH 233155, f, Mendolong, km 14.3: FMNH 243942, f; Luidan river, near Kian, Borneo: MCZ 43612, m, MCZ 43614, f. INDONESIA (SUMATRA): Battak Mts.: NMBE 210a + b, mm. West Sumatra: Bungar-Bondar: SMF 21226, m. Bengkulu Province: KLS02.06*, f, AY371801. Sumatera Barat Province: Padang, West-Sumatra: NMW 23910:2 + 4, mm; NMW 23910:3 + 5, ff; NMW 23917:1 - 2 + 4 - 6 + 9, mm; NMW 23917:3 + 7 - 8 + 10, ff; Pagay [Pulau Pagai, Mentawai Islands]: NMW 23910:1, f.

Popeia inornata: MALAYSIA (WEST): Pahang: Cameron Highlands: AFS93.1*, ?, AY371808; AFS93.2*, ?, AF171888; ZMB 66281, m, AJ627391; ZRC 2.2884, f; Cameron Highlands: Gunung Brinchang: AFS00.12, f, AY371812; AFS00.13, m, AY371819; AFS00.14, f, AY371813; AFS00.15, f, AY371814; road to Gunung Brinchang: BMNH 2003.1*, f, AJ627389; Cameron Highlands: Parit (or Porit) Falls: KLS01-128*, f, AY371811; ZRC 2.5164, f; Cameron Highlands, Tanah Rata: CAS-SU 8863, f; ZRC 2.2886, f; Tanah Rata, Bala's Holiday Chalets: SMF 82934*, f, AJ627390; Tanah Rata, on trail 7, 8, or 9: JAM 1968*, m, AJ627392.

APPENDIX II

Characters Measured for Morphometric Analyses

Scalation

VSC, Number of ventral scales; SCS, Number of pairs of subcaudal scales; BSCK, Keeling of body scales at midbody (recorded as 0 = none; 0.5 = weak; 1 = strong); SUPLAB, Number of supralabial scales (average of left and right hand sides); SUBLAB, Number of infralabial scales (average of left and right hand sides); BORSUPOC, Number of scales bordering the supraocular scales, excluding the preoculars and

postoculars; BTWSUPOC1, Minimum number of intersupraocular scales; BTWSUPOC2, Maximum number of intersupraocular scales; NASPIT, Number of scales between nasal scale and prelacunal; INTNAS, Number of internasal scales; LAB3, Minimum number of scales separating third supralabial and subocular scale; LAB4, Minimum number of scales separating fourth supralabial and subocular scale; LAB5, Minimum number of scales separating fifth supralabial and subocular scale; SOCBORD, Minimum number of scales bordering suboculars, excluding the preoculars and postoculars; GULAR, Number of scales between first ventral and anterior chinshields; VENTEDGE, Number of scales between the edge of the mouth and first ventral scale, including last infralabial.

Scale Reduction Formula

This is recorded as a series of characters, each referring to a specific reduction. Each position of the reduction has two characters, the dorsoventral (DV) position of the reduction (the lowest of the two merging scale rows), and the ventral scale (VS) position (counted from the head), which is the ventral scale to which the scale reduction traces diagonally. Before analysis, the VS position was transformed into the percentage of the total number of ventral scales (%VS) to control for variation. (Subcaudal scale position: SC).

VS25to23, ventral scale position of the reduction from 25 to 23 scale rows; DV25to23, dorsoventral position of the reduction from 25 to 23 scale rows. Then VS23to21, DV23to21, VS21to19, DV21to19, VS19to17, DV19to17, VS17to15, DV17to15, SC12to10, DV12to10, SC10to8, DV10to8, SC8to6, DV8to6, SC6to4, DV6to4.

Color Pattern

STRIPE, Presence of stripe on dorsal scale row one (recorded as 0 = absent; 1 = indistinct; 2 = distinct); SCRSTR, Number of scale rows involved in stripe; OCSTRIPE, Presence of postocular stripe (recorded as 0 = absent; 1 = indistinct; 2 = distinct); SCROC, Number of scale rows involved in postocular stripe; LIPCOL, Number of scales above lip covered by ventral color; DORSPOT, Number of spots on the dorsal surface; SPOTSIZE, Mean number of scales covered by the three largest dorsal spots; SCR1, Proportion of the first scale row covered by the light area.