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Two new species of pitviper of the genus *Cryptelytrops* Cope 1860 (Squamata: Viperidae: Crotalinae) from Southeast Asia

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Abstract

We describe two new species of green pitviper from Southeast Asia that are morphologically similar to *Cryptelytrops macrops,* but can be distinguished from that species by genetic means, multivariate analysis of morphology and some aspects of coloration. *Cryptelytrops cardamomensis* **sp. nov**., is described from southeastern Thailand and the Cardamom Mountains of southwestern Cambodia. *Cryptelytrops rubeus* **sp. nov**. has been recorded from southern Vietnam and eastern Cambodia. These species have previously been confused with *C. macrops,* hence we also present here a redescription of this species, whose range is now restricted to Thailand, southern and central Laos, and northeastern Cambodia. All three species are present in Cambodia, but have disjunct ranges corresponding to three separate highland regions in southwestern (Cardamom Mountains), northeastern (western edge of the Kontum Plateau) and eastern (low elevation hills on the western edge of the Langbian Plateau) Cambodia for *C. cardamomensis*, *C. macrops* and *C. rubeus* respectively. However, there is still considerable morphological variation between geographically separated populations of *C. macrops s.s.,* and greater sampling in southern and northern Thailand in particular may be required before the species diversity of this group is fully clarified.

Key words: *Cryptelytrops cardamomensis* **sp. nov**., *Cryptelytrops macrops*, *Cryptelytrops rubeus* **sp. nov.**, green pitviper, multivariate morphometric analysis, *Trimeresurus*

Introduction

Recently, molecular work has helped to resolve some particularly vexing taxonomic issues among the green pitvipers, formerly all included in the genus *Trimeresurus,* but since 2004 placed in seven distinct genera (Malhotra & Thorpe 2004a). A growing interest in these beautiful animals among herpetoculturists and the increased opportunity to travel in Southeast Asia has led to a better understanding of species distribution and variation (Gumprecht *et al.* 2004). Using both traditional morphology-based systematics and more modern approaches combining molecular and multivariate analyses, a number of cryptic species have been recently identified among Asian pitvipers (David *et al*. 2006; Malhotra & Thorpe 2004b; Sanders *et al.* 2006). Specimens obtained during recent herpetological surveys in Laos, Cambodia and Vietnam (Stuart 1999; Stuart *et al*. 2006a Stuart & Emmett 2006; Stuart *et al.* 2010), have helped to shed light on the taxonomy of another of the green pitvipers, *Cryptelytrops macrops.* Though superficially resembling *C. albolabris*, this species has in fact been shown to be closely related to two banded and narrowly distributed species, *C. venustus* and *C. kanburiensis* (Malhotra & Thorpe 2004a) and in more recent analyses including nuclear as well as mitochondrial sequence data (Malhotra *et al.* 2010), some specimens of *C. macrops* appeared to be paraphyletic with respect to *C. venustus.*

More extensive geographical sampling has made it possible to distinguish at least three genetically distinct units within the specimens currently referred to *C. macrops,* using both mitochondrial (12S and 16S rRNA, NADH4) and nuclear loci (298 AFLP markers) (Mrinalini *et al*., unpublished data). These genetically distinct units are also geographically separated (Fig. 1). Here, we present an analysis of morphological variation among specimens currently referred to *C. macrops,* identify diagnostic differences between genetically distinct OTUs, formally

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describe two new species, redescribe the holotype of *C. macrops s.s.* and recharacterize this species based on the additional material collected since the original description (Kramer 1977).

Material and methods

During the period 1999–2003, specimens were collected in Laos and Cambodia by one of us (BLS) and preserved in 10% buffered formalin. Specimens were deposited at The Field Museum, Chicago (FMNH) several months after preservation, and were transferred to 70% ethanol upon arrival there. Living specimens were also obtained in Lampang Province (1996, AM), Chantaburi Province (1998, AM and RST), and Nakhon Ratchasima Province (1999, AM) in Thailand, and in southern Vietnam (1998, AM). Morphometric measurements and macro photographs were taken while the specimens were under anaesthesia, and they were later released (as required by the conditions of permission). The latter procedure was also followed in 1998 for specimens housed at the Queen Savoabha Memorial Institute that were obtained from the region surrounding Bangkok and putatively from southern Thailand from where the species has not previously been recorded. Additional specimens were also donated by K. Udomritthiruj and G. Vogel.

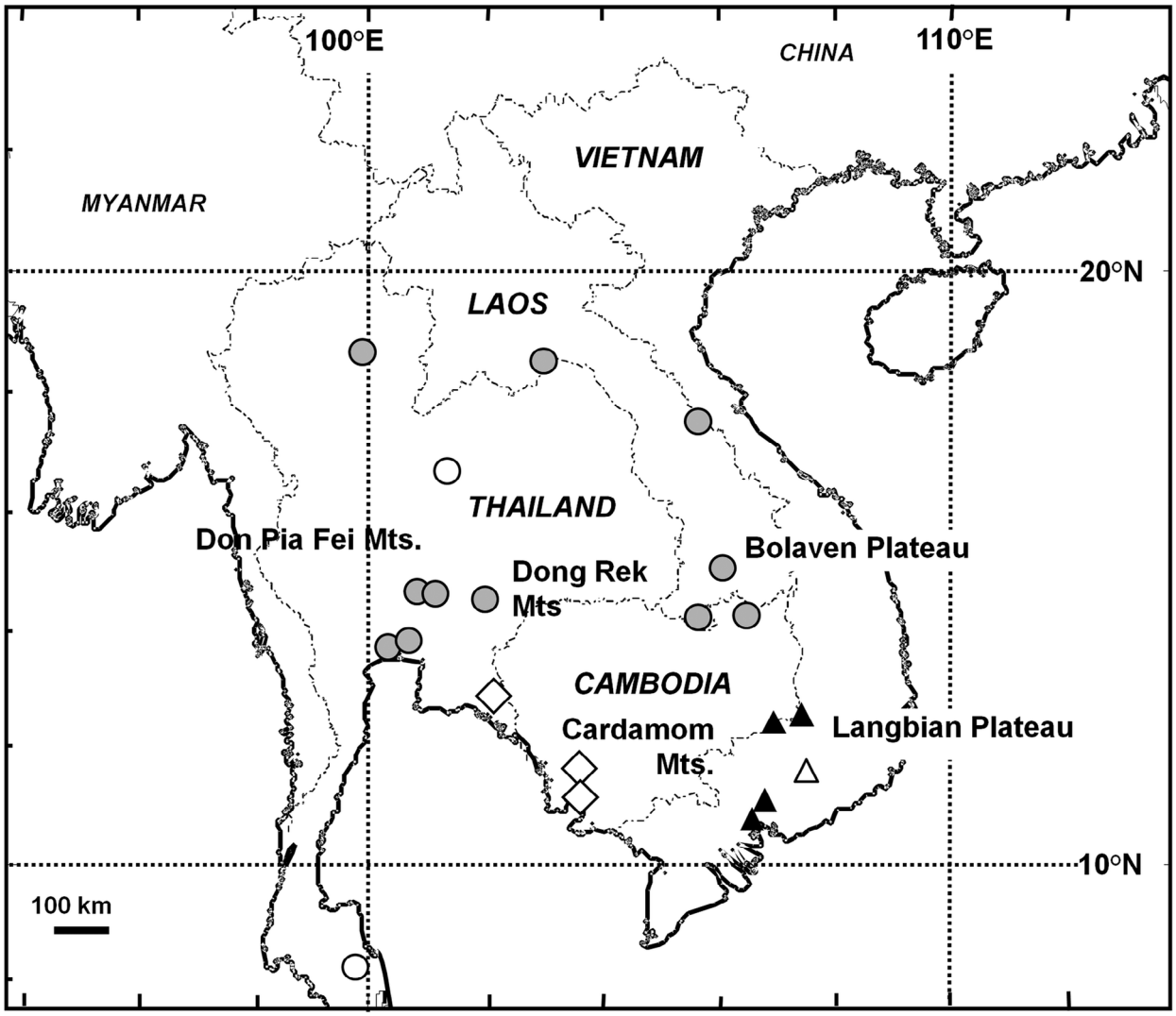

FIGURE 1. Map of Southeast Asia, showing the distribution of the two new species and *Cryptelytrops macrops s.s*. Symbols indicate sampling localities used in the genetic analysis to define species. Grey circles: *C. macrops s.s*; open diamonds: *C. cardamomensis* **sp. nov.**; black triangles: *C. rubeus* **sp. nov.** The empty circle and triangle denotes localities of specimens that have either been referred to the corresponding species on the basis of photographs, or for which the locality is uncertain and requires confirmation.

Additionally, we examined material referred to *C. macrops* in the holdings of the Natural History Museum, London (BMNH), The Field Museum, Chicago (FMNH), Muséum d'Histoire Naturelle de la ville de Geneve (MHNG), Naturhistorisches Museum Basel (NMBA), and Naturhistorisches Museum Wien (NMW). Morphometric and meristic characters were measured as described in Malhotra & Thorpe (2004b). We analyzed external characters in order to maximise sample sizes and because the most useful diagnostic characters are external. We performed a canonical variate analysis (CVA) of morphological characters, using the putative species as groups (sexes were analyzed separately) in order to provide diagnostic characters among the three species. Analysis of variance and covariance (ANOVA/ ANCOVA) was used to identify characters showing significant among-OTU variation. Characters that were not significantly different between species were excluded from subsequent analyses. A list of characters used can be found in Appendix 1.

It was noted that some characters (particularly colour pattern characters) showed some heteroscedascity, which may perturb CVA. Although this should be apparent in the results (e.g., if heteroscedastic characters dominate the axes), the presence of potential perturbation due to heteroscedascity was also checked by carrying out a principal component analysis (PCA) on individuals (i.e., not assigned to groups). This has much less discriminatory power, but is less affected by departures from the assumptions of the model of homoscedascity (Thorpe 1976, 1983) and also allows any misallocation of specimens to groups to be checked. All size–related characters used in the PCA were first adjusted to a common size using the pooled within–group regression slope, with either snout–vent length (SVL) or head length (LHEAD) as the covariate.

Results

Sample sizes are given in Table 1. PCA and CVA results were similar, with no apparent misgrouping or deleterious effect arising from heteroscedascity in the CVAs (Thorpe 1976, 1983), hence only the CVA results are given (Fig. 2). The CVA discriminated among the three putative species with 100% success in both sexes. CV1 in males (72.8% of variance) discriminates among all species while specimens from the Cardamom mountains of Cambodia and adjacent areas of Thailand are further separated on CV2 (53% of variance). In females, CV1 (53% of variance) mainly distinguishes the OTU from the Cardamom mountains and adjacent areas of Thailand, while CV2 (47% of variance) further distinguishes the OTU from eastern Cambodia and southern Vietnam from the remaining group which corresponds to *C. macrops* s.s. Tables 2 and 3 give lists of characters that contribute to the discrimination of the new species and C. *macrops s.s*, as well as their mean value and standard deviations, drawn from the among-species CVA.

We next provide a detailed description of the two new species defined by the above analyses. Since considerable geographic variation within *C. macrops s.s*. was also found, and many specimens included were from new localities outside the range considered in the original description of this species, we also provide a redescription of *C. macrops s.s.*

TABLE 1. Sample sizes for each sex of the three species in the multivariate analyses.

C. macrops s.s.		*C. cardamomensis*		*C. rubeus*	
M	F	M	F	M	F
26	20	2	2	6	5

***Cryptelytrops cardamomensis* sp. nov.** (Cardamom Mountains Green Pitviper)
Figs. 3, 4; Tables 1, 2.

Trimeresurus macrops Kramer 1977: Kramer (1977): 757 (part); Regenass and Kramer (1981):184 (part); Gumprecht (1998): 25 (part); Orlov *et al*. (2002a): 193 (part); Orlov *et al*. (2002b): 353 (part); Gumprecht *et al*. (2004): 230 (part).

Cryptelytrops macrops (Kramer 1977): Stuart and Emmett (2006): 23; Grismer *et al*. (2007): 232; Grismer *et al*. (2008a): 24; Grismer *et al*. (2008b): 166.

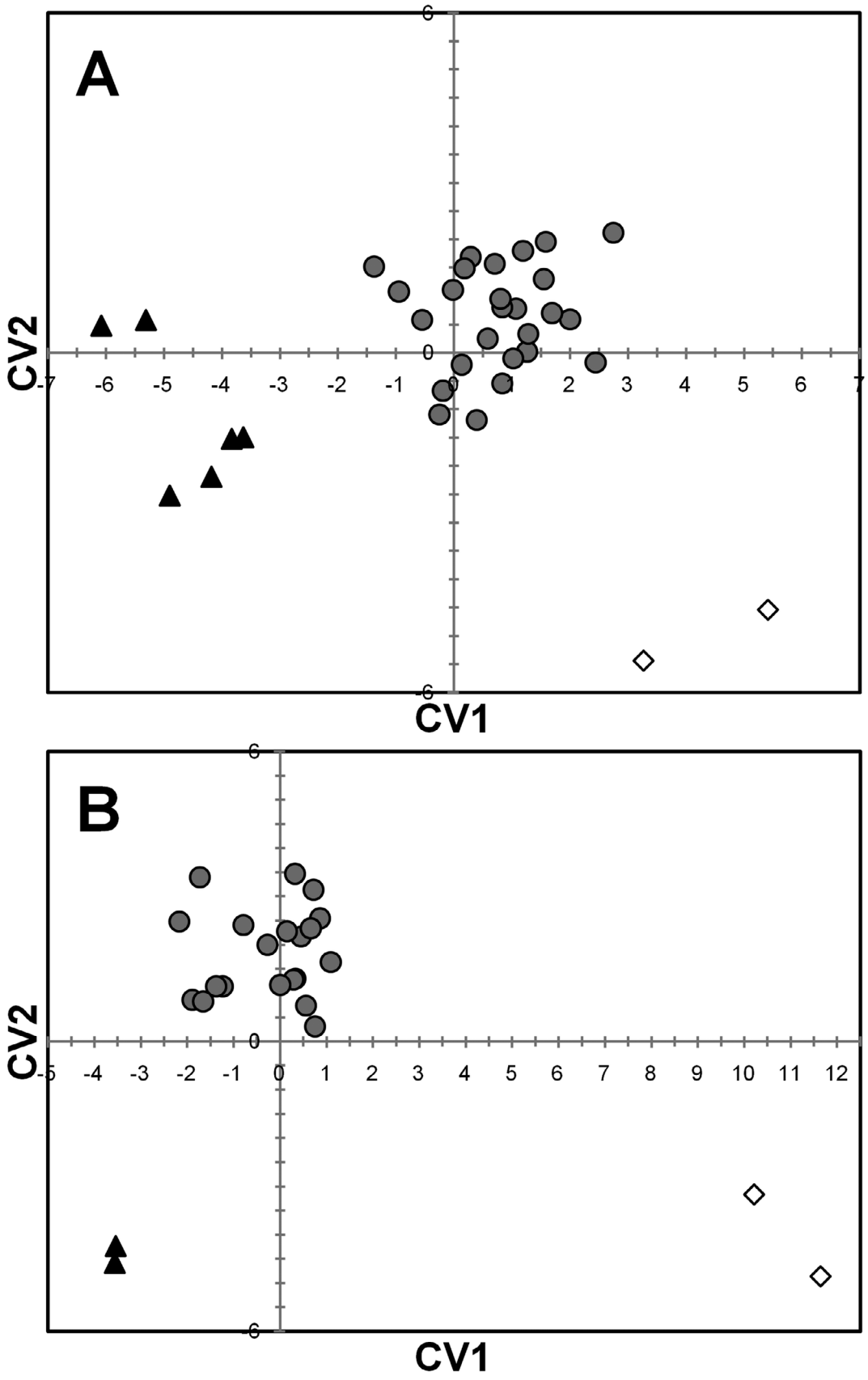

FIGURE 2. Canonical variate plot showing the success of multivariate morphometrics in discriminating the new species (symbols are as given in Fig. 1). Colour pattern and internal characters provide additional resolution, but could not be included in this analysis as they could not be recorded in all specimens. A. Males, B. Females.

Holotype. FMNH 259191, adult female, collected on a root of a strangler fig growing from a tree trunk 1 m above the ground in semi-evergreen forest on Phnom Chan Mountain, Cardamom Mountains, Sre Ambel District, Koh Kong Province, Cambodia (11.44 N, 103.79 E), 100–200 m elevation, on 25 August 2000 by BLS and S. Platt.

Paratype. FMNH 259192, an adult male, collected at 2000 hrs swimming mid–stream in the Prek Kroch River (tributary of the Prek Sre Ambel River) in melaleuca/mangrove coastal swamp forest, Sre Ambel District, Koh Kong Province, Cambodia (11.105 N, 103.659 E), <10 m elevation, on 27 August 2000 by BLS and S. Platt.

Referred material. FMNH 263387, female, collected on bamboo 0.5 m above the ground, 1 m from a small stream in hill evergreen forest, Central Cardamoms Protected Forest, Thmar Baing District, Koh Kong Province, Cambodia (11.67 E 103.71 N), 800 m elevation, on 1 March 2004 by D. Emmett. FMNH 267732, female, collected at 2000 hrs on a tree trunk 0.5 m above the ground, 10 m from a river, in seasonally flooded lowland evergreen forest, Central Cardamoms Protected Forest, Thmar Baing District, Koh Kong Province, Cambodia (11.63 N, 103.5 E), 180 m elevation, on 24 August 2004 by D. Emmett.

Additional material. Two live specimens, an adult male and female, collected at 2215 hrs in low vegetation by the fourth tier of Krathing Waterfall, Khao Kitchakut National Park, Chantaburi Province, Thailand (12.80 N 102.13 E), 75 m elevation, on 11 November 1998, by AM and RST. Data from these living specimens has been used in all analyses, but under the conditions of permission, these specimens could not be preserved as vouchers and were released at the site of capture.

Diagnosis. *Cryptelytrops cardamomensis* **sp. nov.** is distinguished from *C. venustus*, *C. honsonensis* and *C. kanburiensis*, by the absence of purple-red marking (banding on the body and blotches on the head). It is distinguished from all other Asian pitviper species which have the typical "green pitviper" colouration (uniform green dorsal colour and a lateral stripe present on the first few dorsal scale rows in one or both sexes), except other species of *Cryptelytrops* (including *C. albolabris, C. insularis* and *C. septentrionalis*), by the presence of a fused first supralabial and nasal scale. It can be distinguished from *C. albolabris, C. insularis* and *C. septentrionalis* primarily by the relatively larger size of the eye (most obvious in adults), the relatively wider supraoculars, and the shape of the head. The latter is more elongate–oval in *C. albolabris, C. insularis* and *C. septentrionalis*, but widens quite abruptly behind the eyes in *C. cardamomensis, C. macrops s.s.* and *C. rubeus* **sp. nov.** (described below) to give a characteristically triangular shaped head. *Cryptelytrops cardamomensis* can be distinguished from both *C. macrops s.s.* and *C. rubeus* using a combination of the following characters (for further details see Table 2). In males, *C. cardamomensis* tends to have more scales between the rear edges of the supraoculars (BTWSUPOC2), a relatively larger eye (DEYE), and a more prominent postocular white stripe (SCROC) than either *C. macrops s.s*, or *C. rubeus*. Furthermore, compared to *C. macrops s.s*, the scale reduction from 19 to 17 scale rows around the body (VS19TO17) tends to occur further away from the head, it tends to have fewer (larger) scales bordering the supralabial scales (BORSUPOC), and less keeled temporal scales (KTEMP). Compared to *C. rubeus*, the scale reduction from 19 to 17 scale rows around the body tends to involve higher (i.e., more dorsal) scale rows (DV19TO17); it tends to have more keeled body scales at mid-body (BSCK), and more scales between the last supralabial and the chin shields (VENTEDGE). In females, the lateral white stripe is much more prominent (STRIPE), always involving the first two dorsal scale rows. Furthermore, it tends to cover a larger proportion of the first scale row (SCR1) than in females of *C. macrops s.s*. A small scale is present between the nasal scale and the scale bordering the anterior edge of the pit (NASPIT), whereas this is infrequently present in *C. macrops s.s.* and never present in *C. rubeus. Crytpelytrops cardamomensis* tends to have more (smaller) scales bordering the supralabial scales (BORSUPOC) than *C. rubeus*, but fewer (larger) than in *C. macrops s.s*. The scale reduction from 19 to 17 scale rows around the body (DV19TO17) tends to involve lower scale rows in *C. cardamomensis* and the fusion between the first labial and nasal scale tends to be more complete (LABNAS) and involve partial sutures on both sides of the nostril (compare Figs. 3, 5 and 7), than in either *C. macrops s.s*, or *C. rubeus*. Furthermore, compared to *C. macrops s.s*, , the scale reduction from 19 to 17 scale rows around the body (VS19TO17) tends to occur further away from the head, it tends to have more scales between the rear edges of the supraoculars (BTWSUPOC2), a higher number of sublabial scales (SUBLAB), and a relatively smaller eye (DEYE). Compared to *C. rubeus*, it has more keeled body scales at mid-body (BSCK), the scale reduction from 12 to 10 scale rows around the tail (SC12O10) also tends to occur further away from the vent, and there are a larger number of ventral scales in *C. cardamomensis* females than in *C. rubeus* females.

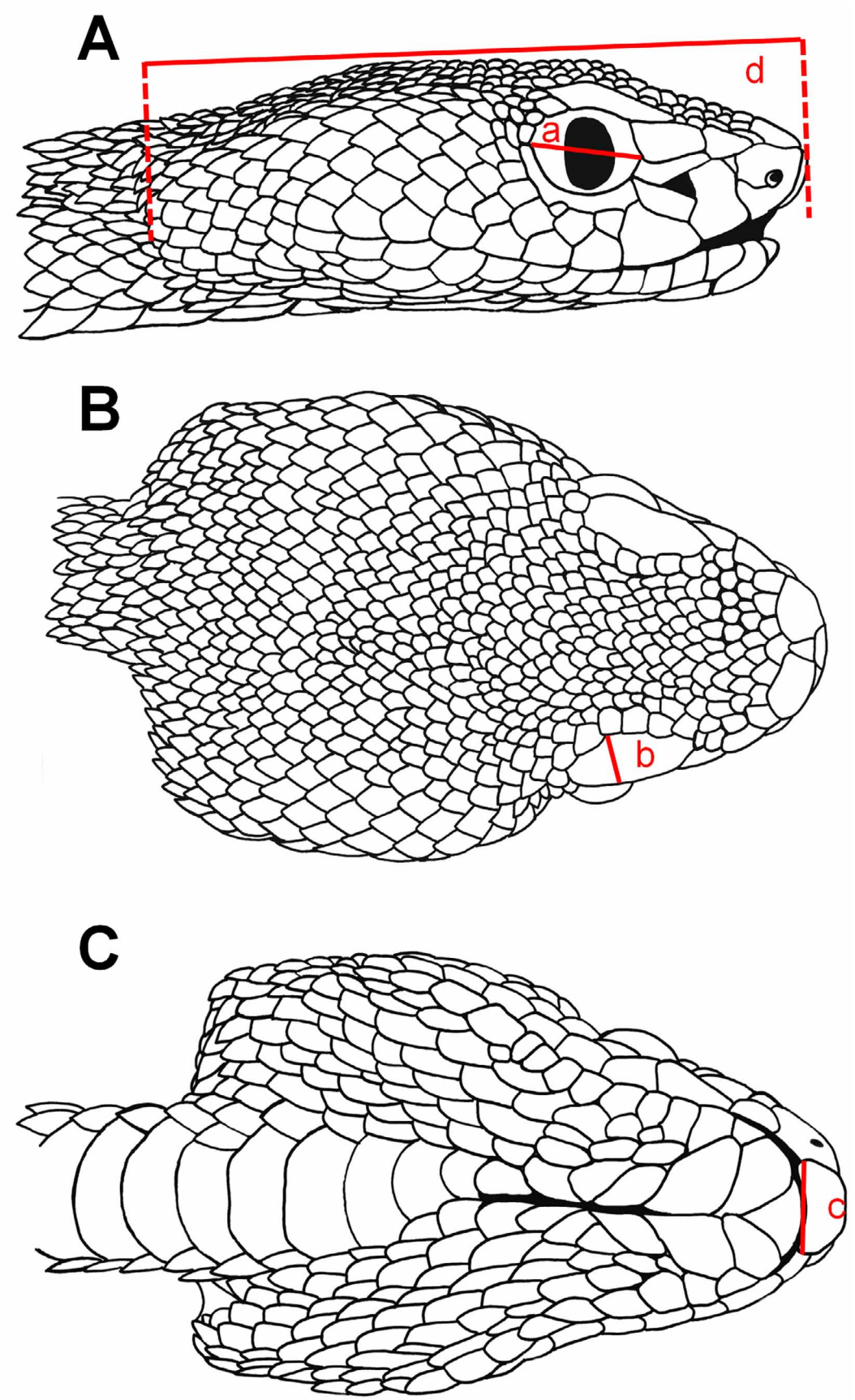

FIGURE 3. Line drawings of the head scalation of the holotype of *Cryptelytrops cardamomensis* **sp. nov.** (FMNH 259191) A. lateral, B. dorsal, C. ventral. Small letters identify the following measurements: a (eye width): 3.3mm , b (supraocular width): 1.55mm, c (bottom edge of rostral): 2.5mm, d: (head length): 18.75 mm.

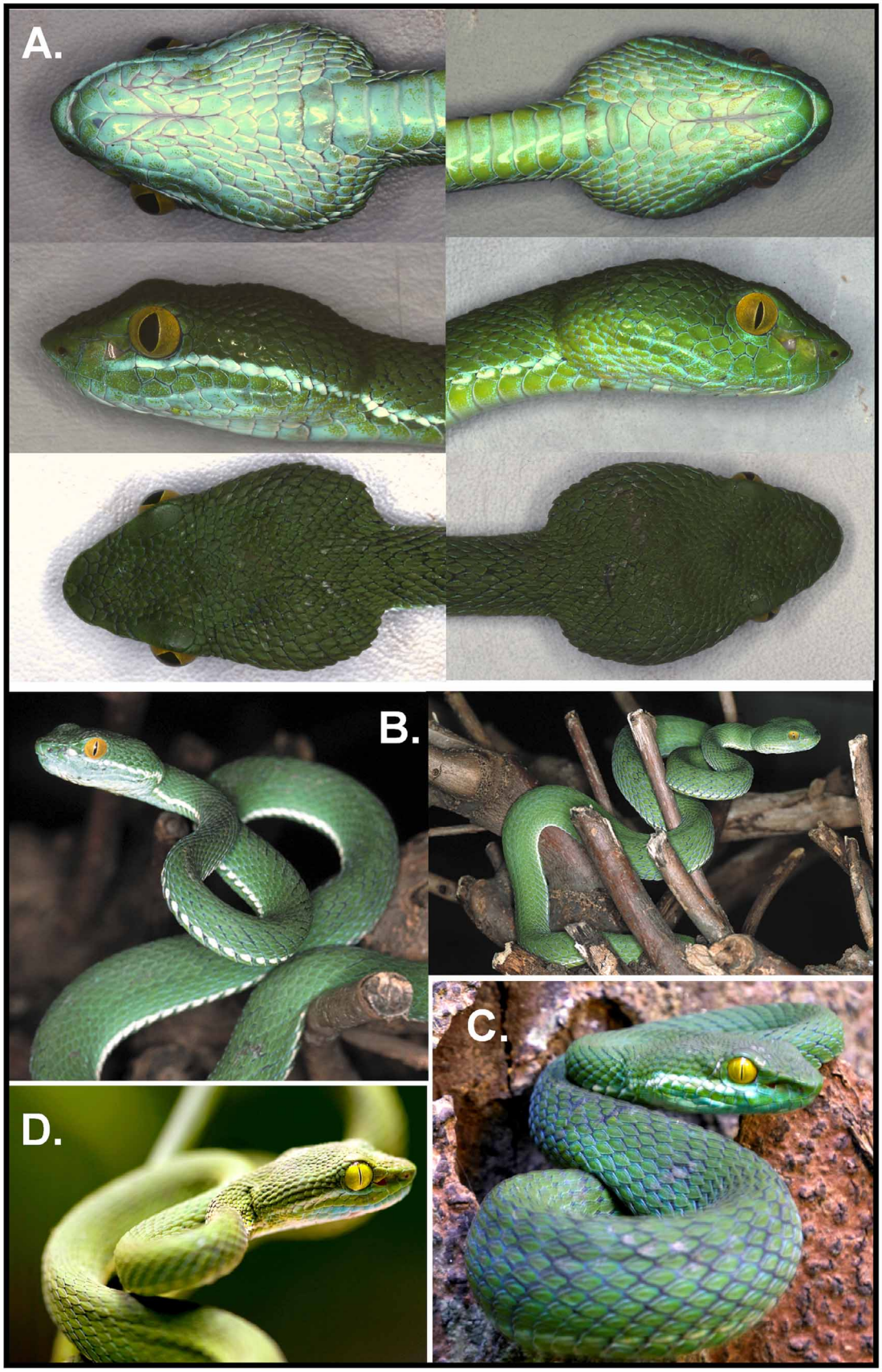

FIGURE 4. *Cryptelytrops cardamomensis* sp.nov. A. Close-up of head and mid-body region of adult male (left) and female (right) from Khao Kitchakut National Park, Chantaburi Prov., Thailand (photos: A Malhotra). B. Adult male (left) and female (right) from Kâmpóng Saôm Bay, Koh Kong Prov., Cambodia (photos: A Gumprecht); C. and D. Adult specimens from Mount Da Lai in Cardamom Mountains, southwest Cambodia (photos: Jeremy Holden).

Description of holotype. Body cylindrical, head triangular in dorsal aspect and very distinct from neck. Canthus rostralis distinct**.** Head scales small (no large dorsal shields), smooth except in temporal region, region between the suprabials and temporal region, and on the rear of head, which show weak tubercular keeling. Dorsal body scales weakly keeled. 171 ventral scales, 63 pairs subcaudal scales, 21 dorsal scales at mid–body. Rostral scale roughly triangular, upper edge about half the width of lower edge**.** Pupil vertically elliptical. Loreal pit present. Nostril completely enclosed in nasal scale. Nasal scale partially fused with first supralabial, bearing a suture present behind the nostril, but not anterior to it. Ten and 11 supralabials on the right and left sides respectively, similarly 13/12 sublabials, three postocular scales. Shield bordering anterior edge of pit fused with second supralabial, but separated from nasal by one small scale on either side. Subocular scale touches third supralabial, but separated by one scale from fourth and fifth supralabials. At least 11 scales between supraoculars, with 14 scales between their posterior edges. Five teeth on palatine, 16 on pterygoid, and 16 on dentary. Snout–vent length 29.1 cm; tail length 5.6 cm. Head length measured from tip of snout to posterior edge of lower jawbone 18.75 mm; head width measured between rear outer edges of supraoculars 8.3 mm, and at widest point of head 12.9 mm. Supraocular scale (on right hand side) 3.9 mm long, 1.55 mm wide. Distance from eye to nostril 3.85 mm, eye to pit 0.9 mm, posterior edge of pit to anterior edge of nostril 3.6 mm. Eye diameter 3.3 mm. Scale reduction formula (derived as in Thorpe [1975]):

31	5+6 (9)	29	14+15 (14)	27	7+8 (12)	25	6+7 (17)	23	4+5 (24)	21	4+5 (110)	19	3+4 (117)	17	4+5 (128)	15
	6+7 (9)		14+15 (14)		7+8 (13)		7+8 (18)		4+5 (24)		4+5 (111)		4+5 (120)		4+5 (131)	

Colour of holotype in preservative. Dark brownish grey dorsally, the ventral surface somewhat paler than the dorsal surface towards anterior of body, but less distinct posteriorly. Pale lateral stripe well developed, covering approximately one–third of first dorsal scale row, increasing in width towards head. Upper and lower labials not distinct in colour from the rest of the head, but chin shields, scales between chin shields and sublabial scales are creamy white.

Colour in life (Fig. 4). No notes or photographs were taken of the holotype in life. This description is based on photographs of the male and female specimens from Khao Kitchakut NP, Thailand as well as photographs on p. 230 Plate II and p. 232 Plate I (adult male from Khao Soi Dao wildlife sanctuary, Chantaburi Province), and p. 233 Plate II, and p. 235 Pl II (adult male and female respectively, from Koh Kong Province, Cambodia) of Gumprecht *et al*. (2004). Dorsal and ventral surface grass green, very similar in shade. Lateral white stripe more prominent in male, extending onto the second dorsal scale row (confined to the first in female). In female, obvious bright blue dot on the upper rear quadrant of first scale row; present in some males, but less obvious. In male only, lateral white stripe extends onto the head as postocular stripe. Upper lip slightly paler than rest of dorsal surface of head, more obvious in female. Sublabials, and to lesser extent supralabials, also suffused with pale blue, mostly confined to edges of scales. Same pale blue also covers most scales on ventral surface of head to first part of body, more saturated and extensive on underside of head than in *C. macrops* s.s. Occasional small patches of white and green pigment on scales of underside of head. Interstitial skin bright blue, black banding sometimes on anterior body, scales here have narrow edging of black pigment at base. Tail solid brick red, to vent on dorsal surface, approximately one-third (male) to half (female) distance to the vent on ventral surface. Eye golden yellow in both sexes.

Variation. Sexual dimorphism is not very obvious in coloration. Females never have postocular stripes, but they may be only indistinct white streaks in males. The lateral white stripe may be much more prominent in males. Females have relatively shorter tails and fewer subcaudals (58–63 in females, versus 69 in the single male in which this count could be made). Females also are likely to reach an overall larger size (maximum recorded 53.6 cm SVL versus 49.9 cm for males), but the sample is small. The number of ventral scales is similar in both sexes, varying between 169 and 173. Keeling of body scales at mid–body is usually strong. Temporal scales and scales in the region between the temporal scales and supralabials show weak tubercular keeling, and keeling is strong on the scales covering the rear of the head. The ratio between the lengths of the upper and lower edges of the rostral scale varies between 0.35 and 0.56. Supralabials vary between 10 and 11 and sublabials between 11 and 14. The suture between the nasal scale and first labial scale is always more extensive to the rear of the nostril, usually absent in front of the nostril, but there may be a slight kink in the anterior margin of the fused scale at the likely position. The minimum number of scales between supraoculars varies between 8–12 and there are 13–16 scales between the posterior edges of the supraoculars. The number of scales between the nasals and shield bordering the anterior of the

pit varies between 0–2, and there are 0–1 scales separating the internasals. There are 0–1 scales between the third supralabial and the subocular, one scale between the fourth supralabial, and 1–2 scales between the fifth supralabial and the subocular scale. Hemipenes were examined in FMNH 259192, in which they were both partly everted, and do not differ notably from those of *C. macrops s.s*. Teeth were also counted in this specimen, and were identical to the holotype except for the number of pterygoid teeth, which numbered 14.

Distribution. *Cryptelytrops cardamomensis* is currently known from Koh Kong Province in southwestern Cambodia and Chantaburi Province in southeastern Thailand. (Fig. 1). The species probably occurs in appropriate habitat throughout the Cardamom Mountains in southwestern Cambodia and adjacent southeastern Thailand, and offshore islands (e.g., Koh Chang).

Ecology. *Cryptelytrops cardamomensis* is currently known from low-lying coastal areas up to 800 m elevation in semi-evergreen, evergreen, and mangrove/melaleuca swamp forest. All specimens were found within a couple of metres above the ground, and most within 10 m of water. No food items were found in the digestive tracts of the types.

Etymology. The name refers to the mountain range wherein the type locality of this species occurs.

***Cryptelytrops rubeus* sp. nov**. (Ruby-eyed Green Pitviper)
Fig. 5, 6; Tables 1–3

Trimeresurus macrops Kramer 1977*:* Kramer (1977): 757 (part); Regenass and Kramer (1981): 184 (part); Orlov *et al*. (2002a): 193 (part); Orlov *et al*. (2002b): 353 (part); Stuart *et al*. (2006a): 152.
Trimeresurus cf. *macrops* Kramer 1977: Gumprecht *et al*. (2004): 236.

Material examined. Cambodia, Mondolkiri Province, Seima Biodiversity Conservation Area, FMNH 262717–21. Vietnam, southern part of country (no precise locality), BMNH 2005.1602. Vietnam, Ho Chi Minh City, NMBA 12461. Vietnam, Cu Chi and Bien Hoa, AFS98.53–55.

Holotype. FMNH 262718, adult female, collected at 1820 hrs on an herbaceous plant 1 m from the O Kamen Stream in hilly evergreen forest, Seima Biodiversity Conservation Area (formerly part of Samling Logging Concession), O'Rang District, Mondolkiri Province, Cambodia (12.326 N, 107. 092 E), 500 m elevation, on 1 November 2003 by BLS, K. Sok, and T. Neang.

Paratypes. FMNH 262717, 262719–262721 (all males, collected from near the type locality in hilly evergreen forest between 450–500 m elevation, near streams between 1–6 November 2003); FMNH 259190 (female, Phnom Nam Lyr Wildlife Sanctuary, Mondolkiri Province, Cambodia); BMNH 2005.1602 (female, from an unknown location in southern Vietnam); NMBA 12461 (Saigon, southern Vietnam).

Additional material. Data for several specimens obtained from dealers in the vicinity of Ho Chi Minh City, southern Vietnam are included in all analyses. The specimens were stated to originate from Cu Chi (10.75 N, 106.67 E) and Bien Hoa (10.95 N, 106.82 E). These specimens were left in the care of Dr T-X. Kiem (Cho–Ray Hospital, Vietnam).

Diagnosis. *Cryptelytrops rubeus* is distinguished from all other Asian pitviper species which have the typical "green pitviper" colouration (uniform green dorsal colour and a lateral stripe present on the first few dorsal scale rows in one or both sexes), except other species of *Cryptelytrops*, by the presence of a fused first supralabial and nasal scale. It can be distinguished from *C. albolabris, C. insularis* and *C. septentrionalis* primarily by the larger size of the eye (most obvious in adults), the wider supraoculars, and the shape of the head. The latter is more elongate–oval in *C. albolabris, C. insularis* and *C. septentrionalis*, but widens quite abruptly behind the eyes in *C. cardamomensis, C. macrops s.s.* and *C. rubeus* to give the latter a characteristically triangular shaped head. *Cryptelytrops rubeus* can be distinguished from *C. cardamomensis* sp.nov. (described above) using the combination of the following characters (further details are given in Table 2). In males, *C. rubeus* tends to have fewer scales between the rear edges of the supraoculars (BTWSUPOC2), a relatively smaller eye (DEYE), and a less prominent postocular white stripe (SCROC). The scale reduction from 19 to 17 dorsal scale rows (DV19TO17) tends to involve lower scale rows, it tends to have less keeled body scales at mid-body (BSCK), and fewer scales between the last supralabial and the chin shields (VENTEDGE). In females, the scale reduction from 19 to 17 dorsal scale rows (DV19TO17) tends to involve higher scale rows in *C. rubeus* than in *C. cardamomensis*, it has a relatively shorter head (LHEAD), a small scale is never present between the nasal scale and the scale bordering the anterior

edge of the pit (NASPIT), the lateral white stripe covers a larger proportion of the first dorsal scale row (SCR1), it tends to have fewer (larger) scales bordering the supralabial scales (BORSUPOC), and less keeled body scales at mid-body (BSCK). The scale reduction from 12 to 10 scale rows around the tail (SC12O10) also tends to occur closer to the vent in females of *C. cardamomensis* than *C. rubeus* and they also have relatively smaller eyes (DEYE).

TABLE 2. Mean values and standard deviations of morphological characters that in combination can be used to distinguish *C. cardamomensis* **sp. nov.** from both *C. macrops s.s.* and *C. rubeus* **sp. nov.** Observed values have a 95% probability of falling within ± 1.96 x SD of the mean, hence this is a more useful measure than the range. LHEAD is adjusted to the grand mean size of SVL (48.72 cm) in females and DEYE to the grand mean size of LHEAD (22.45, 25.45 mm) in males and females respectively. Cm = *C. macrops s.s.*, Cc = *C. cardamomensis*, Cr = *C. rubeus*. Character abbreviations are explained in Appendix 1. Entries in bold identify the taxa which that character helps to discriminate from *C. cardamomensis* (e.g. BTWSUPOC can be used to discriminate both *C. macrops* and *C. rubeus* from *C. cardamomensis* while DV19to17 is only useful to discriminate *C. rubeus* from *C. cardamomensis*).

Character	Cm	Cc	Cr
Males			
BTWSUPOC2	11.96 (±1.22)	14.50 (±2.12)	10.17 (±1.94)
DV19TO17	4.29 (±0.43)	4.25 (±1.06)	3.92 (±0.38)
BSCK	0.80 (±0.25)	1.00 (±0.00)	0.38 (±0.21)
VENTEDGE	7.46 (±0.45)	7.50 (±0.71)	6.92 (±0.49)
DEYE	4.03 (±0.36)	4.46 (±0.13)	4.08 (± 0.19)
SCROC	0.69 (±0.93)	2.00 (±0.00)	0.33 (±0.82)
BORSUPOC	9.65 (±0.90)	8.75 (±0.35)	8.58 (± 0.97)
VS19TO17	68.00 (±1.99)	69.29 (±2.16)	69.29 (±1.53)
KTEMP	0.67 (±0.31)	0.50 (±0.00)	0.46 (±0.29)
b. Females			
STRIPE	0.70 (±0.57)	2.00 (±0.00)	1.00 (±0.71)
SCR1	0.15 (±0.13)	0.25 (±0.07)	0.29 (±0.22)
SC12TO10	5.81 (±1.62)	5.37 (±0.28)	4.65 (±1.71)
SUBLAB	11.75 (±0.60)	13.00 (±0.71)	12.00 (±1.28)
DV19TO17	4.38 (±0.58)	3.50 (±0.00)	4.20 (±0.27)
VS19TO17	67.64 (±2.99)	68.38 (±1.30)	69.26 (±2.74)
NASPIT	0.13 (±0.39)	1.00 (±0.00)	0.00 (±0.00)
BORSUPOC	9.70 (±1.19)	9.00 (±0.71)	8.50 (±0.35)
BSCK	0.75 (±0.30)	0.75 (±0.35)	0.50 (±0.35)
BTWSUPOC2	12.75 (±1.33)	15.00 (±1.41)	13.40 (±3.78)
VSC	169.73 (±4.18)	170.00 (±1.41)	165.30 (±4.55)
LABNAS	0.59 (±0.14)	0.75 (±0.00)	0.66 (±0.22)
DEYE	4.24 (±0.46)	3.69 (±0.75)	3.91 (±0.67)

Compared to *C. macrops s.s* (Table 3), in both sexes *C. rubeus* has a more prominent lateral stripe with the white area covering a larger proportion of the first scale row (SCR1), less keeled body scales at mid-body (BSCK), and the scale reduction from 19 to 17 dorsal scale rows (VS19TO17) occurs further away from the head. In addition, there are never any small scales present between the nasal scale and the scale bordering the anterior edge of the pit (NASPIT) in *C. rubeus*, while they sometimes occur in *C. macrops s.s*. In addition, males tend to have a less prominent postocular stripe (SCROC), fewer sublabial scales (SUBLAB), fewer scales between the rear edges of the supraocular scales (BTWSUPOC2), fewer scales between the last supralabial and the chin shields (VENTEDGE), and less keeled temporal scales (KTEMP). In females, *C. rubeus* tends to have fewer ventral scales, fewer (larger) scales bordering the supraoculars (BORSUPOC), and a larger number of scales between the rear edges of the supraoculars (BTWSUPOC2) than *C. macrops s.s*.

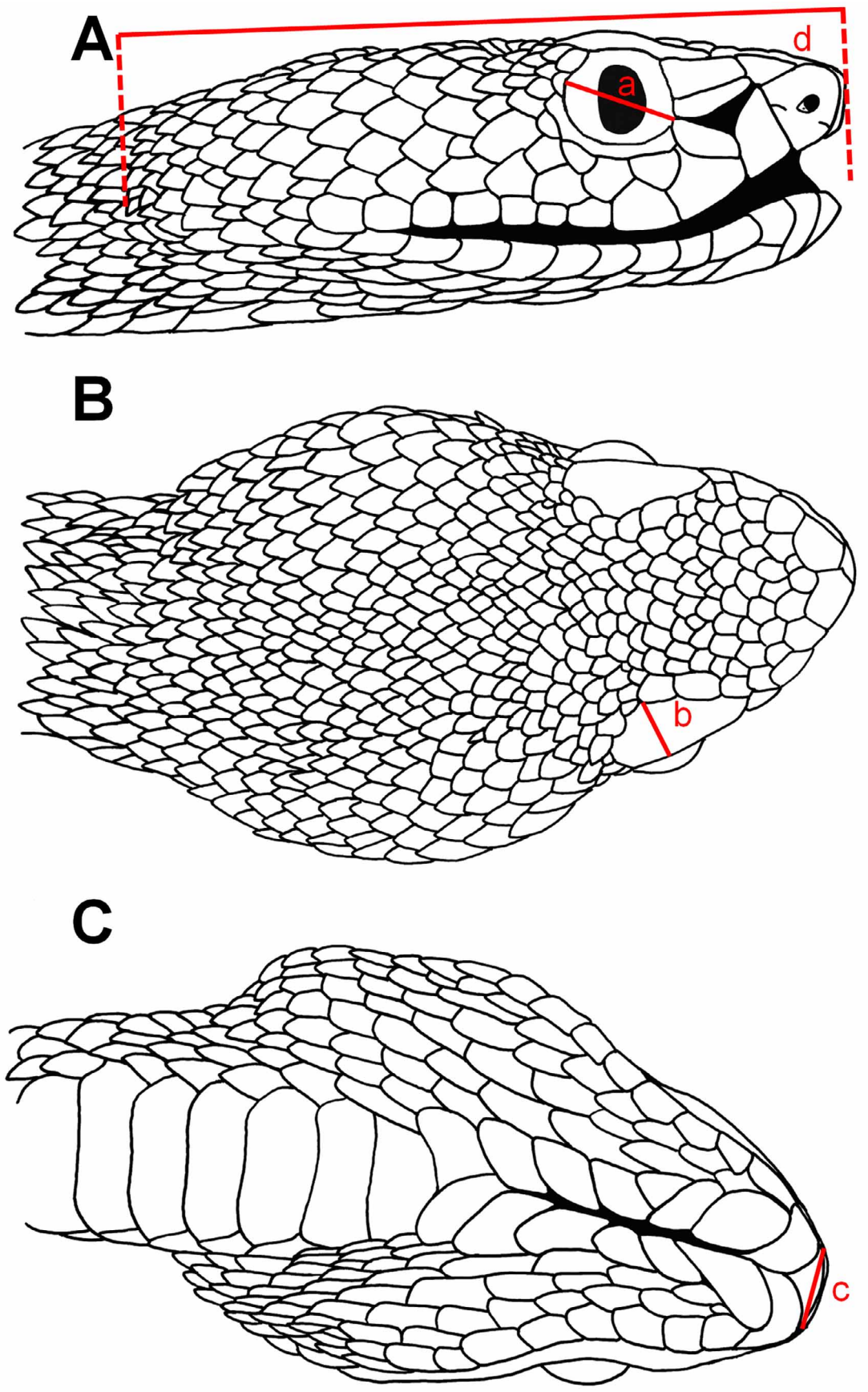

FIGURE 5. Line drawings of the head scalation of the holotype of *Cryptelytrops rubeus* **sp. nov.** (FMNH 262718). Labelling as in Fig. 3 (a: 4.00mm, b: 2.05mm, c: 3.45mm, d: 24.9mm).

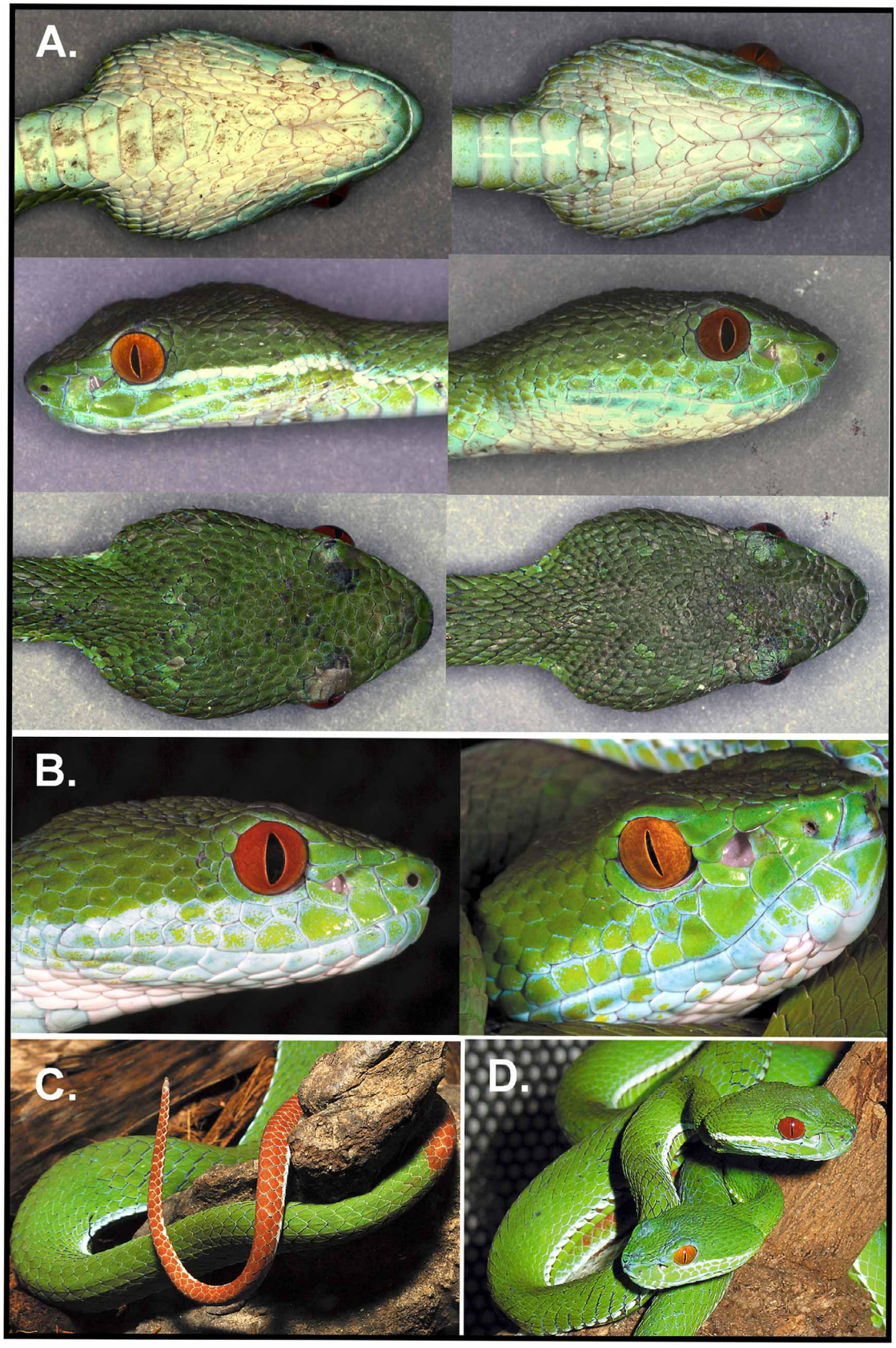

FIGURE 6. *Cryptelytrops rubeus* sp.nov. A. Close-up of head of male (left) and female (right) from vicinity of Ho Chi Minh city, South Vietnam (photos: A Malhotra); B. Close-up of head of male (left) and female (right) from South Vietnam; C. Closeup of tail of male from B; D. Pair from B (male above) (photos: K Udomritthiruj).

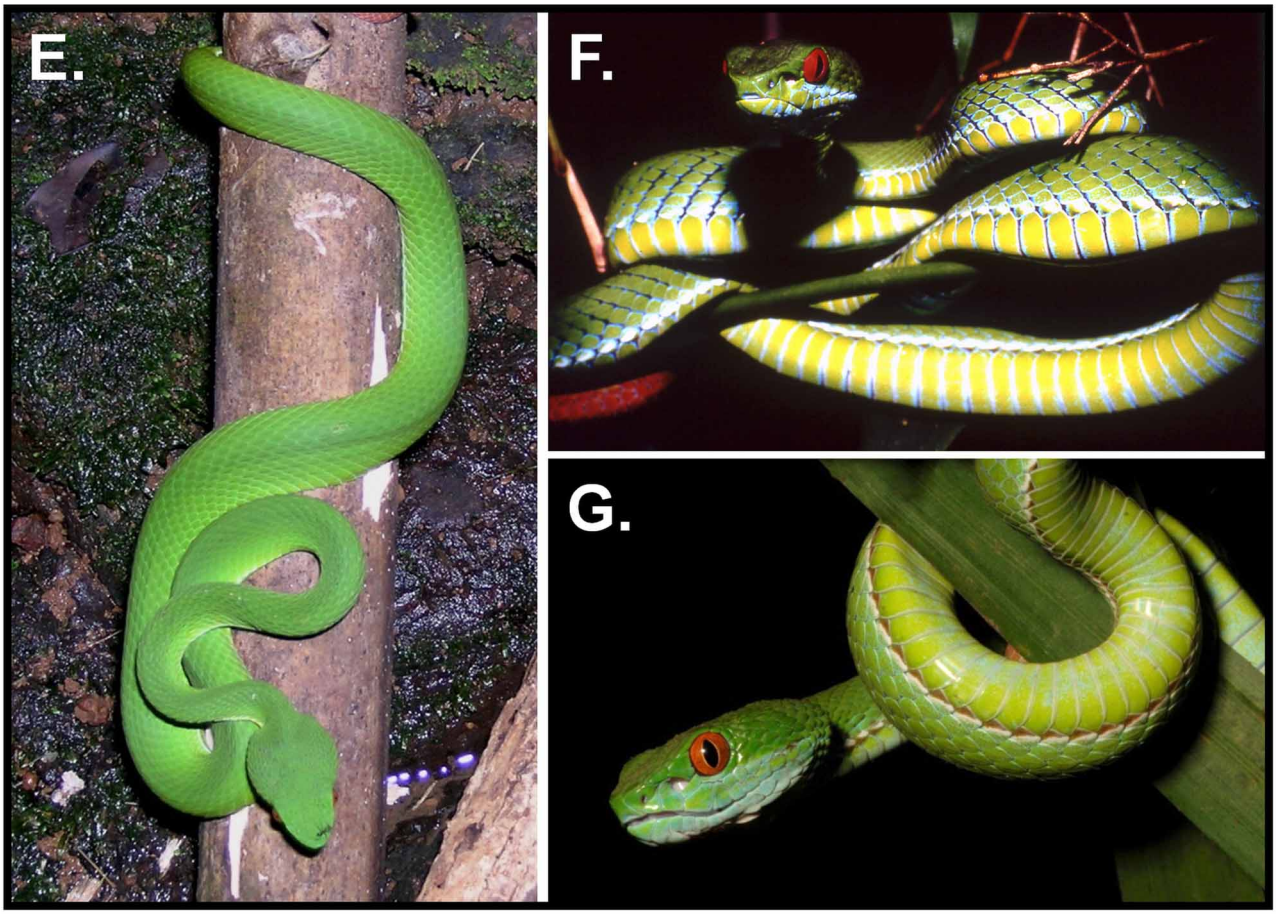

Figure 6 (contd.). Cryptelytrops rubeus sp. nov. E. Adult specimen from Mondolkiri Prov.,Cambodia (photo: Bryan L Stuart); F: Adult male from Nam Cat Tien National Park, Vietnam (photo: Peter Paul van Dijk); G: Adult male from O Reang, Ko Seima Protected Forest. Mondolkiri, northwest Cambodia (photo: Jeremy Holden).

Description of holotype. Body cylindrical; head triangular in dorsal aspect, very distinct from neck. Canthus rostralis distinct**.** Head scales small (no large dorsal shields), smooth except for weakly keeled scales in temporal region, region above suprabials, and rear of head. Dorsal body scales weakly keeled. 163 ventral scales, 58 pairs subcaudal scales, 21 dorsal scales at mid–body. Rostral scale roughly triangular, upper edge about half width of lower edge**.** Pupil vertically elliptical. Loreal pit present. Nostril completely enclosed in nasal scale. Nasal scale partially fused with first supralabial, suture extending part way towards nostril on both sides. Eleven and 12 supralabials on right and left sides respectively, 12 sublabials, two postocular scales. Shield bordering anterior edge of pit fused with second supralabial, lacking any small scales between it and nasal. Subocular scale separated by one scale from third, fourth, and fifth supralabials. At least 8 scales between supraoculars, 14 scales between their posterior edges. Five teeth on palatine, 16 on pterygoid, and 16 on dentary. Snout–vent length 49.9 cm; tail length 9.1 cm. Head length measured from tip of snout to posterior edge of lower jawbone 24.9 mm; head width measured between rear outer edges of supraoculars 11.4 mm, at widest point of head 16.85 mm. Supraocular scale (on right hand side) 5.7 mm long, 2.05 mm wide. Distance from eye to nostril 5.0 mm, eye to pit 1.0 mm, posterior edge of pit to anterior edge of nostril 4.85 mm. Eye diameter 4.0 mm. Scale reduction formula:

31	7+8 (7)	29	1+2 (6)	27	4+5 (8)	25	6+7 (13)	23	4+5 (17)	21	4+5 (108)	19	4+5 (114)	17	3+4 (124)	15
	10+11(9)		3+4 (7)		5+6 (10)		5+6 (12)		4+5 (17)		5+6 (109)		4+5 (115)		4+5 (125)	

Colour of holotype in preservative. Dark brownish grey on dorsal surface of head, fading to steely blue grey laterally. Ventral scales are very similar in colour to the first few dorsal scale rows. Pale lateral stripe present, covering approximately one–quarter of first scale row at mid-body, fading towards the head. Upper and lower labials

not distinct in colour from rest of head. Paired chin shields, scales between the chin shields creamy white in colour, although a single pair of chinshields and the occasional scale blue–grey. Ventral scales uniformly blue–grey.

Colour in life. Photographs of a red–eyed green pitviper which is almost certainly referable to *C. rubeus*, taken in Nam Cat Tien National Park in May 2000, were supplied by P-P. van Dijk. This specimen, together with those pictured in Gumprecht *et al*. (2004) (p. 236–238), photographs taken by AM of the specimens from Cu Chi and Bien Hoa above, of FMNH 262717 by BLS in Cambodia (described in Stuart *et al*. [2006a), and of BMNH 2005.1602, provided by K. Udomritthiruj (Fig. 6), were used to write this description of the colour of the species in life.

Posterior half of the body dark to grass green, similar on ventral and dorsal surface. Lateral white stripe more prominent and may extend onto the second dorsal scale row in males (confined to first row in females). In males, lateral white stripe may be edged below with dull reddish–brown more obvious on the rear half of the body. White stripe may also extend onto head as postocular stripe, passing underneath the eye and fading out on lower preocular scale. Upper lip (supralabials and 1–2 scale rows above) suffused with pale blue and differentiated from rest of head; mostly confined to scale edges, but may be more widespread towards rear of mouth. Pale blue also largely covering sublabials, genials and paired chinshields, extending onto central part of the ventral scales in anterior of body. Scales between the chinshields and the sublabials creamy white. Patches of other colours including deep yellow also present on these scales. Interstitial skin black. Tail solid orange–red, this extending to vent dorsally and ventrally (although in males forming distinct pattern of blotches on the distal half of the tail). Eye bright or deep reddish–orange in both sexes.

Variation. Sexual dimorphism is not very obvious although females lack postocular stripes and have a less prominent lateral stripe, never edged with brick red. Eye colour appears to be the same in both sexes, with the exception of one female from southern Vietnam (BMNH 2005.1602), in which the eye was golden yellow. Females have relatively shorter tails and fewer subcaudals (52–63, versus 63–74 in males). Sexual dimorphism in size may also be low/absent in this species (maximum recorded 50.3 cm SVL versus 50.5 cm for males), but the sample is small. The number of ventral scales is similar in both sexes (159 and 172). Body scales smooth to strongly keeled at mid–body. Temporal scales show weak to strong tubercular keeling, and keeling is also weak to strongly present on the scales covering the rear of the head. In some specimens, the scales in the region between the temporal scales and supralabials are also keeled. The ratio between the lengths of the upper and lower edges of the rostral scale varies between 0.39 and 0.53. Supralabials vary between 8 and 12 and sublabials between 9 and 13. The suture that partially separates the first supralabial and nasal scale is more obliquely inclined than in the other species, where it tends to be more horizontal, and tends to be confined to the rear of the nostril. The minimum number of scales between supraoculars varies between 7 and 12 and there are 7 and 19 scales between the posterior edges of the supraoculars. There are never any small scales between the nasals and shield bordering the anterior of the pit, and exceptionally there was a single scale between the internasals in one specimen. There are 0–1 scales between the third and fourth supralabials and the subocular, and 1–2 scales between the fifth supralabial and the subocular scale. Hemipenes do not differ notably from those of *C. macrops s.s*. There are always five teeth on the palatine bone (as in most other pitvipers of the *Trimeresurus* radiation), while those on the pterygoid vary between and 15–18 (in one specimen, a count of 12 was made on one side, but the other side had 16, a count that was within the range seen in other specimens), and on the dentary between 14–17.

TABLE 3. Mean and standard deviations of morphological characters that in combination can be used to distinguish *C. macrops* s.s. and *C. rubeus* **sp. nov.** Data are for the maximum number of specimens available for that character. Cm = *C. macrops s.s.*, Cr = *C. rubeus*. Character abbreviations are explained in Appendix 1.

Character	Cm	Cr
a. Males		
SCROC	0.69 (±0.93)	0.33 (±0.82)
SCR1	0.19 (±0.19)	0.32 (±0.08)
BSCK	0.8 (±0.25)	0.38 (±0.21)
VS19TO17	68.00 (±1.99)	69.29 (±1.53)
SUPLAB	9.65 (±0.49)	9.58 (± 1.02)
SUBLAB	11.62 (±0.54)	10.92 (±0.74)
BTWSUPOC2	11.96 (±1.22)	10.17 (±1.94)

VENTEDGE	7.46 (±0.45)	6.92 (±0.49)
SC12TO10	5.15 (±1.52)	5.14 (±1.24)
NASPIT	0.19 (±0.47)	0.00 (±0.0)
KTEMP	0.67 (±0.31)	0.46 (±0.29)
b. Females		
SCR1	0.15 (±0.13)	0.29 (±0.23)
VSC	169.73 (±4.18)	165.30 (±4.55)
VS19TO17	67.64 (±2.99)	69.26 (±2.74)
BORSUPOC	9.70 (±1.19)	8.50 (±0.35)
NASPIT	0.13 (±0.39)	0.00 (±0.00)
STRIPE	0.70 (±0.57)	1.00 (±0.71)
BTWSUPOC2	12.75 (±1.33)	13.40 (±3.78)
BSCK	0.75 (±0.30)	0.50 (±0.35)

Distribution. *Cryptelytrops rubeus* is currently known from southern Vietnam from the vicinity of Ho Chi Minh City and the low-elevation hills on the southern and western edges of the Langbian (= Dalat) Plateau in southern Vietnam and eastern Cambodia (Fig. 1). The occurrence of this species in Nam Cat Tien National Park is supported by a photographic record of a red–eyed green pitviper (Fig. 6), which is almost certainly referable to *C. rubeus.*

Ecology. Specimens from Cambodia were collected at night (1810–2040 h) on the soil bank, herbaceous plants, bushes, tree roots, and tree branches. All were found within 10 m of swift, rocky streams (often near waterfalls) at an elevation of 450–500 m. The species was found in sympatry with *Viridovipera vogeli* at this location. FMNH 262720 contained mammal hairs in its hind gut (stomach contents were too digested to allow more accurate identification of prey). The specimen in Nam Cat Tien was found near a small temporary pond, c. 1 km northeast of the park headquarters. It was first noted at 2050 hrs moving on grass adjacent to the pond towards tangled poolside vegetation, and later found at 2230 hrs coiled in bamboo/shrubby undergrowth a few meters away.

Etymology. Rubeus, from Latin, meaning reddish, refers to the reddish eye colouration in both sexes, the presence of at least a partial red lateral stripe in males, and the bright and prominent red coloration on the tail, which differentiates it from other macrops group species.

Cryptelytrops macrops *sensu stricto* (Kramer 1977) (Big-eyed Green Pitviper)
Fig. 7, 8; Tables 1–4

Trimeresurus macrops Kramer 1977 : Kramer (1977): 757 (part); Regenass and Kramer (1981):184 (part); Viravan *et al*. (1992):102; Gumprecht (1998): 25 (part); Orlov *et al*. (2002a): 193 (part); Orlov *et al*. (2002b): 353 (part); Gumprecht *et al*. (2004): 230 (part), Teynié *et al*. (2004): 47.

Material examined. MHNG 1400.85, holotype, adult male, Bangkok, Thailand; MHNG 1400.73, 1400.78, 1400.79, 1400.87, 1400.96 –100, paratypes, Bangkok, Thailand; FMNH 258954–58, Dong Hua Sao National Biodiversity Conservation Area, Bolaven Plateau, Champasak Province, Laos; FMNH 255249, 255251–52, 255256–57, Dong Khanthung National Biodiversity Conservation Area, Champasak Province, Laos; FMNH 255253–55, Phou Khao Khouay National Biodiversity Conservation Area, Bolikhamxai Province, Laos; FMNH 255248, Hin Nam No National Biodiversity Conservation Area, Khammouan Province, Laos; FMNH 262715–16, Virachey National Park, Siem Pang District, Stung Treng Province, Cambodia; NMW 23899:4, NMW 23899:10, NMW 23899:13, Dong Rek Mountains, Thailand; NMW 23897:1, NMW 23897:3, NMW 23897:4, NMW 23897:7, NMW 23897:13, NMW 23897:15, NMW 23897:17, Don Pia Fei Mountains, Thailand. The senior author also examined a number of live Thai specimens under anaesthesia; these included a juvenile male found behind the headquarters of Jae Sorn National Park, Lampang province, on 24th July 1996, two specimens from the vicinity of Sakaerat Experimental Station, Nakhon Ratchasima Province in June 1999, and five specimens obtained from dealers through the Queen Savoabha Memorial Institute (QSMI), Bangkok from Nonthaburi and Ang Thong Provinces,

as well as the outskirts of the city itself, in 1998. Although morphological data from these specimens have been used in all analyses, under the conditions of permission, these specimens could not be taken as vouchers and were returned unharmed to the site of capture, or retained by the QSMI for further study.

Revised diagnosis. *Cryptelytrops macrops s.s.* is distinguished from all other Asian pitviper species which also have the typical "green pitviper" colouration (uniform green dorsal colour and a lateral stripe present on the first few dorsal scale rows in one or both sexes), except other species of *Cryptelytrops*, by the presence of a fused first supralabial and nasal scale. It can be distinguished from *C. albolabris*, *C. insularis* and *C. septentrionalis* primarily by the relatively larger size of the eye (most obvious in adults), the relatively wider supraoculars, and the shape of the head, which is more elongate–oval in *C. albolabris*, *C. insularis* and *C. septentrionalis*, but widens quite abruptly behind the eyes in *C. cardamomensis* **sp. nov.**, *C. macrops s.s.* and *C. rubeus* **sp. nov.** to give a characteristically triangular shaped head. *Cryptelytrops macrops s.s.* can be distinguished from both *C. cardamomensis* **sp. nov.** and *C. rubeus* sp. nov using the characters detailed above (further details are also given in Tables 2 and 3).

Redescription of holotype. We supplement Kramer's (1977) original description (Appendix 2) of the holotype, as follows. Body cylindrical, head triangular in dorsal aspect and very distinct from neck. Canthus rostralis distinct**.** Head scales small (no large dorsal shields), smooth except for weak tubercular keeling in temporal region and region between suprabials and temporal region and strong keeling on rear of head. Body scales also strongly keeled dorsally. 168 ventral scales, 68 pairs of subcaudals, 21 dorsal scales at mid–body. Rostral scale somewhat triangular, upper edge more than half the width of lower edge (ratio between the lengths of the upper to lower edge 0.58)**.** Pupil vertically elliptical. Loreal pit present. Nostril completely enclosed in nasal scale. Nasal scale partially fused with first supralabial, partial suture present behind the nostril, but not to anterior on one side, on both sides of the nostril on the other. Ten supralabials, 13 sublabials, two postocular scales. Shield bordering anterior edge of pit fused with second supralabial, in contact with nasal scale. Subocular scale touches third supralabial, but separated by one scale from fourth and fifth supralabials. At least 7 scales between supraoculars, 13 scales between their posterior edges. Snout–vent length 50.6 cm; tail length 13.3 cm. Head length measured from tip of snout to posterior edge of lower jawbone 23.2 mm; head width measured between rear outer edges of supraoculars 11.55 mm, at widest point of head 16.9 mm. Supraocular scale (on right) 5.05 mm long, 2.3 mm wide. Distance from eye to nostril 4.95 mm, eye to pit 1.1 mm, posterior edge of pit to anterior edge of nostril 5.0 mm. Eye diameter 4.15 mm. Scale reduction formula:

31	2+3 (6)	29	14+15 (11)	27	6+7 (8)	25	6+7 (10)	23	4+5 (23)	21	4+5 (113)	19	5+6 (119)	17	4+5 (126)	15
	2+3 (6)		13+14 (11)		5+6 (9)		6+7 (10)		4+5 (24)		4+5 (111)		4+5 (120)		4+5 (130)	

Colour of holotype in preservative. Dorsal surface of head and body brownish grey; sublabials, last three supralabials, and lateral edges of ventral scales steely blue. Apart from mental, sublabials and a few scale rows below sublabials posterior to eighth sublabial, scales on the underside of the head creamy white. Central part and rear edge of ventral scales same creamy white colour. Postocular stripe and lateral stripe not apparent.

Colour in life. This description is based on colour plates on p. 230–235 (with the exception of those listed above) of Gumprecht *et al*. (2004) of specimens from Lampang, Nakhon Ratchasima (Plate 3), and the vicinity of Bangkok, Thailand, as well as macro photographs of the dorsal, lateral, and ventral aspects of the head and body of specimens from Nakhon Ratchasima, Lampang, Nonthaburi and Ang Thong provinces of Thailand by AM. Ground colour varable, bluish green, grass green or yellow–green, ventral surface slightly paler, often with bluer hue than dorsal surface especially on anterior of body and excepting lateral edges of ventral scales. Prominent lateral white stripe in males (sometimes encroaching onto second dorsal scale row), usually extending onto head as postocular stripe passing below the eye and fading out on lower preocular, below pit. In some specimens, lateral stripe pale blue rather than white. Scales below postocular stripe lighter in colour than rest of head. Females lack obvious postocular stripe, but may have indistinct pale or blue streak. Usually little distinction between colour of supralabials and upper surface of head. Females occasionally have lateral stripes, although covering less than one–third of first scale row at mid–body and not extending onto second scale row. Tail dull brick red, dorsally extending as far as vent, with clear margin on lateral side of tail. Eye golden yellow to light orange in both sexes. Males may have small whitish flecks mid–dorsally, more prominent in juveniles, sometimes retained in adults. Interstitial skin blue–grey, with black banding. Sublabial scales often suffused with pale blue; rest of the scales on the underside of the head (genials, chin shields, and scales between these and sublabials) are white. Scattered blue pigment on some dorsal scales on head may be present, but not as well developed as in other two species.

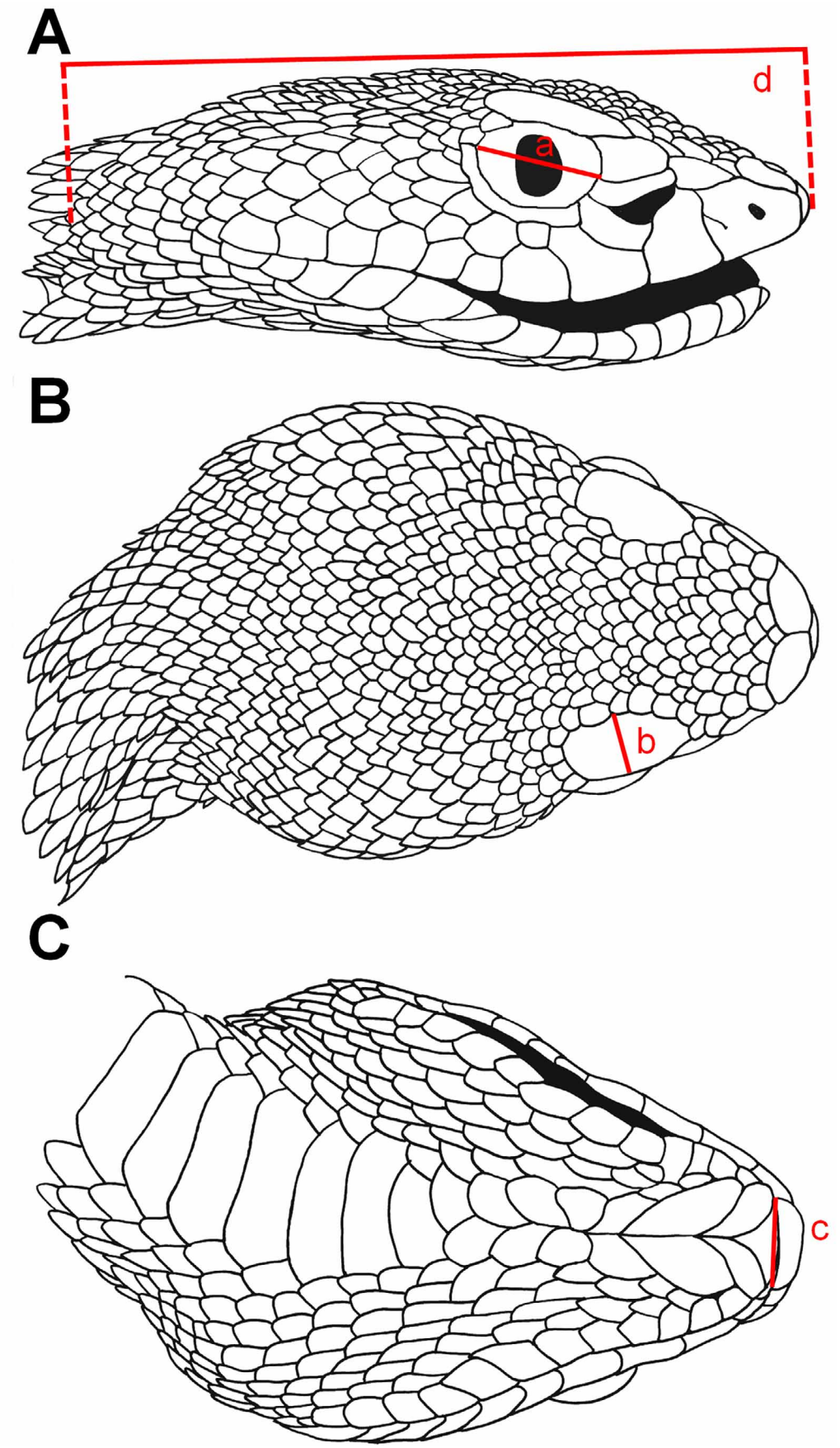

FIGURE 7. Line drawings of the head scalation of the holotype of *Cryptelytrops macrops s. s.* (MHNG 1400.85). Labelling as in Fig. 3 (a: 4.15mm, b: 2.30mm, c: 3.00mm, d: 23.2mm).

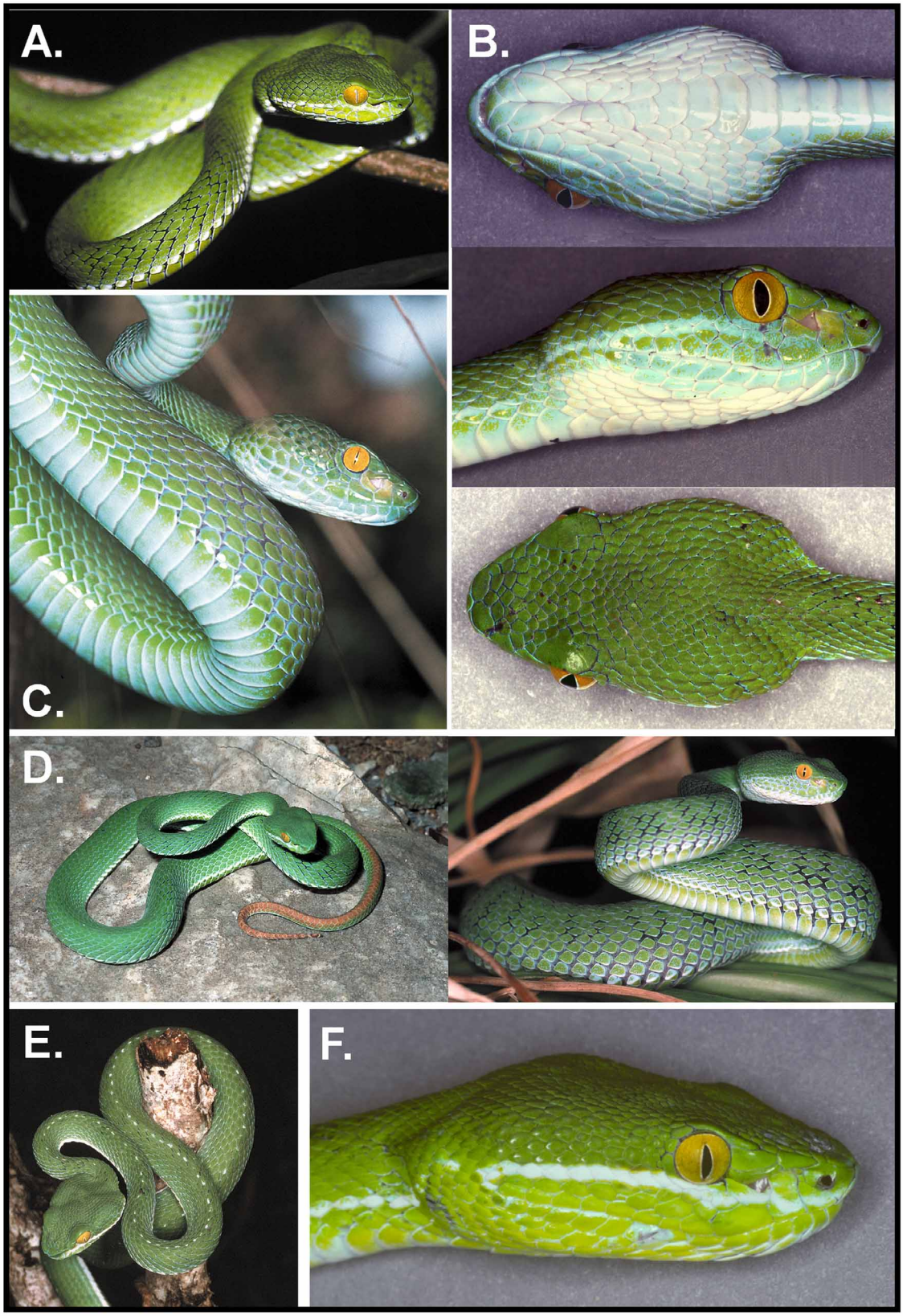

FIGURE 8. *Cryptelytrops macrops* sensu stricto. A. Juvenile male from Jae Sorn National Park, Lampang Prov., Thailand (photo: A Malhotra); B. Adult male from Sakaerat Experimental Station, Nakhon Ratchasima Prov., Thailand (photo: A Malhotra); C. Adult female from the vicinity of Bangkok, Thailand (photo: A Gumprecht); D. Adult male (left) and female (right) from north of Khao Yai National park, Nakhon Ratchasima Prov., Thailand (photos: A Gumprecht); E. Juvenile male from Nakhon Ratchasima Prov., Thailand (photo: A Gumprecht). F. *Cryptelytrops albolabris* from southern Thailand, for comparison. Note the more elongated head, relatively smaller eye, yellower eye and lack of any blue pigmentation (photo: A. Malhotra).

TABLE 4. Range of values for some morphological characters in different populations of *C. macrops s.s.* Keeling of scales is measured as described in Appendix 1. M = male; F = female; n = number of specimens for external/internal characters (the latter is given only if different from the former). The range of the character in all specimens measured is given, except where n = 1, where two numbers separated by a slash denotes different values on the right and left side of the individual. The occurrence of the species in southern Thailand requires further confirmation (See text for fuller details of this individual).

	C Thai		N Thai	S Thai	Dong Rek/Don Pia Fei Mts, Thailand		S. Laos/N Cam		C Laos	N Laos	
	M (n =11/3)	F (n = 4/2)	M (n = 1)	F (n = 1)	M (n = 10/8)	F (n = 7)	M (n = 2)	F (n = 3)	F (n = 1)	M (n = 2)	F (n = 2)
Number of subcaudal scales	55–72	51–55	73	54	66–79	53–65	67–74	56–63	62	68–72	55–57
Maximum SVL (cm)	56.4	55.9	40.4	63.5	54.6	59.8	50.3	62.9	38.9	42.6	46.8
Number of ventral scales	164–170	168–177	169	167.5	159 –176	165–182	159–168	166–168	173.5	169–171	166–170
Keeling of body scales at mid–body	0.5–1.0	0 – 1	0.5	1.0	0.5–1.0	0.5–1.0	1.0	0.5–1.0	1.0	0–0.5	0.5–1.0
Keeling of temporal scales	0.5–1.0	0.5–1.0	0.5	0.5	0–1.0	0–0.5	0–0.5	0–1.0	0.5	0–0.5	0.5
Keeling of scales between supra–labials and temporals	0.0–1.0	0.0–1.0	0	0.5	0–0.5	0–0.5	0–0.5	0–0.5	0.5	0–0.5	0
Keeling of rear head scales	0.5–1.0	0.0–1.0	0.5	1.0	0.0–1.0	0.0–1.0	0.0–1.0	0.0–0.5	0.5	0.0–0.5	0.5
Ratio of the upper and lower edges of rostral scale	0.46 – 0.64	0.42–0.60	0.23	0.52	0.38–0.62	0.37–0.51	0.48–0.51	0.46–0.52	0.47	0.44–0.48	0.37–0.42
Number of supralabials	9– 10	9– 11	9/10	9/10	9–11	9–11	9–10	9–10	10/11	10	10–11
Number of sublabials	11–13	11–13	10/11	12/13	11–12	11–13	11–12	11–12	10/11	11–12	11
Minimum number of scales between supraoculars	6 – 9	9	7	8	6–8	6–10	8–9	8	8	8–9	7–9
Number of scales between posterior edges of supraoculars	10–13	12–15	13	13	10–14	10–14	13	12–14	11	13	12–15
Number of scales between nasals and shield bordering anterior of the pit	0 – 1	0	0	0	0–2	0–2	0–2	0	0	0	0
Number of scales between internasals	0 – 1	0	0	0	0–1	0–1	0	0	0	0–1	0–1
Number of scales between 3rd supralabial and subocular	0 – 1	0 – 1	0	0/1	0–1	0–1	0–1	0	1	0–1	0
Number of scales between 4th supralabial and subocular	0 – 1	1	0/1	1	0–1	0–1	0–1	0–1	1	0–1	0–1
Number of scales between 5th supralabial and subocular	1	1 – 2	1	2	1–2	1	1	1	1	1	1
Number of pterygoid teeth	14	13 – 15	–	–	15–18	13–16	15–19	14–15	17	14–15	14–15
Number of dentary teeth	14 – 16	14	–	–	14–17	14–15	17	15–17	17	14–16	14–15

Variation. There is geographic variation between different populations of *C. macrops s.s.*, summarised in Table 4. Within each population, sexual dimorphism is not pronounced, and is most obvious in the prominence of postocular and lateral stripes in males compared to females, and the relatively shorter tails and more massive girth of females. Females also reach an overall larger size (maximum recorded 62.9 cm SVL compared to 56.4 cm for males).

Distribution. Kramer (1977) reported the species from Thailand (Bangkok) and Vietnam, and it was presumed to occur in the intervening area. However, it is apparent that the species has a wider distribution (Fig. 1). Viravan *et al*. (1992) reported it from western, northern and northeastern Thailand, and although the present study has not been able to confirm its presence in western Thailand (unfortunately, the majority of specimens resulting from Viravan *et al*.'s study, now deposited in the Natural History Museum, London, have since lost their labels carrying the locality information), it is very likely to be present there. One adult female at the QSMI was said to have been obtained from southern Thailand via a dealer based in Thung Song. Mitochondrial DNA analysis showed that it was highly similar to *C. macrops s.s.* from the Bangkok region (Genbank accession numbers AF517184, AF517219, AF517163, and AF517176). Nevertheless, the occurrence of this species in southern Thailand must remain speculative at present until it can be confirmed by the collection of additional specimens in the field. Orlov *et al*. (2002a) also illustrate a specimen (Fig. 20: Pg 191) of *C. macrops* said to be from southern Thailand. However, this specimen seems to be a misidentified male *C. albolabris*. The species is also present in southern (Teynié *et al*. 2004) and central Laos (see also "Material examined", this paper).

Ecology. *Cryptelytrops macrops s.s.* occupies hilly areas up to c. 600 m. It has mainly been found in dry evergreen and mixed deciduous forest mixed with bamboo forest, but also in dry dipterocarp/grassland vegetation. Most specimens were found within a couple of metres of the ground, but occasionally up to 4 m high. Specimens were frequently found in the vicinity of water. Food items found in the digestive tracts of specimens examined included mammals (NMW 23899:4 from the Dong Rek mountains and AFS96.5 from Lampang Province, Thailand), frogs (FMNH 255252 and 255254 from Champasak and Bolikhamxai Provinces, Laos respectively; FMNH 262715 and 262716 from Stung Treng Province, Cambodia) and reptiles (FMNH 255253 from Bolikhamxai Province, Laos).

Discussion

The biogeographic pattern displayed by the group of *Cryptelytrops* species analysed here is an interesting one, contrasting as it does with the apparently wide distribution of some other *Crytptelytrops* species such as *C. albolabris* (however, it should be borne in mind that the intraspecific variation in *C. albolabris* has not yet been fully evaluated). Malhotra & Thorpe (2004a) showed that *C. macrops* was nested in a clade containing also the two phenotypically dissimilar banded species, *C. venustus* and *C. kanburiensis*, and which was quite distinct from other *Cryptelytrops* species. A further recently described banded species of *Cryptelytrops, C. honsonensis* (Grismer *et al*. 2008) from an island off the coast of southern Vietnam, may also be closely related to this species group, sharing a very similar colour pattern to *C. venustus*. Until molecular data confirm the exact relationships among these and the newly described species, any discussion of the biogeography of this subgroup of *Cryptelytrops* should include the banded species.

Within this subgroup of *Cryptelytrops*, a fairly narrow distribution with a high degree of subdivision among slightly separated mountain blocks is evident, with *C. macrops s.s*. being the most widespread. All species appear to be allo- or para-patric. Although all three green species are present in Cambodia, they have disjunct ranges corresponding to three separate highland regions in southwestern (Cardamom Mountains), northeastern (western edge of the Kontum Plateau) and eastern (low elevation hills on the western edge of the Langbian Plateau) Cambodia for *C. cardamomensis*, *C. macrops* and *C. rubeus* respectively. There is little commonality with patterns of distribution in other sympatric pitvipers. For example, *Viridovipera vogeli* is found across several mountain ranges that are occupied by different species in the present paper, for example Dong Pia Fei, Dong Rek, Cardamom mountains and the Bolaven and Langbian Plateaus, despite occupying higher elevations and therefore potentially having a more fragmented range. However, the distribution of *C. cardamomensis* reflects that of a growing number of species of amphibians and reptiles (Ohler *et al*. 2002; Stuart & Emmett 2006; Grismer *et al*. 2010; Wood *et al*. 2010), and stark differences are apparent between the frog and lizard faunas of the Cardamom mountains and the eastern Cambodian/southern Vietnam highlands (Stuart *et al*. 2006a, 2010).

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References

David, P., Vogel, G., Vijayakumar, S.P. & Vidal, N. (2006) A revision of the *Trimeresurus puniceus*-complex (Serpentes: Viperidae: Crotalinae) based on morphological and molecular data. *Zootaxa*, 1293, 1–78.

Dowling, H.G. (1951) A proposed system for counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.

Grismer, L.L, Chav, T., Neang, T., Wood Jr, P.L., Grismer, J.L., Youmans, T.M., Ponce1, A., Daltry, J.C. & Kaiser, H. (2007) The herpetofauna of the Phnom Aural Wildlife Sanctuary and checklist of the herpetofauna of the Cardamom mountains, Cambodia. *Hamadryad*, 31, 216–241.

Grismer, L.L, Neang, T., Chav, T. & Grismer, J.L. (2008a) Checklist of the amphibians and reptiles of the Cardamom region of southwestern Cambodia. *Cambodian Journal of Natural History*, 2008, 12–28.

Grismer, L.L., Neang, T., Chav, T., Wood Jr, P.L., Oaks, J.R., Holden, J., Grismer, J.L., Szutz, T.R. & Youmans, T.M. (2008b) Additional amphibians and reptiles from the Phnom Samkos wildlife sanctuary northwestern Cardamom Mountains, Cambodia, with comments on their taxonomy and the discovery of three new species. *Raffles Bulletin of Zoology*, 56, 161–175.

Grismer, L.L, Ngo, V.T. & Grismer, J.L. (2008c) A new species of insular pitviper of the genus *Cryptelytrops* (Squamata: Viperidae) from southern Vietnam. *Zootaxa*, 1715, 57–68.

Grismer, L.L, Sumontha, M., Cota, M., Grismer, J.L., Wood, P.L., Pauwels, O.S.G. & Kunya, K. (2010) A revision and redescription of the rock gecko *Cnemaspis siamensis* (Taylor 1925) (Squamata: Gekkonidae) from Peninsular Thailand with descriptions of seven new species. *Zootaxa*, 2576, 1–55.

Gumprecht, A. (1998) Die Bambusottern der Gattung *Trimeresurus* Lacépède. Teil II: Die Grossaugen-bambusotter *Trimeresurus macrops* Kramer, 1977. *Sauria*, 20, 25–36.

Gumprecht, A., Tillack, F., Orlov, N.L., Captain, A. & Ryabov, S. (2004) *Asian Pitvipers*. GeitjeBooks, Berlin, 368 pp.

Kramer, E. (1977) Zur Sclangenfauna von Nepal. Rev. *Suisse Zoologie*, 84, 721–761.

Malhotra, A. & Thorpe, R.S. (2004a) A phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pit vipers *Trimeresurus* and *Ovophis*. *Molecular Phylogenetics and Evolution*, 32, 83–100.

Malhotra, A. & Thorpe, R.S. (2004b) Maximising information in systematic revisions: a combined molecular and morphological analysis of a cryptic green pitviper complex (*Trimeresurus stejnegeri*). *Biological Journal of the Linnean Society*, 82, 219–235.

Ohler, A., Swan, S.R. & Daltry, J.C. (2002) A recent survey of the amphibian fauna of the Cardamom mountains, southwest Cambodia, with descriptions of three new species. *Raffles Bulletin of Zoology*, 50, 465–481.

Orlov, N., Ananjeva, N., Barabanov, A., Ryabov, S. & Khalikov, R. (2002a) Diversity of vipers Azemiopinae, Crotalinae in East, Southeast, and South Asia: Annotated checklist and natural history data. Reptilia: Squamata: Serpentes: Viperidae. *Faunistische Abhandlungen des Staatlichen Museums für Tierkunde Dresden*, 23, 177–218.

Orlov, N., Ananjeva, N. & Khalikov, R. (2002b) Natural History of pitvipers in Eastern and Southeastern Asia. *In:* Schuett, G.W., Höggren, M., Douglas, M.E. & Greene, H.W. (Eds.), *Biology of the vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah, pp 345–360.

Regenass, U. & Kramer, E. (1981) Zur Systematik der grunen Grubenottern der Gattung *Trimeresurus* Serpentes, Crotalidae. *Revue Suisse Zoologie*, 88, 163–205.

Sanders, K.L., Malhotra, A. & Thorpe, R.S. (2006) Combining molecular, morphological and ecological data to infer species boundaries in a cryptic tropical pitviper. *Biological Journal of the Linnean Society*, 87, 343–364.

Stuart, B.L. (1999) Amphibians and reptiles. *In*: Duckworth, J.W., Salter, R.E., Khounboline, K. (Eds.), *Wildlife in Lao PDR: 1999 Status Report*. IUCN–The World Conservation Union / Wildlife Conservation Society / Centre for Protected Areas and Watershed Management, Vientiane, Laos, pp 43–67.

Stuart, B.L. & Emmett, D.A. (2006) A collection of amphibians and reptiles from the Cardamom Mountains, southwestern Cambodia. *Fieldiana, New Series*, 109, 1–27.

Stuart, B.L., Sok, K. & Neang, T. (2006a) A collection of amphibians and reptiles from hilly eastern Cambodia. *Raffles Bulletin of Zoology*, 54, 129–155.

Stuart, B.L., Inger, R.F. & Voris, H.K. (2006b) High levels of cryptic species diversity revealed by sympatric lineages of South-east Asian forest frogs. *Biology Letters*, 2, 470–474.

Stuart, B.L., Rowley, J.J.L., Neang, T., Emmett, D.A. & Sitha, S. (2010) A collection of amphibians and reptiles from hilly eastern Cambodia. *Cambodian Journal of Natural History*, 2010, 38–47.

Teynié, A., David, P., Ohler, A. & Luanglath, K. (2004) Notes on a collection of amphibians and reptiles from southern Laos, with a discussion of the occurrence of Indo–Malayan species. *Hamadryad*, 29, 33–62.

Thorpe, R.S. (1975) Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake *Natrix natrix* (L.). *Biological Journal of the Linnean Society*, 7, 27–43.

Thorpe, R.S. (1976) Biometric analysis of geographic variation and racial affinities. *Biological Review*, 51, 407–452.

Thorpe, R.S. (1983) A review of the numerical methods for recognising and analyzing racial differentiation. *In*: Felsenstein, J. (Ed.). *Numerical Taxonomy: Proceedings of a NATO Advanced Studies Institute*. NATO ASI Series, Vol. G1, Berlin, pp 404–423.

Viravan, C., Looareesuwan, S., Kosakarn, W., Wuthiekanun, V., McCarthy, C.J., Stimson, A.F., Bunnag, D., Harinasuta, T. & Warrell, D.A. (1992) A national hospital-based survey of snakes responsible for bites in Thailand. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 86, 100–106.

Wood Jr., P.L., Grismer, L.L., Grismer, J.L., Neang, T., Chav, T. & Holden, J. (2010) A new cryptic species of Acanthosaura Gray, 1831 (Squamata: Agamidae) from Thailand and Cambodia. *Zootaxa*, 2488, 22–38.

APPENDIX 1.

Morphological characters used in multivariate morphometric analyses to discriminate among species, and their abbreviations. A full list of characters screened for significant between-species differences can be found in Malhotra & Thorpe (2004b).

A. SCALATION

VSC: the number of ventral scales (VS), not including anal scale, recorded by the Dowling (1951) method (i.e. the first VS contacts the first dorsal scale row on both sides).

SCS: the number of pairs of subcaudal scales, beginning with the first pair in contact with each other after the vent. Any unpaired scales are treated as a pair (only used to adjust scale reductions on the tail).

SUPLAB : the average number of supralabials on the left and right hand side.

SUBLAB: the average number of sublabials on the left and right hand side.

POSTOC: number of postocular scales.

BORSUPOC: the number of scales bordering the supraocular scales (average of right and left), not counting pre- or post-oculars.

BTWSUPOC2: the number of scales between the posterior edge of the supraoculars.

INTNAS: the number of scales separating the internasal scales.

NASPIT: the number of small scales between the nasal scale and the scale bordering the anterior edge of the pit.

LABNAS: the degree of fusion of the first labial and nasal scale.

ROST: the ratio of the anterior margin of the rostral scale to the posterior margin.

KTEMP: the keeling of the temporal scales.

BSCK: the keeling of the dorsal scales at mid-body.

VENTEDGE: the number of scales between the edge of the mouth and the ventral scales, starting at and including the last sublabial.

B. SCALE REDUCTION FORMULA

These are recorded as a series of characters, each referring to a specific reduction. Each position will have two characters, the dorso-ventral (DV) position of the reduction (the lowest of the two merging scale rows), and the ventral scale or subcaudal scale (VS or CS) position (counted from the head and vent respectively), 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) or subcaudal scales (%SC), to control for variation.

VS19to17: ventral scale position of the reduction from 19 to 17 scale rows.

DV19to17: dorsoventral position of reduction from 19 to 17 scale rows.

C. BODY DIMENSIONS.

All measurements are made on the right side of the head only unless this was damaged, in which case they were done on the left.

SVL: distance between the tip of the snout and the cloaca (only used to size-adjust head dimensions).

LHEAD: length of the head measured between the tip of the snout to the posterior edge of the lower jawbone.

DEYE: diameter of the eye measured between the edges of the scales surrounding it.

D. COLOUR PATTERN

STRIPE: presence of lateral stripe (0, absent; 1, indistinct; 2, distinct).

SCROC: number of scale rows involved in postocular stripe.

SCR1: the proportion of the first scale row covered by the light area.

APPENDIX 2:

Original description of *Trimeresurus macrops* Kramer, 1977.

Translated from the original German (Kramer, 1977): “Nasals fused with the first supralabial, second supralabial borders the pit, third supralabial is the largest. Supraoculars broader than the internasals, from which they are separated by three scales. Eight scales between the supraoculars at the narrowest point. Temporals with tubercular keeling, passing into 21 keeled scale rows around body. Outermost dorsal scale row smooth. Ground colour uniform dark green. Underside green, whitish towards head. Upper part of tail red brown, head as body, slightly bluish green, blue postocular stripe merging into white lateral stripe. Hemipenis divided by the fourth subcaudal, with papillae near the point of division, then calyculate, before the 4th subcaudal the tissue is smooth except for the sulcus, which ends near the 25th subcaudal.”