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REDESCRIPTION OF *TRIMERESURUS HUTTONI* SMITH, 1949 (SERPENTES, CROTALINAE), WITH A DISCUSSION OF ITS RELATIONSHIPS

Patrick David[1] and Gernot Vogel[2]

[1]Laboratoire de Zoologie (Reptiles et Amphibiens), Muséum National d'Histoire Naturelle, 25 Rue Cuvier, F-75005 Paris, France
[2]Society for Southeast Asian Herpetology, Im Sand 3, D-69115 Heidelberg, Germany
(with three text-figures)

ABSTRACT.- The Indian pit viper *Trimeresurus huttoni* Smith, 1949 is known from two specimens. The holotype is redescribed in detail. We suggest that the taxon *huttoni* is not related to other Indian species, but its colour, scalation and morphology agree with the characters of the Indo-Malayan genus *Tropidolaemus*. Consequently, it is here referred to the genus *Tropidolaemus*. The great similarities between *Trimeresurus huttoni* and *Tropidolaemus wagleri* are discussed.

KEY WORDS. - *Trimeresurus huttoni*, *Tropidolaemus*, Crotalinae, India, taxonomy.

INTRODUCTION

The *Trimeresurus*-complex is currently composed of five genera (*Trimeresurus, Ermia, Ovophis, Protobothrops* and *Tropidolaemus*) totalling 43 species (David and Ineich, 1998). The group is widely distributed in tropical and subtropical parts of southern, eastern, and southeastern Asia as far east as Timor Island. On the western border of the *Trimeresurus* complex range, 15 species are currently known from India, of which no fewer than seven are endemic. Four inhabit the Andaman and Nicobar archipelago (two species are endemic to these islands); six are present only in the Himalayan region and north east India; the remaining five (all endemic) inhabit the Western and Eastern Ghats and hills of southern peninsular India.

The most poorly known Indian species is undoubtedly *Trimeresurus huttoni*, described by Malcolm A. Smith (1949) from two juveniles collected by Mr. Angus F. Hutton in the High Wavy Mountains (see below), a small mountain range south-east of Madurai, State of Tamil Nadu, southern India. This species has been mentioned in several checklists of venomous snakes (Klemmer, 1963; Minton et al., 1966; Leviton, 1968; Burger, 1971; Harding and Welch, 1980; Hoge and Romano Hoge, 1981; Welch, 1988; Toriba, 1993), but its status has not been discussed. *T. huttoni* received little attention from Indian herpetologists. It is cited, without comments, by Murthy (1985, 1990a, 1990b, 1994) and Das (1994, 1996), but it is overlooked by Brattstrom (1964), Whitaker (1978), Deoras (1981) and Mahendra (1984). Besides the original description, data on this species can be found only in Hutton (1949), in a paper on animals from the Madurai region. *Trimeresurus huttoni* has not previously been illustrated, nor, as far as we know, rediscovered since the collection of the two original specimens.

This species ranks as one of the rarest Asian pit vipers, and its relationships were never discussed, except rather superficially by Smith (1949). It is interesting to note that the head of the holotype of *Trimeresurus huttoni* was still largely covered with red laterite. Obviously, this specimen has received little attention since its discovery. It is fortunately very well preserved and seems to have retained both its original colours and pattern.

The new taxon is mentioned in Hutton (1949: 460) as a new species. Although the scientific name and ecological data are given, no description is made, therefore the name appearing in Hutton (1949) is a *nomen nudum*. Later, in the same issue of the *Journal of the Bombay Natural History Society*, Smith (1949: 596) gives a formal description based on the two known speci-

mens. It is rather short, and we quote below, in full, the description of the holotype:

"Snout sharp, distinctly upturned, its edge continuous with the equally sharp canthus rostralis. Upper head scales unequal subimbricate, some of them obtusely keeled, 10 or 11 in a line between the supraoculars; these are narrow and entire but have their inner margins indented by the adjacent scales; internasals not twice as large as the adjacent scales, separated from one another by two small scales; supralabials, first entirely separated from the nasal, the third much larger than the others; temporals strongly keeled. Scales in 21: 23: 19 rows, indistinctly keeled on the posterior part of the body. Ventrals 146; anal entire; subcaudals 52 pairs".

"Green above, paler on the sides, with a distinct series of dorso-lateral, paired, small, white spots; pale green below; a white temporal streak, edge with red below; it is continued forwards in front of the eye; tip of snout and end of tail dull red".

"Total length 138, tail 40 mm."

According to the author, the paratype agrees well with the holotype, the differences being the separation of the internasals by a single scale, the presence of 8 scales between the supraoculars (= intersupraoculars), and the numbers of ventrals and subcaudals, respectively 139 and 49.

Smith (1949) did not discuss the relationships of his new species with other members of the *Trimeresurus*-complex, but just noted that the sharp upturned snout gave it a resemblance with *Trimeresurus borneensis*, whereas by its scalation it is related to *Trimeresurus erythrurus*, except for the separation of the first labial from the nasal.

Within the framework of a long-term systematic study of the *Trimeresurus*-complex, we examined types and specimens of most species. In the case of the present species, it is obvious that the original description is very incomplete, and that *Trimeresurus huttoni* shows unusual features for a member of the genus *Trimeresurus* sensu stricto. We therefore redescribe the holotype, and examine its relationships by comparing it with other species of the group.

MATERIALS AND METHODS

The holotype of *Trimeresurus huttoni* (BMNH 1948.1.8.75) was examined for its external features of colouration and morphological and meristic characters. It is here fully redescribed. No attempt was made to obtain data on its skull because of the uniqueness of this specimen. We did not study the paratype that Smith (1949) mentioned as being deposited in Hutton's private collection, which is now in the collection of the Bombay Natural History Society (BNHM), according to Angus Hutton (in litt., 1997).

We compared 23 characters of *Trimeresurus huttoni* with those of 12 species of the *Trimeresurus*-complex, namely those known to occur in southern India, plus a selection of other species known to have a green dorsal colour either in juveniles or adults. The morphology and scalation of *T. huttoni* was also compared in detail with those of specimens of *Tropidolaemus wagleri* from four regions.

The number of ventrals was counted according to Dowling (1951). We did not include the terminal scute in the number of subcaudals. The numbers of dorsal scale rows was counted, respectively, at one head length behind the head, at midbody (at the level of ventral corresponding to one-half the total number of ventrals), and at one head length before vent. Head scalation nomenclature follows Peters (1964).

The list of specimens examined is given in Appendix I. Museum acronyms follow Leviton et al. (1985):

BMNH: British Museum (Natural History), at present, The Natural History Museum, London; BNHM: Bombay Natural History Society, Mumbai; MNHN: Muséum National d'Histoire Naturelle, Paris; NMW: Naturhistoriches Museum, Wien; TNRC: Thai National Reference Collection, Bangkok; SMF: Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main; SMNH: Shanghai Museum of Natural History, Shanghai.

REDESCRIPTION OF THE HOLOTYPE OF *TRIMERESURUS HUTTONI*

(Figs. 1-3)

Body moderately stout, cylindrical; head rather short and wide at its base, about 1.6 times longer

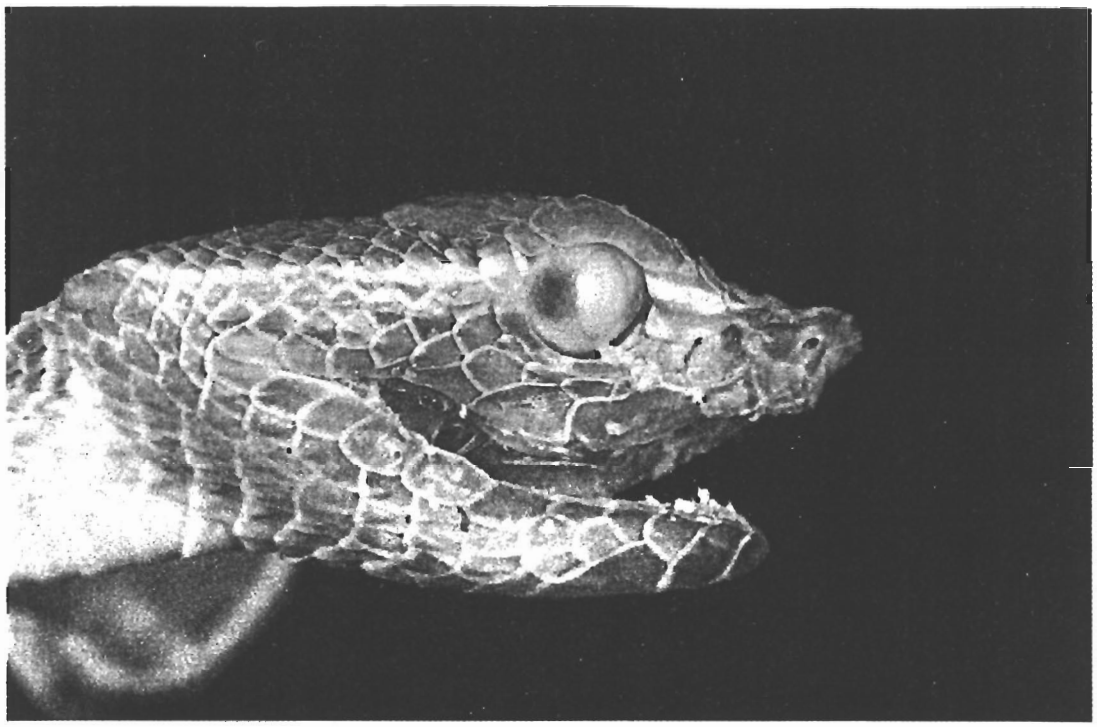

FIGURE 1: Lateral view of head of holotype of *Trimeresurus huttoni* (BMNH 1948.1.8.75).

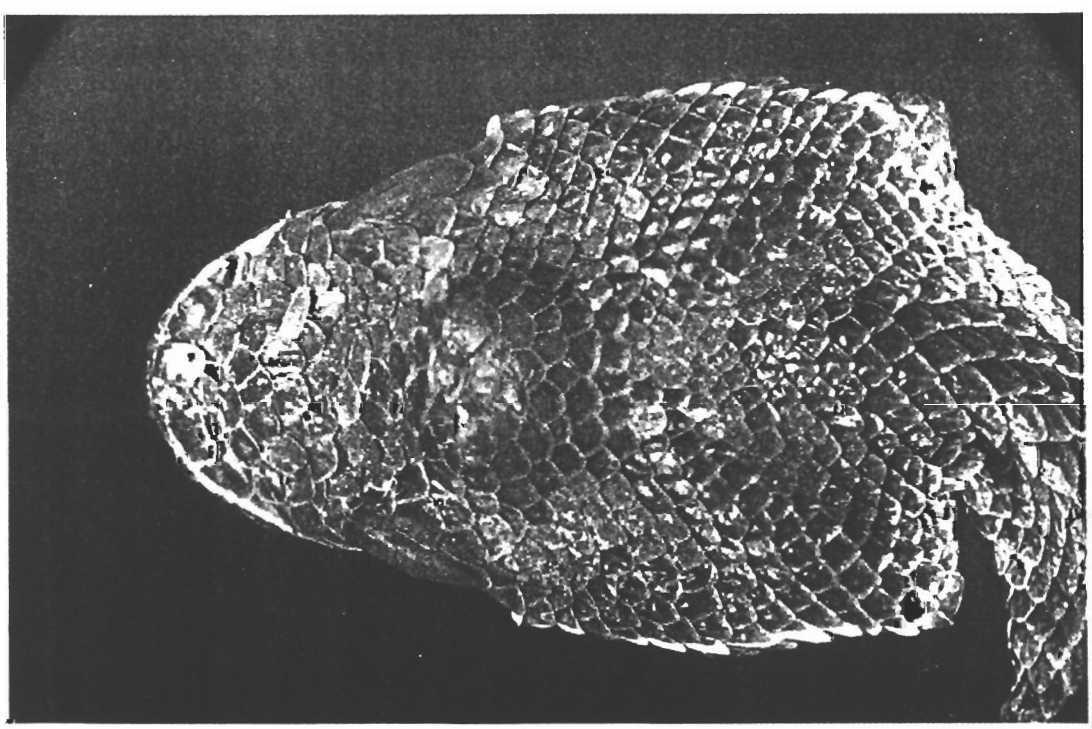

FIGURE 2: Dorsal view of head of holotype of *Trimeresurus huttoni* (BMNH 1948.1.8.75).

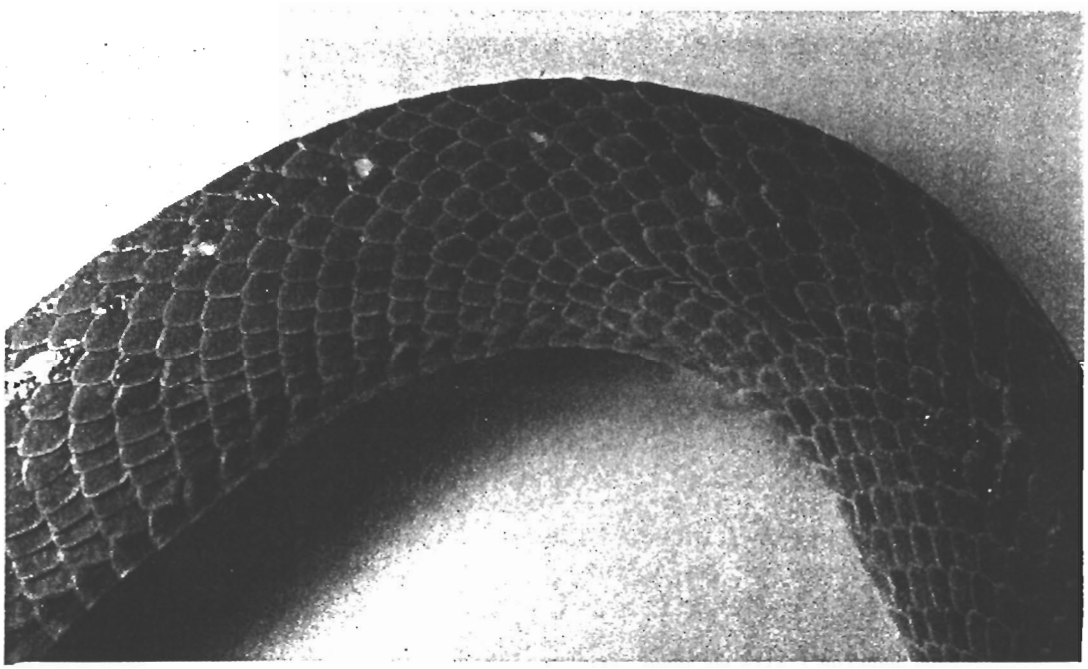

FIGURE 3: Dorsal view at midbody of holotype of *Trimeresurus huttoni* (BMNH 1948.1.8.75).

than wide, triangular, clearly distinct from neck, thick, slightly rounded medially but flattened in front of the eye and depressed in the middle of the snout; snout short, about twice as long as the diameter of the eye, slightly protracted, flattened, its tip only just slightly raised compared with its depressed, concave middle part, rounded and narrow when seen from above, angular and slightly prominent when seen from the side, with a sharp canthus rostralis; eye large (juvenile), diameter similar to the distance between its lower margin and upper lip edge; ratio of nostril-loreal pit distance/nostril-eye distance 0.61 (mean value of each side); tail cylindrical, very long and tapering, prehensile.

Snout-vent length (SVL): 98 mm, tail length (tL): 38 mm; total length (TL): 136 mm.

tL / TL ratio: 0.28.

Ventrals: 146; subcaudals: 52 pairs + one terminal scale; anal entire.

Dorsal scales: 25 [not 21 as written by Smith]-23-19, rhombic and smooth at midbody, some feebly keeled on the posterior part of body.

Rostral as high as wide, triangular, barely visible from above, nasal triangular, undivided, with nostril in its middle; no nasal pore visible; 1 pair of narrow enlarged, internasals, about twice as long but barely wider than adjacent scales on upper snout surface, separated from one another by 1 (not 2 as mentioned in the original description) small scales that are about half as wide as the internasals; 4 subequal canthal scales bordering the canthus rostralis between the internasal and the corresponding supraocular, slightly enlarged compared with adjacent snout scales; 1 small triangular loreal; 2 upper preoculars above the loreal pit, the lower one bordering the upper margin of the loreal pit, the upper one visible from above, both elongated and in contact with the loreal; the lower preocular that normally borders the lower margin of the loreal pit is divided into two small scales; 2 postoculars; 1 supraocular, entire, long and narrow, barely larger than the adjacent dorsal head scales and narrower than internasals, largely indented on its inner margin; dorsal snout and cephalic scales relatively large, irregular and unequal, juxtaposed or barely imbricate, flat, distinctly keeled both on the snout and on the middle and posterior part of the head, more keeled and rather imbricate on posterior part of head; 9 intersupraoculars; temporals in three rows, the lower ones enlarged, as large as

the supralabials, all strongly keeled; 1 thin, elongated, crescent-like subocular; 9 supralabials on each side, the third being the largest; 1st supralabial completely separated from the nasal; 2nd not bordering the anterior margin of the loreal pit and bordered above by a prefoveal that lines the whole of the anterior margin of the loreal pit, one granular scale on each side between the nasal and the 2nd supralabial; 3rd supralabial large, rather low and elongated, about 2.3 times as long as high, separated both from the posterior lower preocular scale and from the subocular by one small scale; 4th supralabial nearly as high and long as the third, separated from the subocular by 1 small scale; 5th and succeeding posterior supralabials much smaller than preceding ones, not larger than lower temporals but smooth; 5th supralabial separated from the subocular by two scale rows and in contact with the first and second lower temporals; 10 pairs of infralabials, those of the first pair in contact with each other and obtusely but distinctly keeled, infralabials of the first, second and third pairs in contact with the chin shield; one pair of elongated, keeled chin shields; 7 rows of gular scales, distinctly keeled.

In preservative, dorsal body and tail surfaces dull green, slightly paler on the sides of the body, with a series of small, vertically elongated white spots located on each side of the 2nd and 3rd scale rows from the vertebral row, separated from each other by about 3-5 scales; no ventrolateral stripes; pale green below; end of tail dull reddish-brown for a length equivalent to the 25 posterior subcaudal scales.

Head dull green above and on its sides; a white postocular streak on the 3rd and 4th rows of temporals from eye to the neck, edged below with a dull, discoloured, rather indistinct red streak; a preocular white streak running forward in front of the eye, on the upper preocular and loreal, vanishing on this latter scale and not reaching the nasal; this anterior white streak is bordered below with a reddish, indistinct streak that makes the snout tip reddish.

RESULTS AND DISCUSSION

Our interest in the *Trimeresurus* complex led us to examine more than 300 specimens of nearly all species of these Asian pit vipers, including the name-bearing types of most valid species. It appeared immediately and totally unexpectedly that, from our study of the holotype, this specimen shows a striking similarity in habitus and colouration to juveniles of *Tropidolaemus wagleri*. In the latter species, juveniles have a characteristic overall green colouration (even if adult animals typically become yellow and black) with red or white spots on the dorsum or vertical bars on the flanks, and a pre- and postocular bicolour streak. Furthermore, these similarities in pattern between *huttoni* and *Tropidolaemus wagleri* are supported by largely identical morphological and meristical characters, namely a second supralabial not bordering the loreal pit and the strongly keeled dorsal head and gular scales.

The genus *Tropidolaemus* Wagler, 1830 was resurrected as a subgenus of *Trimeresurus* by Brattstrom (1964), and considered to be a distinct genus by Burger (1971) on the basis of both anatomical and external features. This genus is currently monospecific, including the sole species *Tropidolaemus wagleri* Wagler, 1830 (see David and Vogel, 1996 and David and Ineich, 1998). According to Brattstrom (1964), the genus *Tropidolaemus* is defined as follows:

"Top of head with numerous small scales of varying size, including many or several in the frontal area. All scales on top of head usually keeled; gular scales keeled. Nasal pore absent. Subcaudals in one or two rows. Pterygoid teeth extending posteriorly past middle of junction of ectopterygoid with pterygoid. Ectopterygoid longer than basal portion of pterygoid. Palatine low, not humped or forked. Frontals with centers depressed. Lower lumen of fang medial. Prefrontals laterally wider than long. Curvature of pit cavity interrupted by a small process or knob. Venom neurotoxic. Color primarily green. Arboreal." (verbatim from Brattstrom, 1964: 251).

Tropidolaemus wagleri is a wide ranging and often common species that occurs from southern Thailand south to Sumatra, then eastwards through Borneo and the Philippine Islands to Sulawesi (David and Ineich, 1998). Several colour morphs are known in this species, some of them seemingly correlated with range. We con-

TABLE 1: Comparison of morphological data and body scalation in pit vipers (genera *Tropidolaemus, Trimeresurus* and *Protobothrops*). Abbreviations: Obc: Overall body colour bright green in life: + yes, - no. - Bws: white and red dorsolateral vertical bars or dorsolateral spots on body: + present, - absent. - Prs: preocular streak: + present, - absent. - Pos: postocular streak: + present, - absent. - Cps: colour of the postocular streak: - absent, 1 black or dark brown, 2 white, 3 white plus reddish-brown or orange, 4 yellow plus black. - tL/TL: ratio tail length/total body length (range). - Npo: presence of a nasal pore: + present, - absent. - Ven: number of ventrals (range). - Sc: number of subcaudals (range). - Co (m): number of dorsal scale rows at midbody. - KCo: dorsal scale rows at midbody keeled: ++ strongly keeled, + weakly keeled, - smooth. Sources of comparitive data listed with Table 2.

TAXON	Obc	Bws	Prs	Pos	Cps	tL/TL	Npo	Ven	Sc	Co (m)	KCo
Tropidolaemus huttoni	+	+	+	+	3	0.28	-	139-146	49-52	23	-/+
Tropidolaemus wagleri	-/+ (a)	+/- (a)	+	+	1-4	0.14-0.19	-	127-154	45-56	21-27	+/++
Trimeresurus gramineus	+	-	-	+/-	1	0.16-0.18	+	145-177	55-71	21	-/+
Trimeresurus labialis	-	-	-	-/+	0/2	0.13-0.19	+	154-174	46-65	21-23	-/+
Trimeresurus macrolepis	+	-	-	-/+	0/1	0.15-0.23	+	133-144	44-56	12-16	+/++
Trimeresurus malabaricus	-/+	-	-	-/+	0/1	0.15-0.18	+	136-159	44-63	(19) 21-23	+/++
Protobothrops strigatus	-	-	-	-/+	0/1	0.12-0.16	+	128-150	32-52	21 (23)	-/+
Trimeresurus trigonocephalus	+	-	-	+	1	0.15-0.17	+	142-170	53-69	(17)-19	-/+
Trimeresurus albolabri albolabris	+	-	-	-	-	0.14-0.21	+	149-173	48-78	21 (23)	+/++
Trimeresurus erythrurus	+	-	-	-	-	0.15-0.21	+	151-180	49-79	(21) 23-25	+
Trimeresurus hageni	+	- (b)	-	+	2	—	+	177-198	63-85	21	+
Trimeresurus stejneger (c)	+	- (d)	-	-/+	0-2/3	0.17-0.22	+	150-172	59-77	21	+

Additional notes.-

(a). - Juvenile specimens, from all populations, and most adult males are bright green. The preocular bicolour streak, and the rows of white or white and reddish-brown vertebral spots or short vertical bars occurs typically in green specimens. In the typical form from Thailand and Malaya, the preocular streak (yellow) is difficult to distinguish from the snout pattern.

(b). - Large, rounded, white or pinkish-white dorsolateral spots are present.

(c). - There could be several undescribed species under this name; we give data for the nominal species *stejnegeri* sensu lato.

(d). - Sometimes white vertebral spots, but not dorsolateral dots as in *huttoni* and *wagleri*.

sider the systematics of this species to be still unresolved (see below for a discussion). Leviton (1964) considered *Tropidolaemus wagleri* a monotypic species, an interpretation followed by most subsequent authors. We retain it here, although it seems quite unsatisfactory. However, it appears that juveniles from all populations exhibit nearly identical colouration and pattern, typically bright green with one row of small white or white and small red spots on each side of the upper parts of the body, or short vertical white or red bars on the flank, a loreal and temporal bicoloured streak, and a reddish tail tip.

We compared only external features of *Trimeresurus huttoni* with those of (1) *Tropidolaemus wagleri* (juveniles and adults),

TABLE 2: Comparison of head scalation and other features in pit vipers (genera *Tropidolaemus, Trimeresurus* and *Protobothrops*). Abbreviations: SpL: number of supralabials (range). - Ssn: separation of the 1st supralabial with the corresponding nasal: + yes, both scales totally differentiated, - no, both scales partly separated by a shallow furrow or totally fused. - CSP: contact of the second supralabial with the loreal pit: + yes, - no. CSob: number of the supralabial(s) that are in contact with the subocular. Is: number of intersupraoculars between the supraoculars (range). Kus: strong keels on upper snout scales: + yes, - no. Kuh: keels on upper head scales: ++ strongly keeled, + weakly keeled, - no. Kte: keels on temporals scales: ++ strongly keeled, + weakly keeled, - absent. InL: number of infralabials. CIn: first pair of infralabials in contact: + yes, - no. Klh: keels on gular and chin scales: ++ strongly keeled, + weakly keeled, - absent.

TAXON	SpL	Ssn	CSP	Is.	CSob	Kus	Kuh	Kte	InL	CIn	Klh
Tropidolaemus huttoni	9	+	-	8-9	0	+	+	+	10	+	+
Tropidolaemus wagleri	8-10	+	-	10-17	0	+	+	+	10-13	+	+
Trimeresurus gramineus	10-12	+	+	8-11	0	-	-	-	9-10	+	-
Trimeresurus labialis	9-12	-	+	8-11	Nr 3 or 3 & 4	-	-	-	11-16	+	-
Trimeresurus macrolepis	7-9	+	-/+	3	Nr 3 or 3 & 4	-	-	-	10-12	+	-
Trimeresurus malabaricus	8-10	+	+	7-9	0	-	-	-/+	10-13	+	-
Protobothrops strigatus	8-10	+	-	8-11	0	-	-	-	9-12	+	-
Trimeresurus trigonocephalus	9-11	+	+	2-6	Nr 3 & 4	-	-	-/+	12	+	-
Trimeresurus albolabri albolabris	7-13	-	+	8-14	0 or Nr 3	-	-	-/+	11-16	+	-
Trimeresurus erythrurus	9-13	-	+	10-15	0	0	0/++	+	12-14	+	0
Trimeresurus hageni	9-11	+	+	4-8	Nr 3	0	0	0	13	+	0
Trimeresurus stejneger (b)	9-12	+	+	9-13	0 or Nr 3	0	0/+	0/+	11-15	+	0

Sources:
Tropidolaemus wagleri: Boulenger (1896); Leviton (1964); De Rooij (1917); Tweedie (1983). - 24 specimens
Trimeresurus trigonocephalus: Wall (1921); Smith (1943); Deraniyagala (1955); A. De Silva (1990a, 1990b); P. H. D. H. De Silva (1980). - 2 specimens.
T. gramineus: Mahendra (1984); Murthy (1990a, 1990b); Pope and Pope (1933); Regenass and Kramer (1981); Smith (1943); WALL (1919).
T. labialis: Mahendra (1984); Murthy (1990b); Smith (1943); Werner (1926). - 6 specimens.
T. macrolepis: Boulenger (1896); Mahendra (1984); Murthy (1990a, 1990c); Smith (1943). - 6 specimens.
T. malabaricus: Mahendra (1984); Murthy (1990a, 1990b); Rao (1917); Smith (1943). - 4 specimens.
Protobothrops strigatus: Boulenger (1896); Mahendra (1984); Murthy (1990a, 1990b); Smith (1943). - 4 specimens.
Trimeresurus albolabris: Pope and Pope (1933); Regenass and Kramer (1981); Smith (1943). - 10 specimens.
T. erythrurus: Pope and Pope (1933); Regenass and Kramer (1981); Smith (1943); Toriba et al. (1990). - 2 specimens.
T. hageni: Tweedie (1983). - 1 specimen.
T. stejnegeri: Pope and Pope (1933); Smith (1943); Regenass and Kramer (1981). - 12 specimens.

TABLE 3: Comparisons between *Tropidolaemus huttoni* and *T. wagleri*. Abbreviations: n: number of specimens examined. Obc: Overall body colour bright green: + yes, - no. Bws: white vertical stripes or dots on body: + present, - absent. Cps: colour of the postocular streak: 1 black, 2 white, 3 reddish-brown + white, 4 yellow + white. tL/TL: tail length/total body length ratio (range). Ven: number of ventrals plates. Sc: number of subcaudals. Co: number of dorsal scale rows at midbody. KCo: carination of dorsal scales at midbody: ++ strongly keeled, + keeled, - smooth. SpL: number of supralabials (left/right). Cep: number of cephalic scales between the supraoculars (range). InL: number of infralabials (range).

Population	Obc	Bws	Cps	tL/TL	Ven	Sc	Co	KCo	SpL	Cep	InL
Trop. huttoni	+	+	3	0.28	139-146	49-52	23	-/+	9	8-9	10
Trop. wagleri (literature data for the whole range)	-/+	-/+	1-4	0.14-0.19	127-154	45-56	21-27	+/++	8-10	10-17	10-13
Thailand/Malay	-/+	-/+	3/4	0.14-0.17	134-141	49-54	25	+	9-10	13-17	11-13
adults (n = 4)	-	-	4	0.14-0.17	134-141	49-54	25	+	9-10	13-17	11-13
juveniles (n = 1)	+	+	3	—	—	—	—	+	—	—	—
Java/Sumatra	-/+	-/+	1/2/4	0.15-0.19	135-138	45-55	23-25	+/++	9-10	12-15	11-13
adults (n = 4)	-	-	4	0.15-0.17	137-138	45-52	25	+	9-10	12-15	11-13
juveniles (n = 2)	+	+	1/2	0.18-0.19	135	54-55	23	+	10	12	11
Borneo	-/+	-/+	1/3	0.14-0.18	130-142	46-53	21-27	+	9-10	10-13	10-12
adults (n = 6)	-	-/+	1/3	0.14-0.18	130-142	46-53	21-27	+	9-10	10-13	10-11
juveniles (n = 1)	+	+	3	0.15	140	48	21	+	9-10	13	12
Philippine Is.	+	-/+	1/3	0.14-0.16	127-137	45-50	23-25	+/++	9-10	12-16	10-11
adults (n = 5)	+	-/+	1/3	0.14-0.16	127-137	45-50	23-25	+/++	9-10	12-16	10-11

(2) all south Indian and Sri Lankan taxa (*Trimeresurus gramineus, T. macrolepis, T. malabaricus, T. trigonocephalus*, plus *T. labialis* from the Andaman Islands, and the taxon *strigatus*, recently tentatively placed in the genus *Protobothrops* [Kraus et al., 1996]), and (3) a selection of green *Trimeresurus* species covering each of the groups recognised by Brattstrom (1964: 244). Among these taxa, we selected *T. albolabris albolabris, T. erythrurus, T. hageni* (a taxon not mentioned by Brattstrom but closely related to *T. sumatranus*) and *T. stejnegeri*. Results are given in Tables 1-2.

Data were taken from an examination of preserved specimens and from the literature (see Table 2) for general meristic data such as number of ventrals, subcaudals and supralabials, and from an examination of preserved specimens for supplementary meristic data and specific characters or data not found in literature. We retained 23 characters that may be considered to be diagnostic in the *Trimeresurus*-complex, bearing respectively on body colouration, morphology and body scalation (Table 1) and head scalation (Table 2). These characters are as follows:

Colouration: Overall body colouration; presence of white stripes or dots on body; presence of a preocular streak; presence of a postocular streak; colour of the postocular streak.

Morphology: Ratio tail length/total body length (limits of range and mean value); presence of a nasal pore; separation of the 1st supralabial from the corresponding nasal; contact of the second supralabial with the loreal pit; presence of keels on upper snout scales; presence of keels on upper head scales; presence of keels on temporals; first pair of infralabials in contact or not; presence of keels on gular and chin scales.

Meristic characters: Number of ventrals; number of subcaudals; number of dorsal scale rows at midbody; number of supralabials; number and shape of loreal(s); intersupraoculars; number of supralabial(s) in contact with the subocular; number of infralabials.

It results from these data that the nominal taxon *huttoni* differs by the combination of six major, diagnostic generic characters (2nd su-

pralabial not bordering the loreal pit, scales keeled on snout, upper head and chin, presence of a preocular streak, dorsolateral white and red spots) from all other members of the *Trimeresurus*-complex with the exception of *Tropidolaemus wagleri*, with which it shares all these characters, at least in the juveniles and the green adult specimens. We examined specimens from more species of the *Trimeresurus*-complex than those here mentioned above for our comparison, and all of them also largely differ from *huttoni*.

The strong morphological similarities between the taxon *huttoni* and *Tropidolaemus wagleri* were thoroughly examined. The question was a possible conspecificity between these taxa. We give in Table 3 a detailed comparison of selected morphological and meristic data between *huttoni* and specimens of *Tropidolaemus wagleri* from several populations. Diagnostic generic characters that are not repeated in this table are: the lack of a nasal pore, the dorsal snout scales, upper head scales and gular scales keeled, the supralabials not in contact with the subocular and the keeled temporals. In this table, specimens regarded as juveniles have a total length below 300 mm.

Because of the presence in the holotype of *Trimeresurus huttoni* of all external generic diagnostic characters of the genus *Tropidolaemus*, we here refer this nominal taxon to the genus *Tropidolaemus* Wagler, 1830. However, the very long tail in *huttoni* and its geographical isolation lead us to regards *huttoni* as specifically distinct from *Tropidolaemus wagleri*. We therefore propose the following new combination:

Tropidolaemus huttoni (Smith, 1949) new combination

"*Trimeresurus huttoni*" Hutton, 1949: 460. *Nomen nudum*, no description.

Trimeresurus huttoni Smith, 1949: 596. - Type locality.- "The High Wavy Mountains, Madura District, South India; altitude 5,200 feet", now a plateau in the western central edge of the Varushanad Hills, just east of Kambam, District of Madurai, State of Tamil Nadu, India, 1590 m. - Holotype. BMNH 1948.1.8.75, sex male; coll. Angus F. Hutton. Paratype.- Originally in the private collection of Angus Hutton (Smith, 1949), at present BNHM 2658; sex unknown, same collector.

Trimeresurus huttoni: Klemmer, 1963: 432; Minton et al., 1966: 118; Leviton, 1968: 566; Burger, 1971: 31; Harding and Welch, 1980: 73; Hoge and Romano Hoge, 1981: 259; Regenass and Kramer, 1981: 165; Murthy, 1985: 69, 1986: 83, 1990a: 63, 1990b: 83, 1994: 35; Welch, 1988: 137, 1994: 115; Toriba, 1993: 100; Murthy et al., 1993: 139; Das, 1994: 38, 1996: 62.

Diagnosis. - A pit viper endemic to southern peninsular India characterised by the absence of a nasal pore, an elongated snout, slightly raised at its tip, upper surface of snout and head covered with small, distinct keels, strongly keeled gular scales, second supralabial not bordering the anterior margin of the loreal pit and bordered above by a prefoveal, a tail length/total length ratio of at least 0.28, green colouration in juveniles, and white and red pre- and postocular streaks.

Variations. - Only two specimens are known. The currently reported variation is: ventrals 139-146; subcaudals 49-52; 8-9 intersupraoculars (Smith, 1949).

Range. - India: State of Tamil Nadu: western Varushanad Hills (in the High Wavy Mountain Range). Known only from the type locality.

The High Wavy Mountains are located just east from the city of Kambam, from where its summit and a waterfall can be seen when looking towards the east (Blatter and Hallberg, 1917). In general, they correspond to an elevated plateau in the centre of the western edge of the Varushanad Hills, at about 09°30'N, 77°30'E. Bates and Harrison (1997), in their gazetteer, gave the coordinates for the High Wavy as 09° 50'N; 77° 26'E. According to Angus Hutton (pers. comm., 1997), the locality of capture was around coordinates 09°36'N, 77°15'E. The High Wavy Mountains are currently owned by a private tea estate.

Blatter and Hallberg (1917) and Hutton (1949) described the High Wavy Mountains as an undulating plateau, approximately 17 square miles (ca. 44 square km), with an average elevation of about 1,500 m (ca. 5,100 ft), that rises steeply from the surrounding plains. The highest point of the plateau, Brooks Peak, is over 1,950 m (ca. 6,100 ft). The wet montane evergreen forest begins at an elevation of 1,200 m. Lower

elevations are covered with grasslands and light deciduous forests, and do not support the evergreen forest suitable for species restricted to primary montane wet forests. According to Hutton's description, only a small area of the plateau was cultivated at that time.

Biological data. - Both types were collected at an elevation of 1590 m in an evergreen wet montane forest. These animals were discovered from beneath leaves of a hill bamboo (*Ochlandra travancorica*) clump, a plant locally known as "Eeta" in Tamil. The diet and other aspects of its biology are unknown.

TAXONOMIC IMPLICATIONS

This new combination modifies the content of the genus *Tropidolaemus*, which, however, still remains uncertain. *Tropidolaemus huttoni*, as currently known, can be separated from juvenile *T. wagleri* only by the much higher tail length/total length ratio in *T. huttoni* (0.28) than in *T. wagleri* (0.14-0.19) and by its geographic range. Otherwise, the holotype of *huttoni* is similar to juveniles of *wagleri* of equivalent size.

The current subspecific systematics of the wide ranging species *Tropidolaemus wagleri* is not resolved. Three subspecies were recognised by Taylor (1922a: 298): *Tropidolaemus wagleri wagleri* Wagler, 1830, *T. wagleri alboviridis* (Taylor, 1917) and *T. wagleri subannulatus* (Gray, 1842), the latter two being endemic to the Philippine Islands. Leviton (1964) considered *Tropidolaemus wagleri* to be a monotypic species, and this arrangement has been followed by subsequent authors. However, there are positive relationships between colour morphs and geographical range, and it is possible that some insular populations deserve a subspecific status.

The status of *Trimesurus philippinensis* Gray, 1842 (Gray, 1842: 48; type locality: Philippine Islands), regarded as valid by Taylor (1922) and Maslin (1942) as *Trimeresurus philippinensis*, is not resolved either. It was placed in the synonymy of *Trimeresurus wagleri* (now *Tropidolaemus wagleri*) by Leviton (1964: 266), who, however, apparently did not examine its holotype. We examined the holotype of *Trimeresurus philippinensis* (BMNH 1946.1.1767) and another specimen (MNHN 4064, Paris; holotype of *Tropidolaemus hombroni* Guichenot in: Dumont d'Urville, 1848). Both specimens display external features diagnostic of the genus *Tropidolaemus*. Compared with *Tropidolaemus wagleri* both specimens from the Philippine Islands display notable differences in the morphology of the head, in the scalation of head and body, and in colouration. They may belong to a valid species, distinct from *Tropidolaemus wagleri*, for which the name *Tropidolaemus philippinensis* is available. The problem will be addressed in a later paper. We therefore take a conservative approach, and for now, retain only two species in the genus *Tropidolaemus*.

Tropidolaemus Wagler, 1830

Tropidolaemus Wagler, 1830: 175.

Type species. - *Tropidolaemus wagleri* Wagler, 1830, by monotypy.

Diagnosis. - A genus of Asian Crotalinae characterised by the absence of a nasal pore, and by the upper surface of the snout and head covered with distinctly keeled small scales, strongly keeled gular scales, the second supralabial not bordering the anterior margin of the loreal pit and bordered above by a prefoveal, green colouration in juveniles, and the presence of a white and red pre- and postocular streak.

Relationships. - Long regarded as a synonym or a subgenus of *Trimeresurus* (Brattstrom, 1964), the genus *Tropidolaemus* was resurrected by Burger (1971) to accomodate the species formerly referred to *Trimeresurus wagleri*. This interpretation was confirmed by phylogenetic analysis based on immunological data and mitrochondrial DNA sequence data, which have shown that *Tropidolaemus wagleri* is only distantly related to species of *Trimeresurus* sensu stricto (Kraus et al., 1996). The distinctiveness of the genus *Tropidolaemus*, which constitute a basal lineage within the Asian crotalines, is now regarded acceptable (Cadle, 1992; Kraus et al., 1996; Vidal, unpublished).

Contents. - Two species: *Tropidolaemus huttoni, T. wagleri.*

Tropidolaemus huttoni (Smith, 1949)

Trimeresurus huttoni Smith, 1949: 596.

Type locality. - "The High Wavy Mountains, Madura District, South India; altitude 5,200

feet", now a plateau in the western central edge of the Varushanad Hills, Madurai District, State of Tamil Nadu, India, 1590 m.

Comments. - This species is monotypic.

Diagnosis. - A species endemic to southern India characterised by a tail length/total length ratio of 28%.

Range. - India (State of Tamil Nadu).

***Tropidolaemus wagleri* Wagler, 1830**

[*Tropidolaemus*] *wagleri* Wagler, 1830: 175.

Type locality. - Asia.

Comments. - We refer the reader to David and Vogel (1996) for a discussion about the authorship of this species, previously credited to Boie (1827) or Schlegel (1837). This species is monotypic (see above).

Diagnosis. - A species of the genus *Tropidolaemus* found in south-eastern Asia and Indonesia characterised by a tail length/total length ratio less than 20%.

Range. - Brunei Darussalam; Federation of Malaysia (Peninsular Malaya and East Malaysia on Borneo Island); Indonesia (Bangka Is., Belitung Is., Butung Is., Kalimantan on Borneo Is., Karimata Is., Mentawai Archipelago, Natuna Archipelago, Nias Is., Sulawesi, Sumatra); Philippine Islands (Balabac Is., Basilan Is., Bohol Is., Dinagat Is., Jolo Is., Leyte Is., Luzon Is., Mindanao Is., Negros Is., Palawan Is., Samar Is., Siasi Is., Sibutu Is., Tawitawi Is.); Singapore; and Thailand.

ZOOGEOGRAPHICAL REMARKS

There is no possibility for an erroneous type locality of *Tropidolaemus huttoni*, and human introduction in this remote locality, once regarded as largely unexplored by Angus Hutton, may be ruled out. This generic reallocation considerably extends the range of the genus *Tropidolaemus* westwards. The previous western limit was extreme southern Thailand, from the Surat Thani Province of southern Thailand (Cox, 1991). The presence of a *Tropidolaemus* species in southern peninsular India is therefore intriguing.

There are other reptile genera that show a similar distribution, occurring in south-east Asia (Indo-China, Malaya and the Indo-Malayan Archipelago) and southern India and Sri Lanka, with an apparent absence from Myanmar and eastern and central India. According to Das (1996), there are 42 genera of Indo-Malayan reptiles represented in the Indian region. Some snake genera of southern India with Indo-Malayan affinities have been discussed by Hora and Jayaram (1949), the most striking examples being the genera *Cylindrophis* and *Chrysopelea* (ranges according to Welch, 1988). The former has a single species endemic to Sri Lanka (*C. maculatus*), seven on various islands of the Sundas and a widespread species (*C. ruffus*) that is found on both mainland (south of latitude 26° N) and insular situations, eastwards up to Sulawesi, across many of the islands of the Indo-Malayan Archipelago. The latter genus has three Indo-Malayan species and one Sri Lankan endemic, in addition to a widespread species (*Chrysopelea ornata*) with a discontinuous range, being found in eastern India to southern China, southwards to Malaya, with populations in south-western India and Sri Lanka.

These and other snake genera discussed by Hora and Jayaram (1949) share a common characteristic in being absent from the area between the Indo-Chinese region and southern peninsular India. Based on such discontinuous ranges, Hora (1937; 1949; 1953) developed the Satpura Hypothesis, which explained the phenomenon by suggesting the existence of an ancient mountain range between the Vindhyas and Satpuras of north-central India, on one side, and the Garo-Khasi Hills of north-eastern India, on the other. The Indo-Malayan species could have migrated from north-eastern India towards the Western Ghats of peninsular India along these wet mountains. This hypothesis is, however, not supported by recent geological data, although Swan (1993) provided some seismographic and zoogeographical evidence in its support. On the other hand, apart from a few shared genera, Das (1996) showed that the reptile faunas of the Western Ghats and of north-eastern India are not similar, and concluded that the occurrence of Indo-Malayan elements in the fauna of southern India and Sri Lanka to be the remnants of an ancient, much wider distribution of plant and animal groups. The mesic forests on the moun-

tains of southern India were the sole refuges to many Indo-Malayan forest-dwelling elements, that are now absent from the adjacent dry lowlands. The extinction along the route is thought linked to climate change following the Eocene, when a recession of tropical evergreen forests took place, being replaced by dry savannas. Many species in the uplands, particularly those with affinities in the east, therefore are considered relicts in terms of distribution, and isolated from their close relatives much further east.

Some evidence in support of this hypothesis is provided by the known distribution pattern shown by members of the *Trimeresurus*- complex (involving the genera *Trimeresurus, Ermia, Ovophis, Protobothrops* and *Tropidolaemus*). Species of one or more of these genera are found as far west as Nepal and northern India, but none have been recorded from central India. However, not less than six endemic species have been described from the evergreen forest-clad hills of the Western and Eastern Ghats. This is in support of the suggestion of Das (1996), of an ancient, more widespread distribution of evergreen forest species within the Indian peninsula. It is worth noting that *Tropidolaemus wagleri* is typically a lowland species, with a maximum recorded elevation of 1,300 m in Sumatra (David and Vogel, 1996), but is more usually found at much lower elevations, while its Indian congener is known only from a montane forest above 1,500 m.

The distribution pattern of *Tropidolaemus* differs notably from those involved in the Satpura Hypothesis in that the ranges of genera discussed by Hora (1953) extend much further north (Myanmar and north-eastern India) than *T. wagleri*, a conspicuous and well-known lowland species that is absent north of peninsular Thailand, and even from apparently ecologically suitable islands, lowlands and hills of southern Myanmar. This distributional disjunction is much wider than those known in genera upon which Hora based his hypothesis. A better knowledge of the distribution of *T. huttoni* through further collections would throw light on the zoogeography of the genus.

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APPENDIX I
SPECIMENS EXAMINED

Protobothrops strigatus: MNHN 4061, "Hindoustan" (= India); SMF 21208, Nilgiri Hills, Tamil Nadu, India; SMF 21209/1-2, Nilgiri Hills, Tamil Nadu, India.

Trimeresurus albolabris albolabris: MNHN 1885.384, near Sisophon, Province of Aranh, Cambodia; MNHN 1980.1343-1344, Cambodia; MNHN 1989.702, Cambodia; MNHN 1897.432, Ban Taxeng, Kas' country, Laos; MNHN 1893.415-416, Bhamo, Myanmar; MNHN 1904.404-405, Province of Cao Bang, Vietnam; MNHN 1974.1350, Province of Ha Tinh, Vietnam.

Trimeresurus erythrurus: MNHN 4058, "Bengale"; SMF 73377, unknown locality.

Trimeresurus hageni: MNHN 1899.269, Malaya, Federation of Malaysia.

Trimeresurus labialis: NMW 18813:1-3, Nicobar Islands, India; NMW 14863:1-3, Nicobar Islands, India.

Trimeresurus macrolepis: MNHN 1913.3-4, Palni Hills, east of Dindigul, State of Tamil Nadu, India, 2000 m; MNHN 1946.82, India; MNHN 1948.338, India; MNHN 1948.339, India; MNHN 1948.340, India.

Trimeresurus malabaricus: MNHN 1913.5, Palni Hills, near Tiruchirapalli, State of Tamil Nadu, India; NMW 23946:1-2, Anaimallai Hills, State of Tamil Nadu, India; NMW 23945, Anaimallai Hills, State of Tamil Nadu, India.

Trimeresurus stejnegeri: MNHN 1912.352, "San Chouen Fou", Province of Guizhou, People's Republic of China; SMNH 4038, Da Jing, Mt. Jing Gang, Province of Jiangxi, People's Republic of China; SMNH 4426, Mt. Feng Yang, Province of Zhejiang, People's Republic of China; MNHN 1969.4, Taiwan; MNHN 1990.4246, Thailand; MNHN 1991.295, Thailand (from pet trade); NRC 1345, Tung Salaeng Luang, Province of Phitsanulok, Thailand; NRC 1347, Pak Chong Chai Sakaerat, Province of Nakhon Ratchasima, Thailand; NRC 1422, Pak Chong Chai Sakaerat, Province of Nakhon Ratchasima, Thailand; NRC 1424, Pak Chong Chai Sakaerat, Province of Nakhon Ratchasima, Thailand; MNHN 1935.110-111, Sapa [Cha Pa] 20 km SW of Lào Cai, Province of Hoang Liên So'n, Vietnam.

Tropidolaemus wagleri: MNHN 4062, Java, Indonesia; MNHN 4063, Sumatra, Indonesia; MNHN 7767, Sumatra, Indonesia; MNHN 1879.708, Bedagneh River, Deli, now Bedagai River, Province of Sumatera Utara, Sumatra, Indonesia; MNHN 1880.43, Sumatra, Indonesia; MNHN 1880.432-434, Borneo; MNHN 1991.2721, Java, Indonesia; MNHN 1880.435, Sandakan, State of Sabah, Borneo, Federation of Malaysia; MNHN 1884.160-161, Malaya, Federation of Malaysia; MNHN 1906.14, No Sang, State of Sabah, Borneo, Federation of Malaysia; MNHN 1880.232, Albay Province, Luzon, Philippine Islands; MNHN 1880.383, Sulu Archipelago, Philippine; MNHN 1884.46, Philippine; MNHN 1884.181-182, Philippine; MNHN 1891.82, Sebroeang, Borneo; MNHN 1957.817, Borneo; MNHN 1990.4250, Thailand (from pet trade); MNHN 1878.365-366, both labelled "Mansinam, Nouvelle Guinée", unknown origin; MNHN 1990.4287, Thailand (from pet trade).

Trimeresurus trigonocephalus: MNHN 245, Sri Lanka; MNHN 1890.68, Sri Lanka.

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