

Description of a New Species of the Genus *Trimeresurus* from Thailand, Related to *Trimeresurus stejnegeri* Schmidt, 1925 (Serpentes, Crotalidae)

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ABSTRACT.—The status of populations from Northeast Thailand previously referred to as *Trimeresurus* cf. *stejnegeri* is reevaluated on the basis of morphological characters. These preliminary data confirm the distinct specific status of these populations, for which a new species is here established. Preliminary comparisons with *T. vogeli*, another taxon from Thailand, and especially *T. stejnegeri* are provided.

KEY WORDS: Reptilia; Serpentes; Crotalidae; *Trimeresurus*; new species; *Trimeresurus stejnegeri*; *Trimeresurus vogeli*; Thailand

INTRODUCTION

The intricate and confusing systematics of the Asian bamboo pitvipers was recently summarized in David et al. (2001). This confusion reaches its apex in Thailand, where these authors described a new species of the informal *Trimeresurus stejnegeri* complex, *T. vogeli* David, Vidal and Pauwels, 2001. This species, known from central eastern and southern Thailand, and also from southwestern Cambodia and central South Vietnam (Gia Lai Province; David et al., in prep.), has long been identified as *T. stejnegeri*.

As indicated in David et al. (2001), the description of *T. vogeli* was merely the first step towards a wide-scale revision of the *T. stejnegeri* complex based on morphological and mtDNA molecular analyses, which will be published in the near future. This first step left unresolved the status of populations of "*T. stejnegeri*" from Northeast Thailand, which were referred to as *T. cf. stejnegeri* in David et al. (2001). That paper showed the morphological homogeneity of populations of *T. stejnegeri* from mainland China and Vietnam on the one hand, and the distinct characters of both *T. vogeli* and *T. cf. stejnegeri* respectively on the other hand. The distinctiveness of these two latter forms is also confirmed by mtDNA molecular analyses, which will be published elsewhere.

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In the present paper, on the basis of the known morphological differences, obtained for a part from new material which was unavailable in the paper cited above, of our unpublished mtDNA analyses, and of data available in the literature, we formally refer these populations from Northeast Thailand to a new species. The relationships of populations from Northeast Thailand with closely related members of the *T. stejnegeri* complex, namely *T. vogeli*, *T. yunnanensis* and *T. stejnegeri* are discussed.

MATERIALS AND METHODS

The present description is established from the examination of 10 specimens (5 adults [4 males, 1 female] and 5 juveniles [2 males, 3 females]) from Northeast Thailand, and from data available in the literature, especially Gumprecht (1997) and Chan-ard et al. (1999). Data on other members of the *stejnegeri* complex stem from David et al. (2001), which should be consulted for variation within *T. stejnegeri* Schmidt, 1925 and the complete list of examined specimens; only Thai specimens are listed in the Appendix of the present paper.

Methods are also discussed in David et al. (2001); here we present only a summary. Ratios involving measurements of the head were considered only in specimens with a body length of at least 400 mm. Ventral scales were counted according to Dowling (1951); the terminal scute is excluded from the number of subcaudals; the numbers of dorsal scale rows are given at one head length behind head, at midbody (i.e. at the level of the ventral plate corresponding to half of the total number of ventrals), and at one head length before vent respectively. Values for symmetric head characters are given in left/right order. Data on the coloration of body and eyes are derived from our observations of living and freshly preserved specimens and from Gumprecht (1997). The terminology used in the description of hemipenes follows Böhme (1988).

Abbreviations used for measures, meristic characters and statistical calculations are:

Measures and ratios: HL (head length), SVL (snout-vent length), TaL (tail length), TL (total length), TaL/TL (ratio tail length/total length).

Meristic characters: Cep (number of cephalic scales on the shortest line separating the middle of supraoculars), DSR (number of dorsal scale rows), MSR (number of dorsal scale rows at midbody), IL (number of infra-labials), IIN (number of scales separating the internasals), SC (number of subcaudals), SL (number of supralabials), VEN (number of ventrals).

Statistical calculations: n (number of specimens), \bar{x} (mean value), s (standard deviation).

Museum abbreviations are as follows:

MNHN: Muséum National d'Histoire Naturelle, Paris, France.

PSGV: Gernot Vogel's private collection, Heidelberg, Germany.

PSUAA: Penn State University at Altoona, Altoona, Pennsylvania, USA.

RFI: Robert F. Inger's collection, deposited under their field numbers in the NHMT, National Science Museum of Thailand, Bangkok, Thailand.

UTA: University of Texas at Arlington, Arlington, Texas, USA.

ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.

RESULTS

Pending the publication of a more detailed study which will include the correlations between the results provided by the mtDNA and morphological analyses of as many as possible populations of *T. stejnegeri*, our morphological results clearly suggest that populations from Northeast Thailand represent an undescribed taxon warranting recognition, distinct from both *T. stejnegeri* and *T. vogeli*. As a consequence, these populations are regarded as a new species, which we describe as:

Trimeresurus gumprechtii sp. nov.
(Figs. 1-8)

Holotype.-MNHN 1999.9072, adult male, from Phu Luang Wildlife Research Station, about 15 km northwest from the city of Phu Luang and 45 km southwest from the city of Loei, Loei Province, Thailand (captive born in May 1996 from a female from this locality collected by Mr. Tanya Chan-ard, died May 1998); deposited by Gernot Vogel, October 1999.

Paratypes.-All from Thailand: MNHN 1999.9073, subadult male, probably from Phu Luang Wildlife Research Station, Loei Province; PSUAA 0047, adult male, no locality; RFI 1345, adult male, Thung Salaeng Luang, Phitsanulok Province; ZFMK 75797, adult female, Phu Luang Wildlife Research Station, Loei Province (same origin as the holotype).

Diagnosis.-A species of the genus *Trimeresurus*, characterized by (1) hemipenes short and strongly spinose; (2) overall bright green coloration in males, deep or dark green in females; (3) interstitial skin black; (4) large size, with a total length greater than 1200 mm in females; (5) conspicuous bicolored postocular stripe in males, thin and white below, wide and bright red above, reversed from the scheme of the ventrolateral stripe (only thin and white in females); (6) vivid, wide bicolored ventrolateral stripe, bright or deep red below/white above in males, extending along the lower part of the first third of the tail, white or blue but well defined in females; (7) eyes deep red in males, yellow in females; (8) tail mostly rusty or reddish-brown (see below); (9) tail long in males, with a ratio TaL/TL ranging from 0.16-0.21, rather short in females, 0.14-0.16; (10) VEN: 162-168; SC: 51-71; (11) first supralabial distinct from nasal; (12) 21 dorsal scale rows at midbody, moderately keeled; (13) snout covered with rather enlarged juxtaposed scales; (14) internasals either in contact or separated by only 1 scale; (15) supraoculars narrower than internasals, separated by 10-12 smooth cephalic scales.

T. gumprechtii differs from all other green pitvipers by the combination of the following characters: (1) short, spinose hemipenis, (2) first supralabials separated from the nasal, (3) the very conspicuous (at least in life) reversed bicolored postocular stripe, white below and wide, bright or deep red above, always present in males (postocular streak only white in females), (4) the ventrolateral stripe, bright red below and white above in males, running under the first third of the tail, white in females, (5) eyes deep red in males, (6) black interstitial skin, (7) upper snout scales enlarged, (8) internasal scales often in contact or separated by at most one scale and (9) greatest part of upper surface of the tail rusty red. These characters and the comparisons with other species are detailed below in the Discussion.

Description of the holotype.-Body moderately elongated, cylindrical; head triangular, wide at its base, thick, rather elongated, 1.5 times as long as wide, clearly distinct from the neck; snout moderately long, accounting for 25.1% of total HL, 2.0 times as long as diameter of eye, flattened, rounded when seen from above, truncated when seen from lateral side, with a very distinct *canthus rostralis*; eye average, with eye diameter/distance lower margin of eye-upper lip border ratio 0.83; nostril-loreal pit distance/nostril-eye distance ratio 0.51 (mean value of both sides); tail rather long, tapering, distinctly prehensile.

SVL: 592 mm; TaL: 134 mm; TL: 726 mm; HL: 29.8 mm; ratio TaL/TL: 0.185.

VEN: 168 (+ 1 preventral); SC: 61, paired, plus one terminal scale; anal shield entire.

DSR: 25 [21 at 2 HL]-21-15 scales, rhomboid, moderately keeled, first row smooth.

Rostral visible from above, about 1.5 times broader than high, triangular; nasals subrectangular, about 1.8 times as long as high, undivided, with nostril in its middle; one pair of enlarged, slightly curved internasals, in contact each with the other, 1.6 times as wide as deep, about 1.3 times as long and as wide as adjacent upper snout scales; 4/4 canthal scales bordering the *canthus rostralis* between the internasal and corresponding supraocular, slightly larger than

adjacent snout scales; 1 triangular loreal between upper preocular and nasal; two upper preoculars above the loreal pit, elongated and in contact with the loreal; lower preocular forming lower margin of loreal pit; 2/2 postoculars; 1 large, entire, long and relatively narrow supraocular on each side, about 3.0 (left)/2.9 (right) times as long as wide, wider than the adjacent upper head scales and about 0.70/0.65 time as wide as the internasals; supraocular indented on their inner margin by the upper head scales; scales on upper snout surface smooth, juxtaposed, irregular in shape, moderately but distinctly enlarged, typically looking like a juxtaposition of irregular paving stones; only 5 snout scales on a line between the scales separating the internasals and a line connecting the anterior margins of eyes; cephalic scales smaller, irregular, juxtaposed, smooth and flat on upper head surface, smooth and flat, or barely swollen (but not keeled) posteriorly on occipital region; 12 cephalic scales in a line between supraoculars; temporals rather small, subequal, in 2 or 3 rows, smooth; one thin, elongated, crescent-like subocular; 10/10 SL; 1st SL triangular, short, totally separated from the corresponding nasal; 2nd SL high, forming the anterior border of loreal pit, in contact with nasal; 3rd SL distinctly enlarged and much larger than the other labials, pentagonal, high and long, approximately 1.1/1.0 times as long as high, in contact with the subocular; 4th SL distinctly shorter, 0.7 times as high as 3rd one, separated from the subocular by one scale on both sides and a row on the right side; the 5th and other posterior supralabials slightly smaller than 4th one, 5th SL separated from the subocular by two scales, others in contact with the first row of temporals; 13/12 infralabials, those of the first pair in contact with each other, the first three pairs in contact with the chin shields; 7/7 rows of smooth gular scales; chin shields irregularly arranged.

In preservative, the dorsal and lateral body surfaces are uniformly dark blue, slightly paler on the bottom of the flanks, progressively replaced, from midbody, by emerald green on the lower half on the flanks, reducing the dark

blue color to a 4-scale wide dorsal stripe (this change of colour being obviously an artefact of the preservative liquid); three small, indistinct white vertebral spots at the rearmost part of the body, absent elsewhere; the interstitial skin is black; a well defined, wide bicolored rusty red and white ventrolateral stripe extending from the angle of the mouth through the first half of the tail, with the rusty red part extending along the lower half of scales of the first row and extreme tips of ventrals and the white part on the upper half of the first row and a very small part in the lower half of scales of the second row of dorsal scales; this stripe ends on the tail as broken bicolored spots. The tail is emerald green like the body, with its whole upper half heavily mottled with rusty red.

The dorsal head surface and temporal regions are uniformly dark blue like dorsal surface, paler bluish-green on the dorsal snout surface; supralabials green anteriorly, becoming dark bluish-green behind the level of the eye; a very conspicuous bicolored postocular streak, well defined but rather thin, white below and wide, bright rusty red above, the red part being wider than the white lower part; this bicolored postocular streak, with its colors reversed from those of the ventrolateral stripe, extends along the second row of temporals, and the second and first row behind, from the rearmost upper part of subocular backwards up to the side of the neck, well behind the angle of the mouth. The lower white part of the postocular streak is connected with the upper white half of the ventrolateral stripe, producing a wider white stripe on the neck behind the angle of the mouth; there is no connexion between the red parts, but they overlap on each side of the common white part.

The chin and throat are pale emerald green; the first quarter of the belly is emerald green, becoming on the second quarter dark bluish-green with posterior margins of ventral plates pale green, then again emerald green; ventral surface of tail emerald green.



FIGURE 1. *T. gumprechtii*, adult male in life. Photograph by Gernot Vogel.



FIGURE 2. *T. gumprechtii*, same specimen as in Fig. 1. Photograph by Gernot Vogel.



FIGURE 3. *T. gumprechtii*, adult female in life. Photograph by Gernot Vogel.



FIGURE 4. *T. gumprechtii*. Holotype (MNHN 1999.9072). General view. Photograph by Renaud Boistel.



FIGURE 5. *T. gumprechtii*. Holotype (MNHN 1999.9072). Lateral view of the head (left side). Photograph by Renaud Boistel.

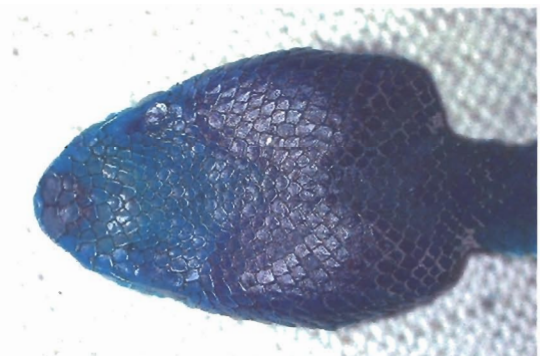


FIGURE 6. *T. gumprechtii*. Holotype (MNHN 1999.9072). Dorsal view of the head. Photograph by Renaud Boistel.

TABLE 1. Morphological characters of the paratypes of *T. gumprehti*.

Collection number	Sex	SVL (mm)	TaL (mm)	TaL/ TL	Postoc. stripe	Lateral stripe	VEN	SC	SL	Cep	IIN	SOc/ IN
MNHN 1999.9073	M	357	69	0.162	bicolored reversed	bicolored	167	59	11/11	12	1	0.72
PSUAA 0047	M	608	159	0.207	bicolored reversed	bicolored	163	71	9/10	12	1	0.69
RFI 1345	M	552	118	0.176	bicolored reversed	bicolored	164	71	11/10	10	1	0.67
ZFMK 75797	F	654	123	0.158	none	white	170	54	11/11	11	0	0.65

Abbreviations: See under Materials and Methods, except SOc/IN : width of supraoculars/width of internasals ratio.

In life, the dorsal color was deep emerald green, paler below, with the streak and stripe much more bright and red than in preservative. Eyes were deep red.

The combination of the reversed colors of the postocular streak with dark red eye and bicolored ventrolateral stripes are diagnostic of this species.

Description of the paratypes.—A summary of morphological characters of the four paratypes is given in Table 1.

All other morphological characters, including the numbers of dorsal scale rows (21, 23 or 25-21-15), coloration and pattern agree with

those of the holotype, except in females where the postocular streak is faint or absent, the ventrolateral stripe, only white, and the eyes, which are yellow. The dorsal color of the paratypes varies from grass green to deep bluish-green.

Variation and general description

Morphology.—The maximal confirmed total length known is 1233 mm (SVL 1047 mm, TaL 186 mm) for a female (ZFMK 68524, from Mt. Phu Luang; not seen, A. Gumprecht, pers. comm., December 2001). The largest known male is 864 mm long (SVL 700 mm, TaL 164 mm; ZFMK 70444, same origin; not seen).

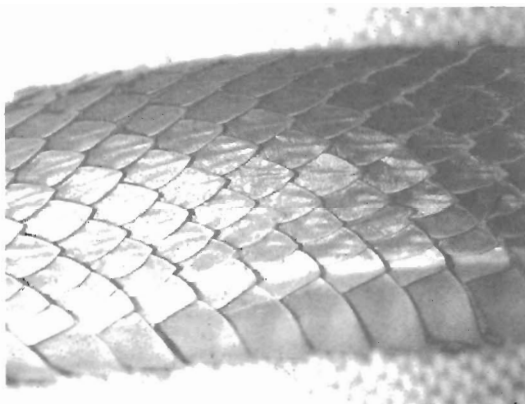


FIGURE 7. *T. gumprehti*. Holotype (MNHN 1999.9072). Lateral view of the body (left side). Photograph by Renaud Boistel.



FIGURE 8. *T. gumprehti*. Hemipenes (from MNHN 1999.9072, holotype). Photograph by Renaud Boistel.

Larger sizes are undoubtedly possible, as A. Gumprecht (pers. comm.) once observed a wild-caught female 1280 mm long. According to the same author, females and males usually reach about 1100 mm and 900 mm (TL) long respectively. The largest specimen examined by us is 777 mm long for a female (ZFMK 75797); the largest examined male measures 767 mm (PSUAA 0047).

The body, compressed laterally, is moderately slender in males but much thicker in females. The triangular head is elongated, 5.0-6.7% of SVL ($x = 5.7\%$), wide at its base, thick and flattened in males, rather convex in females when seen from the side.

The snout is moderately long, accounting for about 24.4-27.5% of HL in both sexes, or 1.8 to 2.4 times as long as diameter of eye, flattened, rounded when seen from above, truncated when seen from the side, with a very distinct *canthus rostralis*. The eye is moderate, with a diameter smaller than the distance between its lower margin to the lip margin. The cylindrical tail is tapering progressively and prehensile. The ratio TaL/TL ranges from 0.14-0.21, and exhibits sexual dimorphism (see below).

DSR: 21-23 (rarely 25)-21-15, moderately keeled at midbody on the upper half of the body, less keeled or nearly smooth ventrolaterally, more keeled posteriorly, smooth on the first outer row.

VEN: 162-168 (plus 1-2 preventrals); SC: 51-71, all paired; anal shield entire.

Head scalation as described for the holotype, with: one pair of enlarged, bean-shaped internasals, 1.5-1.7 times as long and 1.3-1.6 times as wide as adjacent upper snout scales, either in contact (in 4 out of 10 specimens) or separated by 1 small scale (in 6 specimens); snout covered with irregular scales, distinctly larger than the scales on the dorsal surface of the head, typically looking like a juxtaposition of irregular paving stones, with in most specimens only 5 scales (6 scales in 2 specimens) on a line between the internasals or the scale separating the internasals and a line connecting the anterior margins of the eyes; 4 or 5 canthal

scales, slightly larger than adjacent snout scales, bordering the *canthus rostralis* between the internasal and corresponding supraocular; 2, seldom 3 small postoculars (2/2 in 8 specimens; 2/3 in one; 3/3 in one); one large supraocular on each side, long and rather narrow, 2.9-4.1 ($x = 3.15$) times as long as wide, much wider than the adjacent upper head scales and distinctly narrower (0.50-0.80 times; $x = 0.66$) than the internasals, mostly indented on their inner margins by the upper head scales; 10-12 small cephalic scales on a line between supraoculars (10: 2 specimens; 11: 2 specimens; 12: 6 specimens), irregular, juxtaposed, smooth and flat; occipital scales larger than upper head scales, usually swollen backwards, smooth or slightly and obtusely keeled; temporals smooth, not much larger than posterior supralabials, subequal, in 2 or 3 rows; 9-11 SL, with 11/11 in 4 specimens, 10/11 (3 specimens), 10/10 (2 specimens) and 9/10 (1 specimen); 1st SL totally separated from the nasal; 2nd SL high, forming the anterior border of loreal pit, in contact with nasal on both sides (1 specimen), or separated by 1 small scale on one side (5 specimens), or at least 2 scales on one side (4 specimens); 3rd SL longer and higher than other ones, from 1.0-1.3 times as long as high ($x = 1.15$), in contact with the subocular on both sides (9 specimens; partly separated by the tip of a scale on a side of one specimen), or separated by 1 scale on both sides (1 specimen); 4th SL, as long as high, 0.5 to 0.70 time lower than 3rd SL, separated from subocular usually by 1 scale on each side (9 specimens), or 2 scales on each side (1 specimen), without sexual dimorphism; 5th and posterior supralabials slightly smaller than 4th SL, 5th SL separated from subocular by 2 scale rows of similar size; 12-14 IL ($x = 12.7$, $s = 0.8$), those of the first pair in contact with each other, and first three pairs in contact with anterior chinshields; 7-9 rows of smooth gular scales; throat shields irregularly arranged.

Coloration.-In life, the background color is emerald green, dark grass green, deep green or even dark turquoise bluish-green in males, grass or deep green in females (turning to dark

blue or dark bluish-green in alcohol), with sometimes, in males only, faint, irregular dorsal black or purple crossbands. Small white or pale blue vertebral spots may be present in males, but are absent in females. A well defined bicolored ventrolateral stripe, bright red, deep red or chocolate red below (rusty brown in alcohol), white or whitish-yellow above, as described in the holotype, extends from the angle of the mouth through first 1/3-1/2 of the tail. In females, it is replaced by a faint white, bluish-white or yellowish-white stripe on the middle of the first dorsal scale row. The interstitial skin is deep black.

The tail surface is basically the same color as the dorsum, with the whole length of its upper part irregularly mottled with reddish-brown, rusty brown or reddish-violet, which forms backwards a continuous stripe.

The dorsal head surface and temporal regions are of the same colors as the dorsum, sometimes with numerous blue scales, paler on the upper snout surface, with distinctly paler green supralabials. In males, the vivid bicolored reversed postocular streak, narrow and white below, wide and bright red, deep rusty-red or even brownish-red above (rusty brown in alcohol), as described in the holotype, is always present at any age. In males, the white part of the postocular streak and that of the ventrolateral stripe, respectively, may be either confluent, as in the holotype, with red stripes present on its both sides for a short distance, or separated by a short gap on the posterior part of the head, or with white parts fused but respective red parts stopping before the point of confluence. In females, the postocular streak is either absent, or present as very faint, white or bluish-white line. In life, eyes are bright red, fire red or deep red in males, golden yellow or dark yellow in females.

The venter, chin, and throat are a pale, grass green or greenish-blue, slightly lighter than the dorsum in males, grass or deep green in females.

The coloration of juveniles is similar to that of adults, but faint, irregular, dark dorsal crossbands may be present. The postocular streak

and ventrolateral stripes of males are visible as in adults.

Sexual dimorphism.—It is significant in the size, color and pattern, in the relative length of the tail, and in the number of subcaudals.

1. Females reach a greater maximal size (more than 1230 mm vs. about 900 mm) and become thicker than males (Gumprecht, 1997; pers. comm., December 2001).
2. In the specimens examined by us, as well as in those considered by Gumprecht (1997), the reversed, bicolored postocular streak and the bicolored ventrolateral stripes are always present in males. In females, only a thin, white or whitish-blue postocular stripe may be present at best, and a white (never red) ventrolateral stripe is present (see Figs. 1-3).
3. The eye is bright red or deep red in living adult males, deep yellow in living adult females.
4. There is a strong difference in the ratio TaL/TL :

males: 0.157-0.207 ($x = 0.179$; $n = 6$)

females: 0.138-0.158 ($x = 0.147$; $n = 4$)

There are also differences in the number of subcaudals (55-71 [$x = 64.7$] in males vs. 51-60 [$x = 55.0$] in females), but the number of available specimens does not allow us to conclude more precisely. There does not seem to be any difference in any other meristic characters.

Description of the hemipenes (Fig. 8).—From MNHN 1999.9072 (holotype): hemipenes are bilobed, short and thick, 14.4 mm long, rounded at their extremity. Each lobe has, on its proximal side opposite of the sulcus, five enlarged, widely separated spines on its lower third, followed by three medium spines then topped by eight shorter ones. The distal third and the areas near the *sulcus spermaticus* is strongly calyculate. The shallow *sulcus spermaticus* divides at the base of the organ, near the first large spines.

Etymology.—This species is named, upon his own request, after Mr. Andreas Gumprecht (Köln, Germany), who was the first to point out the distinct taxonomic status of this taxon

(Gumprecht, 1997) and who gathered data on its morphology and biology which were largely used in the present paper.

We suggest the following common names in English / French / German respectively:

Gumprecht's green pitviper / Trimérésure de Gumprecht / Gumprechts grüne Grubenotter.

Distribution.—*T. gumprechtii* is currently known only from the Northeast Region of Thailand: Provinces of Loei, Phitsanulok, Phetchabun, and Chaiyaphum.

In the Province of Loei, *T. gumprechtii* is confirmed from Phu Luang Wildlife Research Station and other localities in the Dong Phraya Yenin Range (Gumprecht, 1997: 19, 22). In Phetchabun Province, it is known from Nam Nao National Park. We examined a specimen (RFI 1345) from Thung Salaeng Luang National Park, Phitsanulok Province. In the Province of Chaiyaphum, immediately south of the localities cited above, *T. gumprechtii* has been recorded from Phu Khiao (A. Gumprecht, pers. comm., December 2001). All these localities are situated in a large complex of low to moderate (up to 1571 m a.s.l. for Phu Luang Mt.), nearly contiguous highlands of Northeast Thailand.

This species is most probably also present in hills of northern Thailand, where it should be searched for in the provinces of Uttaradit, Nan, Phayao and others. Moreover, its occurrence in Loei Province makes very likely the presence of this species in Lao People's democratic Republic (Laos), especially in the hills of the western part of the country.

The systematics of members of the *T. stejnegeri* complex in northern Myanmar and northeastern India is still unresolved (David et al., 2001). Quite interestingly, Smith (1943) mentioned, as *T. stejnegeri*, specimens from northern Myanmar or northeastern India that display a reversed bicolored streak. The low number of ventrals cited seems to preclude their identification as *T. gumprechtii*. Such a specimen was again cited by Mathew (1995) from Shillong, in the Khasi Hills, in the Indian state of Meghalaya. Those specimens may be referable to *T. yunnanensis*, a species which also has the reversed bicolored postocular streak,

but further studies are badly required to ascertain the systematics of *T. stejnegeri* in the Eastern Himalayas.

Biology.—A description of the biology of this species, both in the wild and in captivity, was given in Gumprecht (1997). It inhabits hills and mountains mainly between 800 and 1200 m a.s.l. The hills of Northeast Thailand are largely covered with seasonal or dry tropical forests common in several parts of Central Indochina, and are subject to both a drought season and low temperatures (down to 5°C) in winter. Descriptions of Phu Luang Wildlife Research Station and its neighbour Phu Kradueng National Park are given in Gray et al. (1994).

This species is mainly found in rugged, forested areas, often in the vicinity of streams, as well as bamboo thickets. It also occurs near human settlements and along trails. This mostly nocturnal species is definitely arboreal, but can also be found on the ground. Largest known specimens cited above were collected while they were resting on branches near a stream at about 1.5 m above the ground. Rodents and skinks have been recorded as preys. A captive specimen deliberately ingested a congener of similar size. This viviparous species produces litters from 9 to 15 young.

DISCUSSION

Morphological comparisons with other species

Gumprecht (1997) regarded the populations from Northeast Thailand as a subspecies of *T. stejnegeri*. The constant differences in the body morphometry and scalations, and in the unique structure and color of the postocular streak, unknown in populations of *T. stejnegeri* from the mainland, which we regard as a secondary sexual character, lead us to recognize these populations as deserving a specific status distinct from *T. stejnegeri*.

Molecular mtDNA based analyses have shown their usefulness in inferring the phylogeny of the *Trimeresurus* complex (Malhotra and Thorpe, 1996, 2000; Giannasi et al., 2001). Our molecular analyses (David et al., unpub-

lished) are in agreement with morphological data and confirm the distinctiveness of the populations from Northeast Thailand which form a clade sister-group to the remaining populations of *T. stejnegeri*, which were sampled from Zhejiang Province (China, close to the type locality), Tam Dao (North Vietnam) and Taiwan.

Besides *T. gumprechtii*, there are currently in Thailand six named species of entirely or largely green pitviper: *T. albolabris* (Gray, 1842), *T. hageni* (Lidth de Jeude, 1886), *T. macrops* Kramer, 1977, *T. popeiorum* Smith, 1937 (with at least two different "forms", see Vogel, 1990), *T. vogeli* David, Vidal and Pauwels, 2001, and *Tropidolaemus wagleri* Wagler, 1830 (males and juveniles only). To this list, we add the yet undescribed red-eyed *Trimeresurus* species from the vicinity of Chiang Mai, in North Thailand (Malhotra and Thorpe, 1996; Chan-ard et al., 1999: 204).

Characters separating the group of *T. stejnegeri* from *T. albolabris*, *T. macrops*, and *T. erythrurus* (Cantor, 1839), a species occurring close to Thailand western border, as well as *T. hageni* were discussed in David et al. (2001).

T. gumprechtii is distinguished from *T. popeiorum* ssp. (see Vogel, 1990) by the shape of its hemipenes, a thicker head, a shorter tail and a lower number of subcaudals in males. However, it is worth noting that males of some populations of *T. popeiorum* from northern (Doi Inthanon, Chiang Mai Province, MNHN 1987.3836) and southern (Phang-nga Province, see Grossmann and Tillack, 2001) Thailand have the vivid reversed bicolored postocular streak typical of *T. gumprechtii*. We examined the specimen MNHN 1987.3836. Its flat head, elongated snout, narrow tail base and hemipenial structure confirmed by dissection leave no doubt about its identity as a *T. popeiorum*. This great external similarity increases the potential confusion between these two species. Furthermore, it makes quite hazardous the identification of *T. gumprechtii* or *T. popeiorum*, or other green pitvipers from photographed specimens. In preservative, even in adult males, examination of the tail and meristics data remain mandatory to separate these taxa. Our

data suggest that localities may be helpful, as, in Thailand, *T. popeiorum* seems to be restricted to the mountain range crossing the country from north to south in its westernmost part. We did not find any genuine specimen of *T. popeiorum* from Northeast, Central and East Thailand. Juveniles and males of *Tropidolaemus wagleri* also have a bicolored postocular streak, but it is not reversed, namely the red color is below the white part of the streak. As far as we know, the presence and signification of the bicolored postocular streaks, known from only a few, distantly related green species of the *Trimeresurus* complex, has not been discussed. A study of such unusual patterns shared by more or less distantly related reptile or amphibian species sharing the same range would be of great interest (A. Dubois, pers. comm.).

According to morphological and molecular evidence, *T. gumprechtii* is closely related to *T. stejnegeri* Schmidt, 1925, and, to a lesser extent, to *T. vogeli*. From this latter species, *T. gumprechtii* differs by (1) the color, especially in males, paler, more blue and more dull in *T. vogeli*; (2) the stripes of the head and of the body: *T. vogeli* totally lacks the bicolored reversed postocular streak, always present in males of *T. gumprechtii*, and its ventrolateral stripes only rarely have a red part in adult males; (3) the colour of the eyes, never red in males of *T. vogeli*; (4) the colour of the tail: in *T. vogeli*, the tail is mostly green, with only the tip or the last 20% of its length mottled with rusty brown, whereas in *T. gumprechtii*, the whole length of the dorsal part of the tail is irregularly mottled with reddish- or rusty brown or reddish-violet; (5) the presence of the white vertebral spots, diagnostic of *T. vogeli*, which are not systematically present in males of *T. gumprechtii*, and are unknown in females; (6) differences in the ratio TaL/TL; and (7) some meristic characters, such as the numbers of ventrals and subcaudals. Characters separating these two taxa are summarized in Tables 2-4 (data on *T. vogeli* from David et al., 2001). Both species reach large sizes, especially in females.

TABLE 2. Summary of some morphological characters in the *T. stejnegeri* group.

SPECIES	Max SVL (mm)		Ratio TaL/TL		Ventrols (VEN)		Subcaudals (SC)		MSR
	Males	Females	Males	Females	Males	Females	Males	Females	
<i>T. gumprechtii</i>	700	1047	0.157-0.207 (x = 0.179) (n = 6) (s = 0.018)	0.138-0.158 (x = 0.147) (n = 4) (s = 0.010)	162-168 (x = 165.2) (n = 6) (s = 2.2)	163-170 (x = 167.5) (n = 4) (s = 3.1)	55-71 (x = 64.7) (n = 6) (s = 7.2)	51-60 (x = 55.0) (n = 4) (s = 3.7)	21
<i>T. s. stejnegeri</i>	625	765	0.184-0.220 (x = 0.201) (n = 51) (s = 0.009)	0.159-0.194 (x = 0.176) (n = 34) (s = 0.008)	150-170 (x = 161.3) (n = 122) (s = 4.3)	153-171 (x = 161.3) (n = 124) (s = 4.4)	60-77 (x = 68.9) (n = 117) (s = 3.3)	54-74 (x = 64.3) (n = 123) (s = 4.3)	21
<i>T. s. chenbihuii</i>	613	700	0.171-0.214 (x = 0.194) (n = 13) (s = 0.010)	0.161-0.173 (x = 0.168) (n = 7) (s = 0.004)	160-177 (x = 169.8) (n = 18) (s = 4.3)	167-174 (x = 169.4) (n = 8) (s = 2.5)	70-80 (x = 74.4) (n = 17) (s = 3.0)	56-73 (x = 66.0) (n = 6) (s = 5.6)	21
<i>T. vogeli</i>	785	> 950	0.164-0.197 (x = 0.178) (n = 22) (s = 0.009)	0.149-0.164 (x = 0.156) (n = 10) (s = 0.005)	163-173 (x = 169.0) (n = 22) (s = 2.8)	167-173 (x = 170.3) (n = 10) (s = 1.8)	62-72 (x = 66.2) (n = 23) (s = 2.7)	58-64 (x = 60.3) (n = 10) (s = 2.2)	21
<i>T. medoensis</i>	546	530	0.166-0.208 (x = 0.193) (n = 15) (s = 0.014)	0.163-0.183 (x = 0.174) (n = 10) (s = 0.007)	138-149 (x = 143.9) (n = 18) (s = 2.7)	141-149 (x = 143.7) (n = 11) (s = 2.4)	54-65 (x = 59.4) (n = 17) (s = 3.0)	52-60 (x = 54.6) (n = 11) (s = 1.8)	17
<i>T. yunnanensis</i>	602	804	0.174-0.253 (x = 0.195) (n = 9) (s = 0.024)	0.151-0.186 (x = 0.173) (n = 11) (s = 0.011)	154-163 (x = 158.8) (n = 19) (s = 2.8)	150-172 (x = 159.6) (n = 16) (s = 5.1)	61-71 (x = 65.6) (n = 17) (s = 2.7)	52-64 (x = 59.0) (n = 15) (s = 3.8)	19

Notes: Data on *T. s. stejnegeri*, *T. s. chenbihuii* and *T. vogeli* are from David et al. (2001). Data on *T. medoensis*, from David et al. (2002). Data on *T. yunnanensis* are from Pope (1935), Zhao et al. (1998), and examined specimens, all from China.

TABLE 3. Variation of pattern characters in living specimens in relation with the sex.

POPULATIONS	EYE COLOR		POSTOCULAR STREAK		VENTROLATERAL STRIPE	
	Males	Females	Males	Females	Males	Females
<i>T. gumprechti</i>	bright or deep red	golden yellow	white + wide red (reversed)	none or faint white	wide red + white	white
<i>T. s. stejnegeri</i>	bright red or amber (rarely yellow)	yellow or amber	white	none (or very faint)	red + white	red + white or white
<i>T. s. chenbihuii</i>	bright red or amber	yellow or amber	red + white	none	red + white	white, thin
<i>T. vogeli</i>	yellow or yellowish green	yellow	white, thin and faint	none	(red +) white	white
<i>T. medoensis</i>	green or yellowish green	green or yellowish green	none (or faint white)	none	red + white	red + white
<i>T. yunnanensis</i>	bright or deep red	golden yellow	white + red (reversed)	none	red + white	pale green, thin

Notes: Conditions of rare occurrence are placed in parenthesis.

Data on *T. s. stejnegeri*, *T. s. chenbihuii* and *T. vogeli* are from David et al. (2001). Data on *T. medoensis* from David et al. (2002). Data on *T. yunnanensis* are from Pope (1935), Zhao et al. (1998), and examined specimens, all from China.

TABLE 4. Head scalation.

SPECIES (number of specimens)	CEP variation (x) (s)	CONTACT OF INTERNASAL Percentage		TOTAL NUMBER OF SL variation (x)/(s)	CONTACT OF 3rd SL WITH SUBOCULAR Percentage		CONTACT OF 4th SL WITH SUBOCULAR Percentage	
		In contact	Separated		In contact on both sides	Not in contact on 1 side	At most 1 scale on both sides	At least 2 scales on 1 side
<i>T. gumprechti</i> (n = 10)	10-12 (x = 11.4) (s = 0.8)	40.0	60.0	19-22 (x = 21.0) (s = 1.1)	90.0	10.0	90.0	10.0
<i>T. s. stejnegeri</i> (n = 90)	10-15 (x = 11.6) (s = 1.2)	1.1	98.9	17-22 (x = 19.4) (s = 1.2)	93.3	6.7	87.6	12.4
<i>T. s. chenbihuii</i> (n = 21)	11-16 (x = 13.7) (s = 1.2)	0	100.0	17-26 (x = 21.2) (s = 1.9)	95.2	4.8	81.0	19.0
<i>T. vogeli</i> (n = 32)	11-14 (x = 12.6) (s = 0.8)	0	100.0	20-24 (x = 21.7) (s = 1.0)	37.50	62.5	53.1	46.9

The distinction between *T. gumprechtii* and *T. stejnegeri*, as currently understood, needs some further explanations. David et al. (2001) showed the homogeneity and non-clinal variation within the cluster of populations from Eastern China + Southern China + South-western China + Northern Vietnam, namely from most of the range of *T. stejnegeri* as currently defined. From this species, *T. gumprechtii* differs by: (1) the absence in all known specimens of *T. stejnegeri* from the mainland of the reversed bicolored postocular streak; (2) the absence of red in the ventrolateral stripe of females of *T. gumprechtii*, whereas the bottom red part is present in about one third of females of *T. stejnegeri*; (3) interstitial skin deep coal black in *T. gumprechtii*, whereas it is dark grey or greyish-brown in *T. stejnegeri*; (4) a much larger size in *T. gumprechtii*; (5) a much greater difference of size between males and females of *T. gumprechtii* than in *T. stejnegeri*; (6) a lower ratio TaL/TL in *T. gumprechtii* than in *T. stejnegeri* (see Table 2); (7) various scalation characters, as reported in Tables 2 and 4, especially the contact of the internasals, in contact for a significant proportion of specimens in *T. gumprechtii*, whereas this condition is very rare in *T. stejnegeri*; (8) the enlarged, paving stones-like snout scales in *T. gumprechtii*; and (9) slightly different hemipenes. To the contrary, the dorsal background, eye colors and coloration of the tail are quite similar in these two species.

T. gumprechtii differs from *T. yunnanensis* Schmidt, 1925 by several characters summarized in Tables 2 and 3. *T. yunnanensis* is characterized by a lower number of ventrals, a higher ratio TaL/TL, and 19 scale rows at midbody. However, both species share the presence of a bicolored reversed postocular streak in males and enlarged snout scales. The variation of *T. yunnanensis* in Myanmar and northeastern India is not well understood. In these two countries, some specimens referred to this latter species have both the reversed postocular streak and 21 dorsal scale rows at midbody, vs. a constant number of 19 rows in all known Chinese animals (Zhao et al., 1998). The identification of these specimens with 21 scale rows has yet to be

clarified; they might be referable to *T. gumprechtii*. Lastly, *T. gumprechtii* easily differs from *T. medoensis* Djao in Djao and Jiang, 1977 by characters summarized in Tables 2 and 3 (see also David et al., 2001, 2002).

In spite of its vivid coloration and pattern, *T. gumprechtii* seems to have been discovered quite recently, as a result of field trips in remote areas (Gumprecht, pers. comm., December 2001). Consequently, neither Taylor (1965), Regenass and Kramer (1981) nor Cox (1991) wrote anything referable to *T. gumprechtii*. Specimens that Smith (1943: 518) mentioned as "*T. stejnegeri*" with a reversed bicolored postocular streak from either Myanmar or north-eastern India are yet unidentified, but might be referable to *T. yunnanensis*. *T. gumprechtii* has been described or depicted, as *T. stejnegeri*, in Thorpe et al. (1996: front cover and front flap), Gumprecht (1997: 16 and subsequent, description with color photographs), Cox et al. (1998: 21; a female from Phu Luang, Loei Province [W. Wüster, pers. comm., April 2001]), and Chan-ard et al. (1999: 203 and 204 [top]). Illustrations of "*T. stejnegeri*" in Thumwipat and Nutphand (1982) and Nutphand (2001) were discussed in David et al. (2001) and Gumprecht (2001), and none refers to *T. gumprechtii*.

CONCLUSION

The description of *T. gumprechtii* brings to six the number of taxa referable to the informal *T. stejnegeri* subgroup, as defined in Malhotra and Thorpe (2000) and David et al. (2001), which now contains *T. stejnegeri* Schmidt, 1925 (with the subspecies *T. s. stejnegeri* and *T. s. chenbihuii* Zhao, 1995), *T. gumprechtii*, *T. medoensis* Djao in Djao and Jiang, 1977, *T. vogeli* and *T. yunnanensis* Schmidt, 1925. The taxonomic status of Taiwanese populations remains yet unresolved (Malhotra and Thorpe, 2000; Creer et al., 2001).

A next step will be the assessment of the distributional boundaries of the species of the *stejnegeri* group. Morphological and molecular studies of specimens from northeastern India,

Myanmar, Laos, and northern Thailand are critical to affine our understanding of this medically important group of pitvipers and variation within currently recognized species. This wide scale study of morphological variation, correlated with data furnished by molecular studies, will be addressed in a forthcoming paper.

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LITERATURE CITED

- Böhme, W. 1988. Zur Genitalmorphologie der Sauria: funktionelle und stammesgeschichtliche Aspekte. *Bonner zool. Monogr.* 27: 1-176.
- Chan-ard, T., W. Grossmann, A. Gumprecht and K.-D. Schulz. 1999. Amphibians and Reptiles of Peninsular Malaysia and Thailand: An illustrated checklist. Bushmaster Publ., Würselen.
- Cox, M. J. 1991. The Snakes of Thailand and their Husbandry. Krieger Publishing Co., Malabar (Florida).
- Cox, M. J., P. P. van Dijk, J. Nabhitabhata and K. Thirakhupt. 1998. A Photographic Guide to Snakes and other Reptiles of Peninsular Malaysia, Singapore and Thailand. New Holland Publishers, London-Cape Town-Sydney-Singapore.
- Creer, S., A. Malhotra, R. S. Thorpe and W.-H. Chou. 2001. Multiple causation of phylogeographical pattern as revealed by nested clade analysis of the bamboo viper (*Trimeresurus stejnegeri*) within Taiwan. *Mol. Ecol.* 10: 1967-1981.
- David, P., A. Captain and B. B. Bhatt. 2002. On the occurrence of *Trimeresurus medoensis* Djao in: Djao and Jiang, 1977 (Serpentes, Viperidae, Crotalinae) in India, with a redescription of this species and notes on its biology. *Hamadryad* 26 [2001] (2): 222-238.
- David, P., N. Vidal and O. S. G. Pauwels. 2001. A morphological study of Stejneger's pitviper *Trimeresurus stejnegeri* (Serpentes, Viperidae, Crotalinae), with the description of a new species from Thailand. *Russian J. Herpetol.* 8(3): 205-222.
- Deuve, T. 2002. Descriptions de quatre nouveaux *Carabus* L. et *Cychrus* F. de Chine du centre et du sud-ouest (Coleoptera, Carabidae). *Coléoptères* 8: 1-8.
- Dowling, H. G. 1951. A proposed standard system of counting ventrals in snakes. *Brit. J. Herpetol.* 1(5): 97-99.
- Giannasi, N., A. Malhotra and R. S. Thorpe. 2001. Nuclear and mtDNA phylogenies of the *Trimeresurus* complex: implications for the gene versus species tree debate. *Mol. Phyl. Evol.* 19(1): 57-66.
- Gray, D., C. Piprell and M. Graham. 1994. National Parks of Thailand. Revised edition. Industrial Finance Corporation of Thailand, Bangkok.
- Grossmann, W. and F. Tillack. 2001. Bemerkungen zur Herpetofauna des Khao Lak, Phang Nga, thailändische Halbinsel. Teil III: Ergebnisse der Jahre 1999 und 2000. *Sauria* (Berlin) 23(3): 21-34.
- Gumprecht, A. 1997. Die Bambusottern der Gattung *Trimeresurus* Lacépède. Teil I: Die Chinesische Bambusotter *Trimeresurus stejnegeri* Schmidt, 1925. *Sauria* (Berlin) 19(3): 9-30.
- . 2001. Die Bambusottern der Gattung *Trimeresurus* Lacépède. Teil IV: Checkliste der *Trime-*

- resurus*-Arten Thailand. Sauria (Berlin), 23(2): 25-32.
- Jintakune, P. and L. Chanhom. 1995. Ngoo-phit nai Prathet Thai. Queen Saovabha Memorial Institute, Thai Red Cross Society, Bangkok. (in Thai)
Note.-Translation of the title: The venomous snakes of Thailand.
- Malhotra, A. and R. S. Thorpe. 1996. New perspectives on the evolution of south-east Asian pit vipers (genus *Trimeresurus*) from molecular studies. In: R. S. Thorpe, W. Wüster and A. Malhotra (eds.), *Venomous Snakes: Ecology, evolution and snakebite*. Symp. Zool. Soc. London 70 [1997]: 115-128.
- . 2000. A phylogeny of the *Trimeresurus* group of Pit vipers: new evidence from a mitochondrial gene tree. *Mol. Phyl. Evol.* 16(2): 199-211.
- Mao, S.-H. 1962. Sexual dimorphism of Taiwan bamboo vipers. *Bull. Inst. Zool. Acad. Sinica* 1: 41-46.
- Mathew, R. 1995. Reptilia. In: A. K. Gosh (ed.), *Fauna of Meghalaya. Part 1. Vertebrates*, pp. 379-454. Zoological Survey of India, Calcutta, State Fauna Series No.4.
- Nutphand, W. 2001. *Snakes in Thailand*. Amarin Printing and Publishing Public Co., Ltd, Bangkok. (in Thai)
- Pope, C. H. 1935. *The Reptiles of China*. Turtles, crocodylians, snakes, lizards. New York, American Museum of Natural History, Natural History of Central Asia, No.10.
- Regenass, U. and E. Kramer. 1981. Zur Systematik der grünen Grubenottern der Gattung *Trimeresurus* (Serpentes, Crotalidae). *Rev. suisse Zool.* 88(1): 163-205.
- Smith, M. A. 1943. *The Fauna of British India, Ceylon and Burma, including the whole of the Indo-chinese subregion: Reptilia and Amphibia*. Vol. III, Serpentes. Taylor and Francis, London.
- Taylor, E. H. 1965. The serpents of Thailand and adjacent waters. *Univ. Kansas Sci. Bull.* 45(9): 609-1096.
- Thorpe, R. S., W. Wüster and A. Malhotra (eds.). 1996. *Venomous Snakes: Ecology, evolution and snakebite*. Symp. Zool. Soc. London 70 [1997]: 1-276.
- Thumwipat, B. and W. Nutphand. 1982. Treatment of Patients Bitten by Venomous Snakes, and Venomous Snakes of Thailand. Thai Zoological Center, Bangkok. (in Thai)
- Vogel, G. 1990. Über eine verkannte *Trimeresurus*-Art aus Thailand. *Sauria (Berlin)* 12(2): 11-13.
- Zhao, E. M., M. H. Huang, Y. Zong, J. Zheng, Z. J. Huang, D. Yang and D. L. Li (eds.). 1998. *Fauna Sinica: Reptilia. Vol. 3, Squamata Serpentes*. Science Press, Beijing. (in Chinese)

APPENDIX

Specimens examined

Trimeresurus gumprechtii (10 specimens).—Thailand: MNHN 1999.9072 (holotype), Phu Luang Wildlife Research Station, Loei Province (born in captivity from a female from this locality); MNHN 1999.9073 (paratype), MNHN 1999.9074-75, all issued from a female probably from Loei Province; MNHN 1999.9076, Nam Nao National Park, Phetchabun Province.; PSUAA 0047 (paratype), no locality.; RFI 1345 (paratype), Thung Salaeng Luang, Phitsanulok Province; UTA (DLD) 815-816, Thung Salaeng Luang, Phitsanulok Province.; ZFMK 75797 (paratype), Phu Luang Wildlife Research Station, Loei Province (born in captivity from a female from this locality).

Trimeresurus popeiorum (1 specimen).—Thailand: MNHN 1987.3836, Doi Inthanon, Chiang Mai Province.

Trimeresurus vogeli (33 specimens).—Thailand: MNHN 1999.9036, MNHN 1999.9039-40, Khao Yai National Park, Nakhon Ratchasima Province; MNHN 1999.9037-38, MNHN 1999.9041-45, PSGV 294.1-13, ZFMK 74555(1)-(2), Nakhon Ratchasima Province; MNHN 1990.4246, MNHN 1991.295, Thailand, no locality; RFI 1347, 1547, 4573, 8060, Sakaerat, Pak Chong, Nakhon Ratchasima Province; RMNH 16272-73, Pakonschai, Nakhon Ratchasima Province.

See David et al. (2001) for the list of examined specimens of *T. stejnegeri*, *T. medoensis* and *T. yunnanensis*.

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