REDESCRIPTION OF TRIMERERUS HUTTONI SMITH, 1949
(SERPENTES, CROTALINAEE), WITH A DISCUSSION
OF ITS RELATIONSHIPS

Patrick David1 and Gernot Vogel2
1Laboratoire de Zoologie (Reptiles et Amphibians), Muséum National d’Histoire Naturelle, 25 Rue Buffon, F-75005 Paris, France
2Society for Southeast Asian Herpetology, 43850 San Jose, D-49115 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, scaleation and morphology agree with the characters of the Indo-Malayan genus Tropidosaurus. Consequently, it is here referred to the genus Tropidosaurus. The great similarities between Trimeresurus huttoni and Tropidosaurus wagleri are discussed.

KEY WORDS. - Trimeresurus huttoni, Tropidosaurus, Crotalinae, India, taxonomy.

INTRODUCTION
The Trimeresurus-complex is currently composed of five genera (Trimeresurus, Ermetia, Ouophis, Pratoshahypus and Tropidosaurus) totalling 43 species (David and Ineich, 1998). The group is widely distributed in tropical and subtropical parts of southern, eastern, and southeast- ern 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 Gratas 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 Bigh 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 ven- omous 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 Britton (1964), Whittaker (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 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-
pents. 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 row between the supraoculars; there 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; supraalabials, 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. Ventralis 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 dully 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 (= inter supraoculars), 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 its scalation is related to Trimeresurus erythraeus, 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 type specimens of most species. In the case of the present species, it is obvious that the original description is very incomplete, and that Trimeresurus bornensis shows unusual features for a member of the genus Trimeresurus senus ursice. 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 coloration 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 (BNHMS), 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 Trogonophis 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 number 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 ventrais), 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. (1983).


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...
HODSNOTONI (BMNH external faunal and merod described. No son its skull specimen. Wy Smith (1949) a'iton's private collection of the (BNHM), ac-1997. TRIMERERUSAUS Trimeresurus occur in south-species known or in juveniles. caudation of T. i with those of lea from four counted. The a'it counted, re-nd the head, at responding to its), and at one .ation nomen- ed is given in follow: Leviton ral History, at oam, London; society, Mumm- al d'Histoire stanches Mu- nal Reference -Museum und Frankfurt am of Natural.

HOLOTYPE TTONI
al, head rather 6 times longer.

FIGURE 1: Lateral view of holotype of Trimeresurus hauttoni (BMNH 1948.1.8.75).

FIGURE 2: Dorsal view of head of holotype of Trimeresurus hauttoni (BMNH 1948.1.8.75).
FIGURE 3: Dorsal view at midbody of holotype of Trimeresurus austini (BMNH 1948.1.3.75).

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-forehead 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 (TLT): 136 mm.

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

Dorsal scales: 25 (not 2) 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 supracaudal, slightly enlarged compared with adjacent snout scales; 1 small triangular loreal; 2 upper precoculars 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 precocular that normally borders the lower margin of the loreal pit is divided into two small scales; 2 postoculars; 1 supracaudal, 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 interscapulars; temporals in three rows, the lower ones enlarged, as large as

the supralabial-gated, crescent each side, the prelabial composed 2nd not bordered loreal pit and b lines the whole loreal pit, one between the nas supralabial large 2.3 times as long posterior lower subocular by nearly as high from the subo, succeeding pores but sn from the subo contact with the rals; 10 pores of s in contact with tinctly keeled, a third pair in a row of elongate gular scales, d.

In preservative dull green, slight with a series of s spots located o rows from the other by about w stripes; pedio brown for a lar subcaudal scale.

Head dull gray postoculars, the temporals from with a dull, c streak; a pros in front of the loreal, vanishing reaching the n barded below that makes the

RESU Our interest in to examine m
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 preorbital 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 obliquely 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 peculiar 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 nanhae and their three main sister 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 bicolor streak. Furthermore, these similarities in pattern between humoni and Tropidolaemus wagleri are supported by largely identical morphological and meristic 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 Bruton (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 Bruton (1964), the genus Tropidolaemus is defined as follows:


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 color 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 *Trimeresurus* and *Protobothrops*). Abbreviations: Otc: Overall body colour bright green in life + pres. +, no. =, +:- pinkish to red; Bws: white and red dorsolateral vertical bars or dorsolateral spots on body: + present, - absent; Prs: precocular 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; IL/TL: ratio: tail length/totai body length (range). Nps: presence of a nasal pair: + present, - absent. Ven: number of ven- trals (range); Sc: number of subcaudals (range). Co (cm): number of dorsal scale rows at midbody. KCo: dorsal scale rows at midbody keeled: + strongly keeled, +: weakly keeled. Smooth. Sources of comparative data listed with Table 2.

<table>
<thead>
<tr>
<th>TAXON</th>
<th>Otc</th>
<th>Bws</th>
<th>Prs</th>
<th>Pos</th>
<th>Cps</th>
<th>IL/TL</th>
<th>Nps</th>
<th>Ven</th>
<th>Sc</th>
<th>Co (cm)</th>
<th>KCo</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tropidoclonis hamata</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>3</td>
<td>0.28</td>
<td>139-146</td>
<td>40-52</td>
<td>23</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tropidoclonis wagleri</em></td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>1-4</td>
<td>0.14-0.19</td>
<td>127-154</td>
<td>45-56</td>
<td>21-27</td>
<td>+ +</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>0.16-0.18</td>
<td>145-177</td>
<td>55-71</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus melanoleucus</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.13-0.19</td>
<td>154-174</td>
<td>46-65</td>
<td>21-23</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus microlophus</em></td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.15-0.23</td>
<td>173-184</td>
<td>48-78</td>
<td>12-16</td>
<td>+ +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus melanocephalus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>0.15-0.18</td>
<td>136-159</td>
<td>44-63</td>
<td>21-23</td>
<td>+ + +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Protobothrops kii</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.12-0.16</td>
<td>128-150</td>
<td>32-52</td>
<td>21 (23)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus imenoccephalus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>0.15-0.17</td>
<td>142-170</td>
<td>53-69</td>
<td>17-19</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus alticinctus alticinctus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>0.14-0.21</td>
<td>149-173</td>
<td>48-78</td>
<td>21 (23)</td>
<td>+ + +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus erythraeus</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.15-0.21</td>
<td>151-180</td>
<td>49-79</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus hypu</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>197-198</td>
<td>63-83</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus imenoccephalus</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.17-0.22</td>
<td>150-172</td>
<td>59-77</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Additional notes:

(a) - Juvenile specimens, from all populations, and most adult males are bright green. The precocular bicolic 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 precocular 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 *stegniger* sensu later.

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

### TABLE 2: Comparison of morphological data and body scalation in pit vipers (genera *Trimeresurus* and *Protobothrops*). Source: *Tropidoclonis* Smith (1943); *T. melanoleucus*: N. T. (nose); *T. macrolepis*: 1 *T. malaleucus*: *Protobothrops* species, *T. kii*: 1 *T. erythraeus*: 1 *T. alticinctus”: 1 *T. imenoccephalus*: 1 *T. hypu*: 1 *T. imenoccephalus*: 1

<table>
<thead>
<tr>
<th>TAXON</th>
<th>Otc</th>
<th>Bws</th>
<th>Prs</th>
<th>Pos</th>
<th>Cps</th>
<th>IL/TL</th>
<th>Nps</th>
<th>Ven</th>
<th>Sc</th>
<th>Co (cm)</th>
<th>KCo</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tropidoclonis hamata</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>3</td>
<td>0.28</td>
<td>139-146</td>
<td>40-52</td>
<td>23</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tropidoclonis wagleri</em></td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>1-4</td>
<td>0.14-0.19</td>
<td>127-154</td>
<td>45-56</td>
<td>21-27</td>
<td>+ +</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>0.16-0.18</td>
<td>145-177</td>
<td>55-71</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus melanoleucus</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.13-0.19</td>
<td>154-174</td>
<td>46-65</td>
<td>21-23</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus microlophus</em></td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.15-0.23</td>
<td>173-184</td>
<td>48-78</td>
<td>12-16</td>
<td>+ +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus melanocephalus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>0.15-0.18</td>
<td>136-159</td>
<td>44-63</td>
<td>21-23</td>
<td>+ + +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Protobothrops kii</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.12-0.16</td>
<td>128-150</td>
<td>32-52</td>
<td>21 (23)</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus imenoccephalus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>0.15-0.17</td>
<td>142-170</td>
<td>53-69</td>
<td>17-19</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus alticinctus alticinctus</em></td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>0.14-0.21</td>
<td>149-173</td>
<td>48-78</td>
<td>21 (23)</td>
<td>+ + +</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus erythraeus</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.15-0.21</td>
<td>151-180</td>
<td>49-79</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus hypu</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>197-198</td>
<td>63-83</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trimeresurus imenoccephalus</em></td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>0.17-0.22</td>
<td>150-172</td>
<td>59-77</td>
<td>21</td>
<td>+</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


(1) T. hypu. This species is not included in the table due to its small size and lack of distinctive morphological features.
TABLE 2: Comparison of head scation and other features in pit vipers (genera Tropidolepis, Trimeresurus and Pseudoboothopsis). Abbreviations: Sp.: number of supralabials (range). - Sun: separation of the 1st supralabial with the corresponding nasal. + ym., 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. + ym., no. CSoh: number of the supralabials (s) that are in contact with the subocular. Is: number of intersuprac说了 between the supralabials (range). Kmn: strong keels on upper snout scales: + ym., no. Kth: keels on upper head scales: + strongly keeled, ++ weakly keeled, - no. Kth: keels on temporal scales: + strongly keeled, ++ weakly keeled, - absent. Is.: number of infralabials. Cln: first pair of infralabials in contact. + ym., no. Cln: keels on gular and chin scales: + strongly keeled, ++ weakly keeled, - absent.

<table>
<thead>
<tr>
<th>(m)</th>
<th>RCo</th>
<th>Taxon</th>
<th>Sp.</th>
<th>Sun</th>
<th>CSP</th>
<th>Dc.</th>
<th>CSoh</th>
<th>Kmn</th>
<th>Kth</th>
<th>Is</th>
<th>Cln</th>
<th>Cln</th>
<th>Kth</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>+</td>
<td>Tropidolepis huttoni</td>
<td>9</td>
<td>+</td>
<td>-</td>
<td>8-9</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>10</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>27</td>
<td>+</td>
<td>Tropidolepis wagleri</td>
<td>8-10</td>
<td>+</td>
<td>-</td>
<td>10-17</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>10-13</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>2</td>
<td>+</td>
<td>Trimeresurus gramineus</td>
<td>10-12</td>
<td>+</td>
<td>+</td>
<td>8-11</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>9-10</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>+</td>
<td>Trimeresurus labialis</td>
<td>9-12</td>
<td>+</td>
<td>+</td>
<td>8-11</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>11-16</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>14</td>
<td>+</td>
<td>Trimeresurus macleayi</td>
<td>7-9</td>
<td>+</td>
<td>+</td>
<td>3</td>
<td>3</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>10-12</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>21-23</td>
<td>+</td>
<td>Trimeresurus malariorius</td>
<td>8-10</td>
<td>+</td>
<td>+</td>
<td>7-9</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>10-13</td>
<td>-</td>
</tr>
<tr>
<td>20</td>
<td>+</td>
<td>Pseudoboothopsis ingohai</td>
<td>8-10</td>
<td>+</td>
<td>+</td>
<td>8-11</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>9-12</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>&gt;19</td>
<td>+</td>
<td>Trimeresurus iridopleurus</td>
<td>9-11</td>
<td>+</td>
<td>+</td>
<td>2-6</td>
<td>3</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>12</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>25</td>
<td>+</td>
<td>Trimeresurus albolabris</td>
<td>7-13</td>
<td>+</td>
<td>+</td>
<td>8-14</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>11-16</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>23-25</td>
<td>+</td>
<td>Trimeresurus erythraeus</td>
<td>9-13</td>
<td>+</td>
<td>+</td>
<td>10-15</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>+</td>
<td>12-14</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td>+</td>
<td>Trimeresurus hogenii</td>
<td>9-11</td>
<td>+</td>
<td>+</td>
<td>4-8</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>13</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td>+</td>
<td>Trimeresurus sp. (1)</td>
<td>9-12</td>
<td>+</td>
<td>+</td>
<td>9-13</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>11-15</td>
<td>+</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Population</th>
<th>Ocb</th>
<th>Bsw</th>
<th>Cps</th>
<th>tl/TL</th>
<th>Vcm</th>
<th>Sc</th>
<th>Cs</th>
<th>Kca</th>
<th>Sprl</th>
<th>Crp</th>
<th>Int.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trop. huttoni</td>
<td>+</td>
<td>+</td>
<td>3</td>
<td>0.28</td>
<td>139-146</td>
<td>49-52</td>
<td>23</td>
<td>7</td>
<td>6</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Trop. huttoni</td>
<td>+</td>
<td>+</td>
<td>1-4</td>
<td>0.14-0.19</td>
<td>127-156</td>
<td>45-56</td>
<td>21-27</td>
<td>4</td>
<td>8</td>
<td>10-17</td>
<td>10-13</td>
</tr>
<tr>
<td>Thailand/Malay</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>0.14-0.17</td>
<td>134-141</td>
<td>49-54</td>
<td>25</td>
<td>7</td>
<td>9</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Adults (n = 4)</td>
<td>+</td>
<td>+</td>
<td>4</td>
<td>0.14-0.17</td>
<td>134-141</td>
<td>49-54</td>
<td>25</td>
<td>7</td>
<td>9</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Juv./adults (n = 1)</td>
<td>+</td>
<td>+</td>
<td>3</td>
<td>0.14-0.19</td>
<td>135-141</td>
<td>45-55</td>
<td>23-25</td>
<td>4</td>
<td>8</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Laos/Timor</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>0.14-0.19</td>
<td>135-138</td>
<td>45-55</td>
<td>23-25</td>
<td>4</td>
<td>8</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Adults (n = 4)</td>
<td>+</td>
<td>+</td>
<td>4</td>
<td>0.14-0.19</td>
<td>135-138</td>
<td>45-55</td>
<td>23-25</td>
<td>4</td>
<td>8</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Juv./adults (n = 2)</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>0.14-0.19</td>
<td>135</td>
<td>45-55</td>
<td>23-25</td>
<td>4</td>
<td>8</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Borneo</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>0.14-0.19</td>
<td>134-142</td>
<td>46-53</td>
<td>21-27</td>
<td>4</td>
<td>8</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Adults (n = 6)</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>0.14-0.19</td>
<td>134-142</td>
<td>46-53</td>
<td>21-27</td>
<td>4</td>
<td>8</td>
<td>10-13</td>
<td>11-13</td>
</tr>
<tr>
<td>Juv./adults (n = 7)</td>
<td>+</td>
<td>+</td>
<td>3</td>
<td>0.15</td>
<td>140</td>
<td>48</td>
<td>21</td>
<td>9</td>
<td>10</td>
<td>13</td>
<td>12</td>
</tr>
<tr>
<td>Philippines</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>0.14-0.16</td>
<td>127-137</td>
<td>45-50</td>
<td>25-25</td>
<td>4</td>
<td>8</td>
<td>10-16</td>
<td>10-11</td>
</tr>
<tr>
<td>Adults (n = 5)</td>
<td>+</td>
<td>+</td>
<td>1</td>
<td>0.14-0.16</td>
<td>127-137</td>
<td>45-50</td>
<td>25-25</td>
<td>4</td>
<td>8</td>
<td>10-16</td>
<td>10-11</td>
</tr>
</tbody>
</table>

(2) all south Indian and Sri Lankan taxa *Trimeresurus gramineus*, *T. macrolopha*, *T. malabaricus*, *T. nigrocinctus*, plus *T. lahitia* from the Andaman Islands, and the taxon *stigmuroides*, recently tentatively placed in the genus *Protothamnus* (Krane et al., 1998), and (3) a selection of green *Trimeresurus* species covering each of the groups recognised by Brattstrom (1964: 244). Among these taxa, we selected *T. albodorsalis albodorsalis*, *T. erythrurus*, *T. hagenii* (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 subcaudal, 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

---

January, 1998
January, 1949] REDESCRIPTION OF TRIMERESURUS HUTTONI 51

gonal bordering the loreal pit, scales keeled on snout, upper head and sides, of a peculiar 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 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


Diagnosis. - A pit viper endemic to southern peninsular India characterized 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 preocular, a tail length/total length ratio of at least 0.28, green colouration in juveniles, and white and red post- and postocular streaks.

Variations. - Only two specimens are known.

The currently reported variation is: ventrals 139-146; subcaudals 49-52; 8-9 intersupracaudals (Smith, 1949).

Range. - India: State of Tamil Nadu: western Varsudabhad Hills (fin 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, correspond to an elevated plateau in the central part of the Varsudabhad Hills, at about 0°36'S, 77°30'E. Bates and Harrison (1997), in their gazetteer, gave the coordinates, as 0°36'S, 77°32'E. According to Angus Hutton (pers. comm., 1997), the locality of capture was around coordinates 0°36'S, 77°12'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 1,956 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 1500 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 *Tropidolaema*, which, however, still remains uncertain. *Tropidolaema huttoni*, as currently known, can be separated from juvenile *T. wagleri* only by the much higher tail length/tail

T. wagleri (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 *Tropidolaema wagleri* is not resolved. These subspecies were recognised by Taylor (1922a: 298): *Tropidolaema wagleri wagleri* Wagler, 1830, *T. wagleri albozonis* (Taylor, 1917) and *T. wagleri subtunulus* (Gray, 1842), the latter two being endemic to the Philippine Islands. Leviton (1964) considered *Tropidolaema wagleri* to be a monotypic specie,

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

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

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

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

**Tropidolaema huttoni** (Smith, 1949)

Trimeresurus huttoni Smith, 1949: 596.

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

foot", now a pl. of Varia of Tamil Nadu.

**Comments.** - Indian character ratio of 28%. Range. - India.

**Tropidolaema** (Tropididae: Type locality: Commerson. Vogel (1996) i ship of this sps (1827) or Schm. typic (see abov.)

**Diagnosis** - *Tropidolaema*: Indonesia cha length leaves.

Range. - B' Malaysia (Pen. on Borneo Isla. and Sumat... Karimata Is.,... ophaga, Nilgiri Islands. Dinaut Is.,... ipando Is.,... Sana Is.,... Sibin Island, Thailand.

**ZOOLOGIC**

There is no p. locality of Tr. introduction i... by ranked i... regarded ex Tropidolaema... Lim was the Sura Thas... Cox, 1991) - species in sour. inflating.

There are similar distri... Gndo-China, 1
feet", now a plateau in the western central edge of the Varanashahr Hills, Mahratur 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/totallength 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/totallength ratio less than 20%


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, Malayasia) 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 range boundaries 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. nudus) 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) and Sivaprasad (1953) developed the Sapthara Hypothesis, which explained the phenomenon by suggesting the existence of an ancient mountain range between the Vindhya 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 mountainous areas. This hypothesis is, however, not supported by recent geological data, although Swan (1993) provided some taxonomic and zoogeographical evidence in its support. On the other hand, apart from a few shared genera, Das (1996) showed that the reptile fauna 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 refuge 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 scrublands. Many species in the uplands, particularly those with affinities in the east, therefore are considered relics 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 Trimeretronus complex (including the genera Trimeretronus, Erms, Ooophils, Prabotheus and Tropidolemus). Species of one or more of these genera are found as far west as Nepal and northern India, but none have been recorded from the southern parts of India. However, not less than six endemic species have been described from the evergreen forest-clad hills of the Western 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 Tropidolemus 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 Tropidolemus differs notably from those involved in the Satapura 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 lowlands, lowlands and highlands 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. buttoni through further collections would throw light on the zoogeography of the genus.

ACKNOWLEDGMENTS

We are indebted to Alain Dobon, Ivan Lienich and Olivier Pautreau, Laboratoire de Zoologie (Reptiles and Amphibians), Musée National d’Histoire Naturelle (Paris), and Var Wallach, Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts), for their careful reading of the manuscript, their constructive comments and their technical support. We also thank Roger Bear, MNHN, for the photographs of the holotype reproduced here.

LITERATURE CITED


1922. The snakes of the Philippine Islands. Bureau of Printing, Manila. 312 pp; 37 pl.


1931. Opiumia Taprobaneis, or the snakes of Ceylon. H. R. Cottle, Cólombo. xxiii + 581 pp; 1 pl; folding map.


January, 1998

REDESCRIPTION OF TIMMERSERUS HUTTONI

APPENDIX I
SPECIMENS EXAMINED
Protothoraxis stirgutu: MNHN 4061, "Hindoutan" (= India); SMF 21208, Nilgiri Hills, Tamil Nadu, India; SMF 21209/1-2, Nilgiri Hills, Tamil Nadu, India.


Timmerserus 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. Timmerserus malabaricus: MNHN 1913.5, Palni Hills, near Tiruchirappalli, 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. Timmerserus steinigeri: MNHN 1912.352, "San Chozen Fou", Province of Guizhou, People’s Republic of China; SMNH 4038, Da Jing, Mt. Jing Gang, Province of Jiangxi, People’s Republic of China; MNHN 1969.4, Taiwan; MNHN 1990.4246, Thailand; MNHN 1991.295, Thailand (from pet trade); NRC 1345, Tung Salang Luang, Province of Phinuanak, Thailand; NRC 1347, Pak Chong Chai Sakarat, Province of Nakon Ratchasima, Thailand; NRC 1422, Pak Chong Chai Sakarat, Province of Nakon Ratchasima, Thailand; NRC 1424, Pak Chong Chai Sakarat, Province of Nakon Ratchasima, Thailand; MNHN 1955.110-111, Sap [Cha Pa] 20 km SW of Lao Cai, Province of Hsou Lieu So’n, Vietnam. Tropidosurus nogneri: MNHN 4062, Java, Indonesia; MNHN 4063, Sumatra, Indonesia; MNHN 1879.708, Bedageth River, Deli, now Bedagai River, Province of Sumatera Utara, Sumatra, Indonesia; MNHN 1880.43, Sumatra, Indonesia; MNHN 1880.432-434, Borneo; MNHN 1991.2712, 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 1880.327, Alor Province, Luzon, Philippine Islands; MNHN 1880.383, Sulu Archipelago, Philippine; MNHN 1884.46, Philippine; MNHN 1884.181-182, Philippine; MNHN 1891.82, Seboenak, Borneo; MNHN 1957.817, Borneo; MNHN 1990.4250, Thailand (from pet trade); MNHN 1878.365-366, both labelled "Masinian, Nouvelle Guinée", unknown origin; MNHN 1990.4287, Thailand (from pet trade). Timmerserus trigonocephalus: MNHN 245, Sri Lanka; MNHN 1890.68, Sri Lanka.

Received: 28 October, 1997. Accepted: 20 December, 1997.