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A REVIEW OF THE COMPLEX OF *Trimeresurus hageni* (LIDTH DE JEUDE, 1886) (SQUAMATA: VIPERIDAE) WITH DESCRIPTIONS OF THREE NEW INSULAR SPECIES FROM INDONESIA

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Abstract
Variations in morphological characters were investigated among 124 specimens covering the whole range of the large, Indo-Malayan pitviper complex of species currently known as *Trimeresurus hageni* (Lidth de Jeude, 1886). Herein, we redefine *T. hageni* and discuss and confirm the validities of its description and name-bearing type; the lectotype is redescribed. Morphological analyses show that at least four taxa, distinct at species level, are currently confused under the combination *T. hageni*. As a consequence, three new insular species are described, from Nias Island, Siberut Island, and Simeulue Island. All these three new species differ from *T. hageni* sensu stricto by a combination of differences in scalation and pattern. *T. hageni* sensu stricto inhabits Sumatra and Bangka Island, as well as West Malaysia, Singapore and southern Thailand. The new species are compared with *T. sumatranus* and *T. gunaleni*, also present on Sumatra.

Key words: Great Sunda, Nias, Siberut, Simeulue, Sumatra, *Trimeresurus sumatranus*, West Malaysia

Introduction

The nomen *Bothrops hageni* was first applied by Lidth de Jeude (1886) to a collection of nine specimens. However, his description was clearly conditional as he was not sure if the specimens he had at hand represented a distinct species or were merely young specimens of *Trimeresurus sumatranus* (Raffles, 1822). The validity of this conditional description, in the sense of the *Code* (ICZN 1999), is discussed below. Nevertheless, on the basis of this uncertain identification, Boulenger (1896) synonymized *B. hageni* with *T. sumatranus*. This fact is quite surprising as there are several differences in scalation and also in dorsal colour and pattern; the adults of each species have a totally different colouration and

habitus. However, Boulenger had only one single juvenile of *T. sumatranus* at hand and whereas the adults are quite different in colouration, juveniles of both species are green and nearly patternless. Boulenger's decision was followed by subsequent authors, until Lidth de Jeude (1922), and especially Brongersma (1933a), addressed the status of *Bothrops hageni*. This latter author was the first to show that *T. sumatranus* and *T. hageni* were valid species, and he provided new characters separating both species from one another.

Subsequently, the status and variation in the groups of *T. sumatranus* and *T. hageni* have only been addressed in two recent papers (Sanders *et al*. 2002, 2004). As far as *T. hageni* is concerned, results of the first publication, which was based on scalation characters and colour pattern, can be summarized as follows: (1) *T. sumatranus* and *T. hageni* are clearly separate as shown by canonical multivariate analysis; (2) *T. hageni* is found in North and South Sumatra, Thailand, West Malaysia, Singapore, and the islands of Nias and Siberut; (3) morphological differences, especially in males, were pointed out between populations from the islands of Nias and Siberut on the one hand, and all other populations on the other hand. In these islands, specimens referable to *T. hageni* show some characters of the pattern typical to *T. sumatranus*, such as black dorsal crossbars and the presence of dark edges on head scales. This partial similarity has led to erroneous records of *T. sumatranus* from these islands.

The second publication included molecular analyses and compared all species referred to the genus *Parias*, which we consider to be a subgenus (see David *et al*. 2011). Regarding the species treated here, the results of Sanders *et al*. (2004) can be summarized as follows:

(1) For *T. hageni*, the same distribution as in Sanders *et al*. (2002) was given on the map, but in contrast to the work of 2002, the authors found little morphological variation within *T. hageni*. So, they referred all populations of the Mentawai Archipelago as *T. hageni*.

(2) For *T. sumatranus* they excluded the mainland of Thailand and West Malaysia from the distribution area for unknown reasons. They found differences in ecology between Bornean populations and Sumatran populations. Genetically they found a difference of 3.3% in the distance between the specimens of these two populations based on the mitochondrial cytochrome b gene. It must be emphasized that only two populations of *T. hageni* and two populations of *T. sumatranus* were compared genetically.

Finally, Vogel *et al*. (2014) addressed the systematics and the nomenclatural history of *T. sumatranus*. This species, as defined in the literature, was shown to be a composite of two species on Sumatra. One was described as *T. gunaleni* (Vogel, David and Sidik, 2014). Here, we address the systematics of various populations of *T. hageni*, and especially the insular populations from several islands of the Mentawai Archipelago. At least three of them are shown to warrant a distinct, specific status.

Material and Methods

The present paper is based on 124 preserved specimens of the *Trimeresurus hageni* complex consisting of 45 males and 79 females, and an additional series of 69 specimens of the *T. sumatranus* complex covering the whole range of both species. Preserved examined specimens of the *T. hageni* complex are listed under their respective account; specimens of *T. sumatranus* and *T. gunaleni* are listed in the Appendix II.

Morphology. We retained standard morphological characters used in the genus *Trimeresurus* by Brongersma (1933a), Pope & Pope (1933) and Regenass & Kramer (1981), along with other morphometric characters adapted from Vogel *et al*. (2004, 2014). We made a pre-selection of characters based on a limited number of specimens. Characters not suitable, due to variability or uniformity were deleted and a set of 30 characters was retained (Appendix I, see also abbreviations). Measurements, except body and tail lengths, were taken with a slide-calliper to the nearest 0.1 mm; all measures on body were taken to the nearest millimetre. To minimize inter-observer error, all measurements considered here were made by GV. Ventral plates were counted according to Dowling (1951). The first subcaudal was defined as the first scale posterior to the vent that touched the opposite scale. The terminal scute is excluded from the number of subcaudals. The numbers of dorsal scale rows are given at one head length behind the head, at midbody (*i.e*. at the level of SVL/2) and at one head length anterior to the vent respectively. Values for symmetric head characters are given in left/right order. The real coloration of body and eyes were observed only on living animals or very freshly preserved specimens.

Morphometric, meristic and colouration characters retained for this study are listed in Appendix I. Altogether, 30 variables were considered, either standing on their own or derived from the raw characters listed above. Not all variables listed in this table proved to be useful to separate at least one taxon of the *T. hageni* group from the others, but all were investigated and used in combinations of characters and/or were used in univariate analyses.

The colour of the eyes has been shown before to be a diagnostic character (Vogel *et al*. 2004). However, this is problematic as it cannot be observed in preserved specimens. According to our observations, the eye colour in adult animals is stable, for the same sex, for most species of pitvipers (Vogel *et al*. 2004) with the notable exceptions of *T. stejnegeri* and *T. insularis*, species not belonging to the group treated here. In the species treated here, there was no sexual dimorphism in eye colouration. The colour of the tail is also diagnostic.

Museum abbreviations. BMNH (now NHMUK), the Natural History Museum, London, UK; CAS, California Academy of Sciences, San Francisco, USA; FMNH, Field Museum of Natural History, Chicago, USA; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMB, Naturhistorisches Museum, Basel, Switzerland; NMW, Naturhistorisches Museum Wien, Austria; MZB.OPHI, Museum Zoologicum Bogoriense, Cibinong, Indonesia; OMNH, Osaka Museum of Natural History, Osaka, Japan; PSGV, Gernot Vogel's private collection, Heidelberg, Germany; RMNH, Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Netherlands; SMF, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, Germany; USNM, United States National Museum, Washington, D.C., USA; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; ZMA, Zoölogisch Museum Amsterdam, Amsterdam, The Netherlands; ZMB, Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; ZMH, Zoologisches Institut und Museum, Universität Hamburg, Hamburg, Germany; ZRC: Zoological Reference Collection, National University of Singapore, Singapore; ZSM, Zoologische Staatssammlung, München, Germany.

Results

Based on the analysis of morphological characters of specimens originating from the whole of the distribution range of the complex of *Trimeresurus hageni* auctorum, we conclude that three populations inhabiting islands off the west of Sumatra, namely the populations of Siberut, Simeulue and Nias Islands, constantly differ in several morphological and colouration characters from those of Sumatra and West Malaysia. We consider that these isolated populations should be given full species status. A fourth population, also possibly distinct at species level, inhabits Batu Island but we do not have enough material from this population to come to a final conclusion and thus refrain from naming it. The status of this population will be addressed elsewhere. On this basis, we provide a new definition of *T. hageni* sensu stricto, which is redescribed, and we describe the three new species, as follows:

Trimeresurus hageni (Lidth de Jeude, 1886)
(Figs. 1–3, 12A; Table 1)

Bothrops hageni Lidth de Jeude, 1886: 53

Lectotype [designation of Brongersma (1933a: 7)]. RMNH RENA 819 (former cabinet of Lidth de Jeude Nr 301), adult female, collected by D. Hagen from "Deli, Sumatra" [by virtue of the designation of a lectotype by Brongersma (1933a)], at present Medan, North Sumatra (Sumatera Utara) Province, Sumatra Island, Indonesia.

Other material examined (*n*=76). **INDONESIA**. ***Sumatra***. BMNH 89.12.26.20, District of Deli, now Medan; BMNH 93.6.5.11, East coast of Sumatra; MNHN 1880.0042, Sumatra; MZB.OPHI 1740, Padang Bukit Sebelah; MZB.OPHI 1892a–b, Ketambe, Aceh Tenggara; MZB.OPHI 1898, Aceh Barut; MZB.OPHI 2886a–b, Kembang Manis, Bengkulu; MZB.OPHI 3716, Kubu Perahu, Lampung; NHMB 5108, Palembang, South Sumatra; NHMB 9423, Sumatra; NMW 23909:1–2, Medan; NMW 23909:3, Deli; NMW 28150:1–3; Padang; NMW 28155:3, Medan; RMNH 5587A, Deli; RMNH RENA 819 (lectotype), "Deli", now Medan; ZFMK 32508, Sumatra; ZMB 15884, Sukuranda, Oberer Langkat, O-Sumatra; ZMB 29642, Padang; ZMB 32193a, b, Sumatra; ZMB 62699, Aceh; ZMB 66176, Bengkulu province; ZMH R06937, Serdang; ZSM 109/1927, Goenoeng Rintels, S.

Deli; ZSM 202–1979a, Lau Rakit, near Deli; ZSM 202–1979b, Gunoeng Rinteh. ***Bangka Island***. RMNH 4697, Bangka; ZSM 365/1907 (4), ZSM 365/1908 (1–3) Simpang, Bangka. **SINGAPORE**. BMNH 80.9.10.6, Singapore. **MALAYSIA**. ***West Malaysia***. BMNH 1936.9.12.5, "Kualla Taku, Malay Penin."; BMNH 1936.9.91, Perak; BMNH 1967.2290–1, Gunong Benom; CAS 16831, Silensing, Pahang; MNHN 1899.0269, Peninsular Malaysia; MNHN 1974.0044, Kuala Lumpur; MNHN 2002.0406, West Malaysia; NMW 28158:1–2, Kedah; PSGV 393, Kuala Lumpur; SMF 64464–5, Perak; ZFMK 16680, Yombak; ZFMK 68522, north of Kuala Lumpur; ZMB 70235, Kepong, Selangor; ZRC 2.2928, Tasik Bera, Pahang; ZRC 2.2930, Tembeling, Pahang; ZRC 2.2932, Bukit Lagong Forest, Selangor; ZRC 2.2933–4, Ulu Langat, Selangor; ZRC 2.2935, Cameron Highlands, Pahang; ZRC 2.2943, Negeri Sembilan, Gunung Angsi; ZRC 2.5362, Bellum, Perak; ZRC 2.5397, Kepong, Frim, Selangor. **THAILAND**. BMNH 1936.9.12.4, Betong, Yala; BMNH 1988.858–62, Trang; IRSNB 3059 Betong. **NO SPECIFIC LOCALITY**: ZFMK 18835, no locality; ZFMK 21497, Sunda Islands.

Diagnosis. A large species of pitviper of the genus *Trimeresurus* (subgenus *Parias* Gray, 1849), characterized by the combination of (1) body elongate, head long and massive in adults; (2) body deep green or dark green in life, without sexual dimorphism in colouration and pattern; (3) on each side, a series of dorsolateral spots, white or pink, irregular in shape and size, usually conspicuous; (4) a broad, pale ventrolateral stripe on first two dorsal scale rows; (5) 21 (in a sole specimen 23) DSR at midbody; (6) 1st supralabial distinct from nasal scale; (7) large internasals, most usually in contact, only exceptionally separated by 1 scale (6 out of 42 specimens); (8) 1 or 2 (3rd or 3rd–4th SL), rarely 3 supralabials (3rd–4th–5th SL) in contact with subocular, (9) supraoculars elongate, not distinctly broad, separated by 5–9 (usually 6–7) scales; (10) tail average, with a ratio TaL/TL between 0.190 and 0.225 in males and 0.143 and 0.185 in females, with a clear sexual dimorphism; (11) 176–196 VEN; (10) 59–91 SC (males: 72–91; females: 59–78); (12) in life, eye dark grey pale yellow or yellowish-green; (13) a narrow postocular streak, white, cream, pale yellow, uniform or mixed with reddish-brown or salmon (pink or cream in preservative) usually present in males, present or absent in females; (14) venter yellowish-green or pale green, without any black margins; and (16) tail green as the body anteriorly, with large pinkish-red, salmon or red blotches (cream in preservative) on the upper surface of its anterior half, becoming fused and turning the tail entirely into hues of red on its posterior half.

Characters separating *T. hageni* from the three new species described below, and from *T. sumatranus* and *T. gunaleni* are discussed below and summarized in Table 1.

Taxonomic and nomenclatural comments. The 'description' of *Bothrops hageni* is rather odd and may be challenging on a nomenclatural basis. According to the *Code* (ICZN 1999), the specific nomen was in fact first published both as a "name proposed conditionally" and as a "name published as a junior synonym", here of *Bothrops sumatranus*. Lidth de Jeude saw the possibility that the syntypes might be juveniles of *T. sumatranus* (Raffles, 1822), but stated that the nomen *Bothrops hageni* would be available if these specimens proved to be distinct from *T. sumatranus*. Nevertheless, according to Art. 11.5.1, "a name proposed conditionally for a taxon before 1961 is not to be excluded on that account alone", provided that its description is valid according to other requirements of Art. 11. Furthermore, according to Art. 11.6.1, if a name published as a junior synonym has been treated before 1961 as an available name of a taxon, it is made available. This is the case here as *Bothrops hageni* and its chresonyms in various genera, mostly as *Trimeresurus hageni*, have been widely regarded as a valid species since Brongersma (1933a), for example by Loveridge (1946), Haas (1950), Klemmer (1963), Werler & Keegan (1963), Taylor (1965), Minton *et al*. (1966), Leviton (1968), Grandison (1978), Hoge & Romano Hoge (1981), Tweedie (1983), Golay *et al*. (1993), David & Vogel (1996), Manthey & Grossmann (1997), David & Ineich (1999), McDiarmid *et al*. (1999) and David *et al*. (2011), and, in the genus *Parias* Gray, 1849, by Malhotra & Thorpe (2004) and Wallach *et al*. (2014) (non-exhaustive list). Therefore, the combination *Bothrops hageni* Lidth de Jeude, 1886 is both available and valid.

Lidth de Jeude had at hand nine specimens of this new species, eight from "Sumatra" and one from "Banka" (now Bangka Island), which should all be considered to be syntypes. Brongersma (1933a: 7) designated specimen RMNH 819 (now renamed RMNH RENA 819) as "Type". According to Art. 74.5 of the *Code*,

an indication, such as "type" given to one of the syntypes before 2000, define the designation of a lectotype.

The original type locality (Lidth de Jeude, 1886: 54) should stand as "Sumatra" and "Banka", restricted by Brongersma (1933a: 7) to "Deli" by virtue of the designation of this lectotype. There is no doubt about the distinct specific status of *T. sumatranus* and *T. hageni*. *Trimeresurus hageni*, as here redefined, is monotypic. We could not find differences between populations of *T. hageni* from Sumatra and those from West Malaysia (Table 1).

Redescription of the lectotype. Rostral barely visible from above, triangular, about as high as broad; nasals pentagonal, large, elongate, entire with elements of a very shallow furrow barely visible; 2 internasals, trapezium-like, large, laterally elongate, about 1.5 times wider than long, broadly in contact each with the other; each internasal followed by small, irregular snout scales, not enlarged; scales on upper snout surface smooth, juxtaposed or barely imbricate, subrectangular, with 4 scales along a longitudinal line extending from the internasals to a line connecting the anterior margins of eyes; 2/2 canthal scales bordering the *canthus rostralis* between internasal and corresponding supraocular, not larger than adjacent snout scales; on each side, 1 elongate, triangular loreal scale between nasal and the upper preocular; 2/2 preoculars above the loreal pit, the upper one visible from above, both scales elongate and in contact with loreal; lower preocular forming the lower margin of loreal pit; 1/1 thin, elongate subocular; 2/2 small postoculars; 1/1 supraocular, elongate, rather irregularly shaped, 2.8/2.9 times as long as wide, about 0.8 times as wide as internasal, distinctly indented by upper head scales; 7 cephalic scales on a line between the middle of supraoculars, smooth, flat and juxtaposed; occipital scales flat, smooth, imbricate; temporal scales in 2 or 3 rows, smooth, lower ones much enlarged; 10/10 SL, 1st SL triangular, rather short, completely separated from the nasal; 2nd SL tall, bordering entirely the loreal pit and anteriorly in contact with nasal; 3rd SL longest and highest, about 1.1 times longer than high, in contact on both sides with subocular; 4th SL as high as 3rd SL but not as long, in contact with the subocular on both sides; 5th SL much shorter (0.6 times) than 4th one, separated from the subocular by 1 scale on both sides; 14/14 infralabials, those of the first pair longitudinally in contact, 1st–3rd IL in contact with anterior chin shields; 3 or 4 rows of smooth gular scales; throat shields irregularly arranged.

Body elongate, laterally compressed; head elongate, flattened, relatively narrow seen from above, massive and thick seen from the side, distinctly triangular, wide at its base, clearly distinct from the neck, 1.7 times as long as wide; snout quite long, rounded when seen from above, obliquely truncated when seen from the side, with a moderate canthus rostralis, amounting for 25.5 % of head length and 2.4 times as long as diameter of eye; a large, oval nostril piercing in the middle of nasal scale; nostril-loreal pit distance about 0.5 times the distance between the nostril and the eye; eye average, amounting for 0.6 times the distance between the lower margin of eye and upper lip border; tail, tapering and prehensile. SVL 831 mm, TaL 140 mm, TL 971 mm; ratio TaL/TL 0.144. DSR: 21-21-15 scales, rhomboid, moderately and narrowly keeled with the exception of scales of 1st dorsal scale row which are smooth and not enlarged; 186 ventrals (+ 0 preventral); 60 subcaudals, all paired; anal entire.

***Coloration*.** The head is uniform brown as the anterior part of the body above and on the upper temporal region, bluish green above the snout and lower temporals; on each side, a cream, oblique temporal streak extends from the eye to the corner of the mouth on the 3rd and 2nd rows of temporals behind the eye then on 2nd row only; supralabials pale bluish-green, distinctly paler than upper head surface, without darker edges; preoculars brown mixed with bluish-green. Chin, throat and infralabials uniform bluish green, with some faint darker spots posteriorly.

The body is bluish-green on the lower part of the sides, i.e. on 1st–4th DSR, becoming quickly darker, dark greyish- or greenish-blue above 4th DSR, but this colour turns into pale brown or bluish-brown on the two anterior thirds of the body; on each side, a series of irregularly rounded, cream blotches on 5th–6th DSR, visible only on the posterior half of the body, more or less widely separated each from the other by 5 to 18 scale rows; a cream, conspicuous ventrolateral stripe covering much of 1st DSR and the lower half of 2nd DSR, extending from neck up to vent. The tail is dark greyish blue on its immediate anterior part then covered with four wide and broad, cream blotches covering both the sides and the upper part of the tail; the ventrolateral stripe of the body extends for a

short length on the lower sides of tail; posteriorly, the tail is entirely cream.

The venter is uniform pale bluish green; subcaudals not edged with a darker hue; the tail is uniform pale bluish green on its anterior part then quickly turns to cream.

Species description and variation. According to Brongersma (1933a), Tweedie (1983), Sanders *et al*. (2002), Gumprecht *et al*. (2003, 2004) and our material, this large species reaches a maximum total length of 1,230 mm. Gumprecht *et al*. (2003) mentioned a total length of 1,400 mm but we could not find such a large specimen. Males are seemingly shorter, the longest male seen by us being only 956 mm long. Adults usually reach a maximum total length of 750–1,050 mm.

Rostral barely visible from above, triangular, about as high as broad; nasals subrectangular or pentagonal, entire or with traces of a shallow furrow; 1 large internasal on each side, subrectangular or trapezium-like, laterally elongate, 1.2–1.5 times wider than long; internasals usually in contact (in 65/72 examined specimens) or separated by 1 small scale (7/72); internasals followed by upper snout scales, irregular, distinctly enlarged, smooth, juxtaposed or barely imbricate, subrectangular, with 4–5 scales along a longitudinal line extending from the internasals to a line connecting the anterior margins of the eyes; 2 (rarely 3) canthal scales bordering the *canthus rostralis* of similar size; 2 (exceptionally 3) postoculars on each side; 1 large, elongate supraocular on each side, 2.2–2.6 times as long as wide, 0.7–1.0 times as wide as internasal, not indented by adjacent cephalic scales; 5–9 (usually 6–7) cephalic scales on a line between supraoculars, smooth, flat and juxtaposed or barely imbricate; occipital scales larger than cephalic scales, smooth; temporal scales smooth, large, subequal, in 2 rows anteriorly, 3 rows posteriorly; 9–13 (usually 10 or 11) supralabials; 1st SL always separated from nasal; 2nd SL tall, entirely bordering the anterior margin of the loreal pit, always in contact with nasal; 3rd SL longest and highest, elongate, 1.2–1.5 times as long as high, usually in contact with subocular, separated by 1 scale in 14/144 occurrences; 4th SL as long as high, as high or barely shorter than 3rd SL, either in contact with subocular (in 60/144 occurrences) or separated by 1 small scale (in 84/144 occurrences); 5th SL usually separated from subocular by 1 scale, rarely in contact (in 18/144 occurrences); 11–15 (usually 12–13; 16 IL in one specimen) IL; scales of the 1st pair longitudinally in contact or barely separated by the apex of the long mental scale; first three pairs of infralabials in contact with anterior chin shields; 3–6 rows of smooth gular scales; throat shields irregularly arranged.

The body is robust but elongate in both males and females, or slightly thinner in males. In adults, the snout is 24.0–26.0% as long as head or 2.0–2.6 times as long as diameter of the eye. Eye large in males and juvenile specimens, average in females but rather protruding laterally, amounting for 0.6–0.9 times the distance eye–lower edge of the lip in both sexes. Ratio TaL/TL: 0.143–0.225, with a clear sexual dimorphism: males: 0.190–0.225; females: 0.143–0.185. DSR: 21–23 (exceptionally 20 or 23) -21 (exceptionally 23) -15 (exceptionally 14 or 17); scales moderately keeled, smooth on 1st DSR; VEN: 176–196 (plus 0–2 preventrals); SC: 59–91, all paired, with a sexual dimorphism (males: 72–91; females: 59–78); anal entire. In our sample of 72 specimens, we examined only one specimen with 23 DSR at midbody; its dorsal scale formula is 25–23–17 (RMNH 7589). In our material, one specimen has 14 scale rows before vent, three have 17 rows.

Coloration. In life, adult specimens are pale green, bright green, grass green, dark yellowish green or olive green (deep green, bluish green or dark brown in preservative) above and on the sides, either more or less uniform, although slightly or barely paler on the lower part of the sides, or with more conspicuous paler areas, often triangular in shape with apex pointing upwards up to 4th–6th DSR, separated by areas of a darker green hue, producing a faint banded pattern; scales of the body not edged with black; interstitial skin dark grey; on each side, a series of large, more or less rounded or vertically elongate dorsolateral blotches, white, cream, pink or salmon (white or cream in preservative) on 5th–8th DSR, about 1 to 1.5 dorsal scale long and 1.5 to 2.5 scales high, longitudinally separated by 2 to 4 dorsal scales, usually more or less set off from each other on each side across vertebral line; these blotches are sometimes poorly defined or present only on the posterior half of the body; a conspicuous, broad, white, cream or pale yellow ventrolateral stripe extending from the base of the neck to the vent on the whole or greatest part of scales of the 1st DSR and on the lower part of 2nd DSR; sometimes, some irregular black spots on the anterior margin of scales of the 1st DSR, making

the ventrolateral stripe broken. The background colour of the tail is of the same green as the upper body; 5 to 8 large, pinkish-red, salmon or red blotches (cream in preservative) on the upper and lateral surface of its anterior half, forming incomplete rings, becoming progressively wider and fused, and turning entirely the tail into these hues of red on its posterior half, marked with irregular paler areas of the same colour than the under surface of the tail; the ventrolateral pale stripe of the body extends along the anterior half of the tail.

The upper snout and head surfaces and upper temporal regions are in the same hues of green as the body; snout and cephalic scales uniform or, rarely, narrowly edged with black; rostral, sides of the snout, supralabials and lower temporal regions are pale green, pale greenish yellow, or, often, pale blue or greenish-blue, distinctly paler than the upper head surface, without dark edges; upper snout scales, preoculars, loreals and supraoculars sometimes marbled with yellowish-ochre or pale yellowish-brown; a narrow temporal streak, more or less well-defined, sometimes faint, rather straight or barely oblique, white, cream, pale yellow, uniform or mixed with reddish-brown or salmon, or entirely reddish-brown, (pink or cream in preservative), extends from the eye to the corner of the mouth on the 3rd row of temporals behind the eye then on 2nd row only posteriorly; this postocular streak is present in 28 out of 30 males and 31 out of 72 females. The chin and throat are pale yellow or creamish-yellow, pale yellowish-green or, often, very pale blue or pale bluish green, with some faint darker spots posteriorly; infralabials green or distinctly pale blue. In life, the eye is dark grey, pale yellow or yellowish green.

The venter is pale green, pale bluish green, pale greenish yellow or yellowish green in life (green, yellowish green or bluish green in preservative), without any black margin on ventrals. The under surface of the tail is of the same colours as the body on its anterior part, with subcaudal scales not edged with a darker hue, then quickly turns to pale pinkish-red or salmon (cream in preservative), distinctly paler than on its upper surface.

Juveniles show a very similar pattern. The dorsum is usually more uniform than in adults and the pale dorsolateral spots or blotches may be missing. The pink or salmon colour of the tail is brighter than in adults but less uniform, with darker spots.

***Hemipenis*.** Based on specimen RMNH 4697, hemipenes are long and very slender, deeply forked, extending up to 25th subcaudal, forked opposite 8 or 9th subcaudal; the distal half is wider than the proximal one. It is distinctly calyculate on its proximal half, a short part near the end of this proximal half bearing 6 or 7 soft spines, three of them rather enlarged; distal half strongly papillose, the papillae largest on the side opposite to the sulcus; sulcus rather small and straight.

Distribution. Indonesia: *Sumatra*. Known from the provinces of Aceh, North Sumatra (Sumatera Utara), West Sumatra (Sumatera Barat), Bengkulu, and South Sumatra (Sumatera Selatan); probably also in Jambi Province. *Bangka Island*. Simpang. **Federation of Malaysia**. *West Malaysia*. Definitely recorded from the States of Kedah, Kelantan, Kuala Lumpur, Perak, Selangor, Johor, Negri Sembilan and Pahang. **Thailand**. Recorded only from the south of the Peninsula: provinces of Phang-nga, Krabi, Surat Thani, Songkhla, Satun, Trang, and Yala. **Singapore**. Mentioned in the list of reptile species (Lim & Lim 1992, 2002, Baker & Lim 2008, Charlton 2019) as *T. sumatranus*, but probably no longer present; not cited in the list of Singaporean vipers in Ng *et al*. (2011: 499).

Natural history. This species is found from sea level up to about 1,000 m a.s.l., with a predilection for lowland, hilly or rugged areas. It inhabits primary lowland rainforests, tropical evergreen forests, tropical semi-evergreen and monsoon forests, secondary forests, swamps, various plantations and the vicinity of villages. It often occurs in forest clearings and among tangled vegetation near water or in riparian places.

This nocturnal species is largely arboreal and lives in bushes and foliage of the lower canopy. It feeds mainly on small mammals and birds, but also preys upon lizards and frogs. It is oviparous, and clutches of 13 to 24 eggs have been reported (Sommerauer 1997).

T. hageni is uncommon throughout most of its range. It is an aggressive snake, striking and biting fiercely. There is a recent report of a bite by Sommerauer (1997). The patient recovered after about one week. Hagen (1890) described a bite inflicted on the hand of one of his hunters. It produced only a moderate swelling and hardly any general effects, but the snake had previously bitten a stick several times. Because of its large size and close relationships to *T. sumatranus*, *T. hageni* should be considered dangerous.

Table 1. Main characters to distinguish between species of the *Trimeresurus hageni* group. Source: Specimens listed under examined materials and Appendix II

Characters	*T. hageni*	*T. hageni*	*T. calamitas* sp. nov.	*T. kirscheyi* sp. nov.	*T. whitteni* sp. nov.	*T. sumatranus*[1]	*T. gunaleni*
Distribution	Sumatra	Malay Peninsula	Nias Is.	Simeulue Is.	Siberut Is.	Sundaic region	Sumatra
N = (m)/(f)	13/22	16/21	7/21	2/5	4/3	12/48	5/4
Midbody DSR	21 (23[2])	21	21	21	21	21 (20, 23)	21
Ventrals (m)	177–187; $\bar{x}$ = 181.0	178–189; $\bar{x}$ = 182.5	174–187; $\bar{x}$ = 180.7	180–183; $\bar{x}$ = 181.5	178–182; $\bar{x}$ = 180.8	178–185; $\bar{x}$ = 182.6	162–179; $\bar{x}$=168.4
Ventrals (f)	181–196; $\bar{x}$ = 186.8	176–194; $\bar{x}$ = 185.5	185–192; $\bar{x}$ = 188.5	184–187; $\bar{x}$ = 184.8	185–191; $\bar{x}$ = 187.3	175–191; $\bar{x}$ = 183.4	164–174; $\bar{x}$= 169.5
Subcaudals (m)	73–85; $\bar{x}$ = 79.0	77–91; $\bar{x}$ = 81.7	75–77; $\bar{x}$ = 75.9	81–82; $\bar{x}$ = 81.5	74–77; $\bar{x}$ = 75.5	66–72; $\bar{x}$ = 68.8	71–72; $\bar{x}$ = 71.5
Subcaudals (f)	59–71; $\bar{x}$ = 65.5	65–78; $\bar{x}$ = 70.8	61–71; $\bar{x}$ = 65.3	64–68; $\bar{x}$ = 65.8	63–67; $\bar{x}$ = 64.3	54–68; $\bar{x}$ = 60.1	58–66; $\bar{x}$ = 60.5
Total length (max)	1230	1207	1142	1138	1031	1350	1170
TaL/TL (m)	0.19–0.22; $\bar{x}$ = 0.20	0.19–0.21; $\bar{x}$ = 0.20	0.18–0.21; $\bar{x}$ = 0.20	0.21–0.22; $\bar{x}$ = 0.21	0.19–0.20; $\bar{x}$ = 0.20	0.14–0.16; $\bar{x}$ = 0.16	0.20–0.21; $\bar{x}$ = 0.20
TaL/TL (f)	0.14–0.17; $\bar{x}$ = 0.15	0.15–0.18; $\bar{x}$ = 0.16	0.14–0.16; $\bar{x}$ = 0.15	0.14–0.15; $\bar{x}$ = 0.15	0.14–0.15; $\bar{x}$ = 0.14	0.12–0.16; $\bar{x}$ = 0.14	0.14–0.18; $\bar{x}$ = 0.16
No of cephals between supraoculars	6–8(5); $\bar{x}$ = 7.00	6–8 (9); $\bar{x}$ = 6.92	5–7 (4); $\bar{x}$ = 5.71	7 (6,8); $\bar{x}$ = 7.00	8 (7); $\bar{x}$ = 7.71	4–7 (3); $\bar{x}$ = 5.62	5–7; $\bar{x}$ = 6.22
Internasals separate	0 (1)[3]	0 (1)[4]	0	1	0	1 (0)	1[5]
supralabials	10–11 (9,12,13) $\bar{x}$ = 10.51	10–11 (9,12,13) $\bar{x}$ = 10.58	9–10 (8) $\bar{x}$ = 9.38	10–11 (9, 12) $\bar{x}$ = 10.50	10–11 $\bar{x}$ = 10.36	8–10 (7,11) $\bar{x}$ = 8.97	8–10 $\bar{x}$ = 9.11
Supralabials touch subocular	2–6 (8)[6]; $\bar{x}$ = 3.0	0–6; $\bar{x}$ = 2.43	4 (2,3,5)[7]; $\bar{x}$ =3,93	2; $\bar{x}$ =2.00	2–4; $\bar{x}$ = 2,75	6 (5,7); $\bar{x}$ =5.95	6 (7); $\bar{x}$ =6.11
Infralabials	13–14 (11,12,15) $\bar{x}$ = 13.0	12–14 (11,15,16) $\bar{x}$ = 13.0	10–12 $\bar{x}$ = 11.0	12–14 $\bar{x}$ = 13.0	12–15 $\bar{x}$ = 13.0	10–12 (9,13,14) $\bar{x}$ = 11.2	10–11 (12) $\bar{x}$ = 10.9
Cephalic scales with thick dark margins	No	No	Yes	No	No	Yes	Yes
Temporal streak (m)	White (none)	White (none)	None	No	Rusty/none	None	None
Temporal streak (f)	Yes/no	Yes/no	No	No	Yes/no	No	No
White lateral line	Broad	Broad	half of the males, rarely in females	Weak	Broad	Broad	Thin
Dorsolateral pale dots (m)	Yes (no)[8]	Yes (no)[8]	No	No	No	No	No
Dorsolateral pale dots (f)	No (yes)	Yes (no)	No	No	No	No	No

[1] The data are slightly different from Vogel *et al*. (2014), as more material was examined meanwhile; [2] the 23 DSR were counted in one specimen out of 37; [3] only in one out of 38 specimens the IN are separate, but nearly meeting; [4] In 6 out of 37 specimens the IN are separate; [5] in the description of *T gunaleni* there was written that one out of 9 specimens the internasals were not separate, re-examination of this specimen in poor state showed them to be also separated; [6] in the paralectotype of T. hageni (RMNH 4985) exceptionally 8 supralabials touch the subocular; [7] 23 out of 28 specimens have 4 SL touching subocular; [8] missing only in one male

Trimeresurus calamitas sp. nov.
[urn:lsid:zoobank.org:act:CC12AAC9-2747-4EA7-8689-58607240936E]
(Figs. 4, 5 ; Tables 1, 2)

Trimeresurus erythrurus var. ? — Müller, 1887: 280
Bothrops formosus — Modigliani, 1889: 121.
Trimeresurus hageni — Sanders *et al*. 2002: 109 [*partim*], 2004: 729 [*partim*]

Holotype. NMW 28157:5, adult female, from Nias Island, Indonesia. Don. F. Steindachner, 1901, purchased from "Raff.".

Note: One may suspect that this specimen was purchased from a collection made by Sir Stamford Raffles, the founder of Singapore and famous researcher who collected numerous specimens on Sumatra. However, as he died in 1826, the specimen was obviously not purchased from him or his family. It was most likely obtained from the collection of the institution then known as the *Raffles Library and Museum*, established in 1849 in Singapore (Georg Gassner, pers. comm.) and now known as the *National Museum of Singapore*.

Paratypes (6 specimens). NHMB 9179 (male) "South Nias", ZMH R06935 (male), ZFMK 32509 (female), BMNH 84.1.8.46 (female); MZB.OPHI 445 (female); ZMB 52039 (female) all from "Nias" without locality except MZB.OPHI 445, from Idano Gawo, Nias.

Other material examined (5 males and 18 females). BMNH 84.12.31.14 (male); BMNH 84.1.8.47 (female); BMNH 84.12.31.13 (female); MNHN 5794, female; NMW 28155:2; NMW 28156:2; NMW 28157:4 (all males); NMW 28156:1, 3–4; NMW 28157:1–3; NMW 28159:4; NMW 28160:1–4 (all females); ZFMK 32509–10 (females); ZMB 65721 (male); ZMB 52039–41 (all females), all from Nias except MNHN 5794, with merely "Sumatra" as locality, and NMW 28159:2, from "Padang", and NMW 28159:4, which is said to come from "Deli, Sumatra", now Medan, North Sumatra Province, both most probably in error.

Diagnosis. A large species of pitviper of the genus *Trimeresurus*, characterized by the combination of (1) body elongate, head long and massive in adults; (2) dorsal surfaces deep or dark green, or dark bluish-green, with dorsal scales largely edged with black but non forming a pattern of crossbands; (3) 21 DSR at midbody; (4) 1st supralabial totally separated from nasal scale; (5) large internasals, always in contact; (6) usually 2 supralabials, 3rd–4th SL in contact with subocular (rarely 1st or 3rd SL only); (7) supraoculars large but elongate, separated by 5–7 cephalic scales; (8) tail long, with a ratio TaL/TL between 0.189 and 0.208 in males and 0.143 and 0.166 in females; (9) 174–192 VEN; (10) 61–77 SC (males: 75–77; females: 61–71); (11) eye colour greenish-gold in preservative (unknown in life); (12) cephalic scales strongly and broadly edged with black but not forming streaks; (13) no postocular streak; (15) no ventrolateral stripe or, rarely, a poorly defined stripe due to a cream or pale greenish-yellow spot on each scale of the 1st DSR; (16) tail dark green as the body, with scales edged with black, marked with several, large rusty brown or reddish-brown blotches (pinkish-salmon in preservative), narrowly separated with dark green, becoming fused on the last quarter of the tail, which is entirely of the same colour as the blotches; and (17) venter pale yellowish green or pale bluish green; each ventral narrowly edged with black, especially on their central part, sometimes on the whole of their posterior margin.

Comparison. Main characters separating *Trimeresurus calamitas* sp. nov. from other taxa of the groups of *T. sumatranus* and *T. hageni* are summarized in Table 1. *Trimeresurus calamitas* sp. nov. mainly differs from *T. sumatranus* by (1) a higher number of subcaudals in males (75–77, $\bar{x}$ = 75.9 vs. 66–72, $\bar{x}$ = 68.8; z = -3.6, P <0.005); (2) a higher value of the ratio TaL/TL in males (0.189–0.212, $\bar{x}$ = 0.201 vs. 0.144–0.169, $\bar{x}$ = 0.160); (3) the internasals always in contact vs. usually separate; (4) usually 4 supralabials touching the subocular ($\bar{x}$ = 3.93) vs. 5–7 ($\bar{x}$ = 5.95); (5) a white lateral line usually absent in females (in 18 out of 22) vs. present; (6) bands on body absent vs. present.

T. calamitas sp. nov. differs from *T. gunaleni* by (1) a higher number of ventrals in males 174–187 ($\bar{x}$ = 180.7) vs. 162–179 ($\bar{x}$ = 168.4); (2) a higher number of ventrals in females 185–192 ($\bar{x}$ = 188.5) vs. 164–174 ($\bar{x}$ = 169.5); (3) the number of subcaudals in males 75–77 ($\bar{x}$ = 75.9) vs. 71–72 ($\bar{x}$ = 71.5); (4) the internasals always in contact vs. always separate; (5) usually 4 supralabials touching the subocular ($\bar{x}$ = 3.9) vs. usually 6, rarely 7 ($\bar{x}$ = 6.1).

T. calamitas sp. nov. differs from *T. hageni* by (1) the number of supralabials, 9–10 ($\bar{x}$ = 9.4) vs. 10–11 ($\bar{x}$ = 10.55); (2) the number of

infralabials 10–12 ($\bar{x}$ = 11.0) vs. usually 12–14 ($\bar{x}$ = 13.1); (3) supralabials and cephalic scales strongly and broadly edged with black vs. no black borders; (4) a missing pale temporal streak vs. temporal streak usually present; (5) a pale ventrolateral stripe usually absent in females (in 18 out of 22) vs. present; (6) the absence of alternating dorsolateral blotches vs. large blotches usually present (in 28 out of 30 males and 30 out of 42 females); (7) each ventral pale and narrowly edged with black vs. green without black edges; and (8) in the number of cephalic scales 5–7 ($\bar{x}$ = 5.7) vs. 6–8 ($\bar{x}$ = 6.8).

T. calamitas sp. nov. differs from *T. whitteni* sp. nov. by (1) the number of supralabials 9–10 ($\bar{x}$ = 9.4) vs. 10–11 ($\bar{x}$ = 10.4); (2) in the number of cephalic scales 5–7 ($\bar{x}$ = 5.7) vs. 8 (rarely 7) ($\bar{x}$ = 7.7); (3) usually 4 supralabials touching the subocular ($\bar{x}$ = 3.9) vs. 2–4 ($\bar{x}$ = 2.8); (4) the number of infralabials 10–12 ($\bar{x}$ = 11.0) vs. usually 12–15 ($\bar{x}$ = 13.0); (5) supralabials and cephalic scales strongly and broadly edged with black vs. no black borders; (6) a pale lateral stripe usually absent in females (in 18 out of 22) vs. a broad lateral stripe present; (7) each ventral pale and narrowly edged with black vs. green without black edges.

T. calamitas sp. nov. differs from *T. kirscheyi* sp. nov. by (1) the number of subcaudals in males 75–77 ($\bar{x}$ = 75.9) vs. 80–82 ($\bar{x}$ = 81.5); (2) in the relative tail length of males 0.189–0.212 ($\bar{x}$ = 0.201) vs. 0.212–0.221 ($\bar{x}$ = 0.217); (3) in the number of cephalic scales 5–7 ($\bar{x}$ = 5.7) vs. 7 (rarely 6 or 8) ($\bar{x}$ = 7.0); (4) the internasals always in contact vs. always separate; (5) the number of supralabials, 9–10 ($\bar{x}$ = 9.38) vs. 10–11 ($\bar{x}$ = 10.5) (6) usually 4 supralabials touching the subocular ($\bar{x}$ = 3.9) vs. 2 ($\bar{x}$ = 2.0); (7) the number of infralabials 10–12 ($\bar{x}$ = 11.0) vs. 12–14 ($\bar{x}$ = 13.0); (8) supralabials and cephalic scales strongly and broadly edged with black vs. no black borders; (9) females with a weak lateral line vs. usually without lateral line.

Description of the holotype. Rostral barely visible from above, triangular, distinctly broader than high; nasals pentagonal, elongate, 1.5 times longer than high, partly divided by a shallow furrow, especially above the nostril; on each side, 1 large, subtriangular internasal, laterally elongate, about 1.2 times wider than long, the rounded apex pointing outwards; internasals in broad contact; internasals followed by subrectangular, enlarged snout scales, smooth, juxtaposed or barely imbricate, with only 4 scales along a longitudinal line extending from the internasals to a line connecting the anterior margins of eyes; 2 / 2 canthal scales bordering the *canthus rostralis*, not larger than the large adjacent snout scales on each side, 1 elongate, pentagonal loreal scale between nasal and the upper preocular; 2 / 2 preoculars above the loreal pit, the upper one visible from above, both scales elongate and in contact with loreal; lower preocular forming the lower margin of loreal pit; 1 / 1 thin, elongate, rather straight subocular; 2 / 2 small postoculars, upper one smaller, followed by 3 / 3 small scales between postoculars and the true anterior temporals, larger than these scales; 1 / 1 large, elongate supraocular on each side, 2.3 times longer than wide, 0.8 times as wide as internasal, not indented by adjacent cephalic scales; only 4 cephalic scales on a line between supraoculars, smaller than upper snout scales, smooth, flat and juxtaposed; occipital scales larger than cephalic scales, smooth; temporal scales smooth, large, subequal, arranged in 2 rows anteriorly, 3 rows posteriorly; 9 / 10 supralabials, 3rd–4th SL in contact with subocular; 1st SL entirely separated from nasal; 2nd SL tall, entirely bordering the anterior margin of the loreal pit, in contact with nasal; 3rd SL elongate, longest and highest, 1.4 / 1.3 times longer than high; 4th SL tall and relatively narrow, 1.3 / 1.2 times higher than long, 0.9 / 0.9 time as high as 3rd SL; 5th SL relatively narrow; 12 / 11 IL; scales of the 1st pair longitudinally in contact; first three pairs of infralabials in contact with anterior chin shields at left, only first two pairs at right, the 3rd IL being separated from the chin shield by a small scale; 6 rows of smooth gular scales; throat shields irregularly arranged.

Body elongate, laterally compressed; head elongate, distinctly triangular, relatively narrow seen from above, massive and thick seen from the side, wide at its base, clearly distinct from the neck, flattened anteriorly, thick posteriorly, 1.6 times as long as wide; snout long, with a moderate canthus rostralis, rounded when seen from above, strongly obliquely truncated when seen from the side, amounting for 28.7 % of head length and 2.1 times as long as diameter of eye; a large oval nostril piercing in the middle of nasal scale; nostril-loreal pit distance about 0.6 times the distance between the nostril and the eye; eye rather large, amounting for 1.0 times the distance between the lower margin of eye and upper lip border; tail rather long, tapering

and prehensile. SVL 973 mm, TaL 169 mm, TL 1,142 mm; largest head width 17.8 mm; ratio TaL/TL 0.148. DSR: 21-21-15 scales, rhomboid, distinctly keeled with the exception of scales of 1st DSR which are all smooth; 191 ventrals (+2 preventrals); 67 subcaudals, all paired; anal entire.

***Coloration*.** The head is deep green above, deep bluish green on the temporal regions; scales of the upper snout surface, upper preoculars, supraoculars, cephalic, occipital and temporal scales strongly edged with black, producing a reticulate pattern but not forming streaks; no postocular streak; rostral, posterior part of the nasal, lower preocular and supralabials pale yellowish-green, distinctly paler than upper parts of the head, variegated with dark green excepted on lower half of supralabials; 1st–3rd SL distinctly edged with black both anteriorly and posteriorly, other supralabials edged only on their posterior margin. Chin and throat pale yellowish green; chin shields, mental and infralabials greenish yellow, more yellow than the venter; chin shields and infralabials distinctly edged with black, other scales more or less so; gular scales more green than yellow, also distinctly edged with black.

The body is deep bluish green on the back and on the upper part of sides from 6th DSR upwards, distinctly paler bluish green below, the 2nd scale row being more yellowish green; many scales of the darker dorsal area more or less broadly edged with black, producing an overall slightly reticulate pattern but not forming cross bands as in *T. sumatranus*; some scales of the lower sides also edged with black but much more narrowly; upper half of scales of the 1st DSR and lower part of some scales of the 2nd DSR, especially posteriorly, pale greenish yellow, producing a faint and poorly distinct ventrolateral stripe that extends from the neck to the vent. The tail is dark bluish green as the body, with scales edged with black; 8 large, pinkish salmon blotches narrowly separated with dark green on the top and sides of the tail, becoming progressively fused on the dorsal part of the tail then entirely fused on the last quarter of the tail, entirely pinkish salmon.

The venter is pale yellowish green, not much paler than the 1st dorsal scale row; each ventral narrowly edged with black on the whole of their posterior margin and on the edges of their corner. The ventral surface of the tail is yellowish green anteriorly, with subcaudal scales edged with black on their posterior margin; from the 6th blotch onwards, the dorsal pinkish-salmon blotches extends on the ventral surface, forming rings; ventral surface of the last quarter of the tail entirely pinkish-salmon, with dark edges on subcaudal scales.

Description of the paratypes. A summary of morphological and meristic data of the paratypes is given in Table 2. None of the paratypes significantly differs from the description given for the holotype.

Species description and variation. The maximal confirmed total length known is 1,142 mm (SVL 973 mm, TaL 169 mm; holotype). The second and third largest females both have a total length of 1,111 mm (SVL 972 mm, TaL 182 mm; NMW 28159:2, from "Padang"). The largest known male is 927 mm long (SVL 940 and 942 mm, TaL 171 and 169 mm respectively; ZMB 52040 and ZMB 52039). In our sample of 9 specimens, there is a noteworthy difference of size between males and females (see below, sexual dimorphism).

As described for the holotype, with the following variation for major characters: internasals in contact in all specimens; only 2 canthal scales on each side in all examined specimens, not larger than adjacent snout scales or slightly smaller, bordering the *canthus rostralis* between the internasal and

Table 2. Morphological characters of the paratypes of *Trimeresurus calamitas* sp. nov.; M: male, F: female. For other abbreviations see Appendix I.

Collection No.	Sex	SVL (mm)	TaL (mm)	TaL /TL	VEN	SC	SL	SL touch orbit	Cep	IL	DSR
NHMB 9179	M	538	138	0.204	181	75	9/9	4	4	12/12	21
ZMH R06935	M	626	155	0.198	181	76	9/9	6	4	10/11	21
ZFMK 32509	F	798	133	0.143	188	62	9/9	5	4	11/11	21
BMNH 84.1.8.46	F	912	173	0.159	187	68	9/10	5	4	11/12	21
ZMB 52039	F	942	169	1.52	186	63	10/9	5	4	12/11	21
MZB.OPHI 445	F	932	189	0.169	191	65	9/9	6	4	11/11	21

corresponding supraocular; 3–4 enlarged scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of the eyes, smooth and juxtaposed; 2 small postoculars, in contact with first temporals or followed by 2–3 small scales between postoculars and first temporals; 1 large, elongate supraocular on each side, 2.0–2.5 times as long as wide, 0.8– 1.1 times as wide as internasal, not indented by adjacent cephalic scales; 4–7 cephalic scales (4: 1/28 specimens; 5: 9/28; 7: 5/28 [all in females]) on a line between supraoculars, smooth, flat and juxtaposed; occipital scales barely enlarged and smooth; temporal scales smooth, large, subequal, in 2 or 3 rows; 8–10 supralabials (8: 2/56 occurrences; 9: 31/56; 10: 23/56); 3rd SL in contact with subocular in all cases, 4th SL in contact in 48 of 56 cases (in 2 specimens mixed on both sides), 5th3rdSL in contact with subocular in two specimens on one side in each specimen; 1st SL always separated from nasal; 2nd SL tall, entirely bordering the anterior margin of the loreal pit, always in contact with nasal; 3rd SL longest and highest, 1.2–1.4 times as long as high; 4th SL higher than long; 5th SL tall and narrow; 10–12 IL, usually 11 or 12, (10 in only 8 out of 56 cases); scales of the 1st pair longitudinally in contact; first three pairs of infralabials in contact with anterior chin shields; 6–8 rows of smooth gular scales; throat shields irregularly arranged.

The body is robust but elongate in both males and in females. In adults, the snout is 24.0–29.9 % as long as head or 2.0–2.8 times as long as the diameter of the eye. Eye average, amounting for 0.7–1.0 times the distance eye–lower edge of the lip in both sexes. Ratio TaL/TL: 0.143–0.212, with a sexual dimorphism (see below). DSR: (20–23)-21-15 scales, distinctly keeled, smooth on 1st DSR; VEN: 174–192 (plus 1 or 2 preventrals), without a sexual dimorphism; SC: 61–77, all paired, with a sexual dimorphism (see below); anal entire. In our sample of 29 specimens, only one specimen has 20 and 4 have 23 DSR on the neck, all others have 21 rows.

***Coloration*.** The head is deep green or deep bluish green above and on the temporal region, or more bluish green on the temporal region; scales of the upper snout surface, preoculars, supraoculars, cephalic, occipital and lower temporal scales strongly edged with black, producing a reticulate pattern but not forming defined streaks; no postocular streak in all examined specimens; rostral, posterior part of the nasal, lower preocular and supralabials usually more or less distinctly paler than upper parts of the head pale, i.e. green, pale bluish green or yellowish green, variegated or stippled with dark green excepted on lower part of supralabials, or, in 7 / 28 specimens, of the same colour than upper head surface; 1st–3rd SL distinctly edged with black both anteriorly and posteriorly, other supralabials edged only on their posterior margin. Chin and throat pale green, bluish green or pale yellowish green; chin shields, mental and infralabials greenish yellow, distinctly or strongly edged with black, other scales more or less edged; gular scales more green than yellow, also distinctly edged with black.

The body is deep green, emerald green or bluish green in life, paler green on the sides; most dorsal scales distinctly edged with black, usually more strongly on the dorsum than the sides, but not producing distinct cross bands; no pale ventrolateral stripe or sometimes (in 8 / 28 specimens), a white, cream or pale greenish yellow spot on the posterior part of the upper half of each scale of the 1st DSR and on lower edge of scales of the 2nd DSR, producing a faint, discontinuous ventrolateral stripe that extends from the neck to the vent.

The tail is deep or dark green, or bluish green as the body above and on its sides, with scales distinctly edged with black; 6–8 large, reddish brown, rusty brown, orange or salmon blotches (paler and more pinkish red in preservative), narrowly separated with the dark green hue on the top and sides of the tail, becoming progressively fused on the dorsal part of the tail then entirely fused on the last quarter of the tail, entirely in the hues of red or orange.

The venter is pale yellowish green or pale bluish green; each ventral narrowly edged with black, especially on their central part, sometimes on the whole of their posterior margin. The ventral surface of the tail is yellowish green or pale bluish green anteriorly, with subcaudal scales edged with black on their posterior margin; progressively the dorsal red or orange blotches extends on the ventral surface, forming a few rings; ventral surface of the last quarter of the tail entirely red, orange or salmon, with dark edges on subcaudal scales.

***Hemipenis*.** Unknown.

In specimen ZMH R06935, the hemipenis reaches at least the level of the 27th subcaudal scale.

***Sexual dimorphism*.** Males and females differ in the relative length of the tail, in total length, and in the number of ventrals and subcaudals: (1) Strong difference in the ratio TaL/TL: males: 0.189–0.204 ($\bar{x}$ = 0.202); females: 0.143–0.166 ($\bar{x}$ = 0.154). (2) Total length: Largest male: 781 mm vs. largest female 1,142 mm. (3) Differences in the number of ventrals: 174–187 ($\bar{x}$ = 180.7) in 7 males vs. 185–192 ($\bar{x}$ = 188.8) in 22 females. (4) Differences in the number of subcaudals: 75–77 ($\bar{x}$ = 75.9) in 7 males vs. 61–71 ($\bar{x}$ = 60.5) in 22 females. There is a slight difference in the numbers of supralabials with males ($\bar{x}$ = 18.0) and females ($\bar{x}$ = 19.0) but not in the pattern.

Etymology. The specific nomen is the noun in classical Latin *calamitas* (*calamitatis*), which means "a tragedy". This specific epithet is a noun in apposition and not an adjective. We here dedicate this new species to all victims from the tsunami which struck coasts of the eastern Indian Ocean on December the 26th, 2004. Nias Island was especially hit hard by this event and again by another seismic event, also followed by a tsunami, on March the 28th, 2005. A technical description of the 2004 tsunami and of its effects on northwest Sumatra and islands off its western coast can be found in Jaffe *et al*. (2006).

Suggested common names: English: Nias Pitviper. Bahasa Indonesia: Ular Hijau Nias. Nias: ulô owuge'e sobiso. French: Trimérésure de Nias. German: Nias Grubenotter.

Distribution. Indonesia. *Nias Island* (North Sumatra Province). This species is currently endemic to this island, located about 125 km off the west coast of Sumatra.

Natural history. *Trimeresurus calamitas* sp. nov. inhabits regions typically covered with tropical rainforest. Very little is known on the biology of this species, but it is very likely similar to that of *T. hageni*. It occurs in lowland and hill forested areas, probably including disturbed forests. *T. calamitas* should be arboreal, however Modigliani (1889) stated that it was fairly common in areas covered with tall grasses. This author also reported that his Javanese hunters used to catch this pitviper by hand and immediately firmly grasped it at the neck, as they used to do with other species, without ever looking afraid. Werner (1892) found a mouse in the stomach of a small specimen.

Trimeresurus kirscheyi sp. nov.
[urn:lsid:zoobank.org:act:7C89BD62-B268-424B-ADE6-E65D0E2FDB03]
(Figs. 6, 7; Tables 1, 3)

Holotype. ZMA.RENA.21754, adult female, from Simeulue Timur, Simeulue Island, Aceh Province, Indonesia, collected by S. Jacobson, July 1913.

Paratypes (6 specimens). RMNH 5174–75 (males), 5656 a–d (females), all from Sinabang, Simalue Island, Aceh Province, Indonesia.

Diagnosis. A large species of pitviper of the genus *Trimeresurus*, characterized by the combination of (1) body elongate and quite slender, head long and massive in adults; (2) an overall green coloration, uniform and without dark crossbands; (3) a white, black or white and black ventrolateral stripe; (4) no postocular streak in both sexes; (5) 21 DSR at midbody; (6) 1st supralabial completely separated from nasal scale; (7) large internasals, separated by one large scale in all examined specimens; (8) 12–14 supralabials, only 3rd SL in contact with subocular; (9) supraoculars large but elongate, separated by 6–8 cephalic scales; (10) tail long, with a ratio TaL/TL between 0.212 and 0.221 in males and 0.145 and 0.152 in females; (11) 180–187 VEN; (12) 64–82 SC (males: 81–82; females: 64–68); (13) cephalic scales not edged with black; (14) venter pale greenish yellow, uniform; and (15) tail green as the body anteriorly, its upper surface and sides becoming quickly covered with irregular rusty brown or reddish brown blotches, progressively fused posteriorly making the tail entirely rusty brown.

Comparison. Main characters separating *Trimeresurus kirscheyi* sp. nov. from other taxa of the *T. sumatranus* and *T. hageni* groups are summarized in Table 1. *Trimeresurus kirscheyi* sp. nov. mainly differs from *T. sumatranus* by (1) a higher number of SC in males (81–82, $\bar{x}$ = 81.5 vs. 66–72, $\bar{x}$ = 68.8; (2) a higher value of the ratio TaL/TL in males (0.212–0.221, $\bar{x}$ = 0.217 vs. 0.144–0.169, $\bar{x}$ = 0.160); (3) 2 supralabials touching the subocular ($\bar{x}$ = 2.00) vs. 5–7 ($\bar{x}$ = 5.95); (4) a higher number of supralabials (10–11, $\bar{x}$ = 10.5 vs. 8–10, $\bar{x}$ = 5.95); (5) bands on body absent vs. present; (6) supralabials and cephalic without black borders vs. scales strongly and broadly edged with black.

Trimeresurus kirscheyi sp. nov. differs from *T. hageni* by (1) the internasals always separate vs. in contact; (2) the missing temporal

streak which is in *T. hageni* usually white to light pink; (3) the missing white dorsolateral dots which are present in 13 of the 14 males of *T. hageni* and in about two thirds of the females; (4) the colour of the upper labials of the females, which are more or less in the colour of the body in *T. kirscheyi* sp. nov. vs. bluish white in *T. hageni*.

T. kirscheyi sp. nov. differs from *T. gunaleni* mainly by (1) a higher number of VEN in males (180–183, $\bar{x}$ = 181.5 vs. 162–179, $\bar{x}$ = 168.4) and females (184–187, $\bar{x}$ = 184.8 vs. 164–174, $\bar{x}$ = 169.5); (2) a higher of SC in males (81–82, $\bar{x}$ = 81.5 vs. 71–72, $\bar{x}$ = 71.5) and with some overlap also in females (64–68, $\bar{x}$ = 65.8 vs. 58–66, $\bar{x}$ = 60.5); (3) 2 supralabials touching the subocular ($\bar{x}$ = 2.00) vs. 6, rarely 7 ($\bar{x}$ = 6.11); (4) the number of infralabials (12–14, $\bar{x}$ = 13.0 vs. 10–11, $\bar{x}$ = 10.9); (5) supralabials and cephalic without black borders vs. scales strongly and broadly edged with black.

The comparison between *T. kirscheyi* sp. nov. and *T. calamitas* sp. nov. and *T. whitteni* sp. nov., respectively, was given above in the accounts of these species.

Description of the holotype. Rostral slightly visible from above, triangular, much broader at its base than high; nasals pentagonal, barely divided by a faint furrow above the nostril, their upper anterior margin curved onto the top of the head behind the rostral; on each side, 1 large, pentagonal, elongate, internasal, pointing anteriorly; internasals widely separated by a single, large, triangular scale behind the top of the rostral; on each side, 2/2 canthal scales bordering the *canthus rostralis*, larger than the adjacent snout scales; 1 elongate, triangular loreal scale between the nasal and the upper preocular, its apex touching the nasal; 2/2 preoculars above the loreal pit, the upper one largest and visible from above, both scales elongate and in contact with loreal; lower preocular forming the lower margin of loreal pit; 1 thin, elongate, crescent-like subocular at left, subocular divided into three small scales at right; 2/2 small postoculars (at right, the upper scale forming the subocular may also be considered a postocular), followed by a series of 2/3 small scales between postoculars and first temporals; on each side, 1 large, elongate and wide, supraocular, broadly irregular but irregularly-shaped, 2.1/2.2 times as long as wide respectively, 1.6/1.8 times wider than internasals, strongly indented by adjacent cephalic scales; 4 scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of eyes, those of the first row between the large scale separating the internasal scales distinctly enlarged, other barely enlarged, all smooth and juxtaposed; 9 cephalic scales on a line between supraoculars, much irregular in size, some distinctly smaller than the upper snout scales, other scales as large as these latter scales, all smooth, flat and juxtaposed; occipital scales not larger than cephalic scales, obtusely but distinctly keeled; temporal scales smooth, large, subequal, arranged along 3 rows anteriorly, 4 rows posteriorly; 12/11 supralabials, only the 3rd supralabials are in contact with subocular, the 4th and 5th supralabials are separated from the subocular by 1 large scale on each side; 1st supralabials entirely separated from nasal; 2nd supralabials tall, entirely bordering the anterior margin of the loreal pit, in contact with nasal on both sides; 3rd SL longest and highest, 1.2/1.2 times longer than high; 4th SL short and narrow at left, short and long at right, 1.2/0.7 times higher than long, respectively; 4th SL 0.8/0.7 times as high as 3rd SL; 5th SL relatively narrow; 13/13 infralabials; scales of the 1st pair longitudinally in contact; first three pairs of infralabials in contact with anterior chin shields at left, only first two pairs at right; 7 or 8 rows of smooth gular scales; throat shields regularly arranged along the gular groove.

Body elongate, relatively slender distinctly laterally compressed; head elongate, subtriangular, wide at its base, clearly distinct from the thin neck, slightly flattened anteriorly, thick posteriorly, 1.7 times as long as wide; snout average, round when seen from above, obliquely truncated when seen from the side, with a poorly distinct canthus rostralis, amounting for 24.5 % of head length and 2.3 times as long as diameter of eye; a large, slightly vertically oval, nostril piercing in the middle of the nasal scale; distance nostril-loreal pit about 0.6 times the distance between the nostril and the eye; eye average, amounting for 0.75 times the distance between the lower margin of eye and upper lip border; tail long, relatively thick anteriorly then tapering and prehensile.

SVL 965 mm, TaL 173 mm, TL 1,138 mm; largest head width 27.93 mm; ratio TaL/TL 0.152. DSR: 21-21-15 scales, rhomboid, distinctly keeled with the exception of scales of

1st DSR which are smooth; 178 VEN (+ 3 preventrals); 74 SC, all paired; anal entire.

***Coloration*.** The head is uniform dark greyish green or verdigris, slightly darker than the dorsal surface, without dark edges on cephalic or snout scales; scales of the sides of the snout and anterior supralabials somewhat paler green; lower part of posterior yellowish green; supralabials not or very slightly edged with black but irregular dark grey spots or streaks on some supralabials, more conspicuous posteriorly; no postocular streak. Chin and throat pale greenish yellow, uniform with only a few irregular, dark grey spots or blotches, especially on the gular scales.

The body is uniform dark greyish green or verdigris, somewhat paler and more green on the lower part of the sides; many dorsolateral scales on the anterior third part of the length of the body are edged posteriorly with black but they are irregularly arranged and do not produce crossbars; no pale dorsal blotches or spots; a narrow, discontinuous ventrolateral stripe, composed of small black areas along the lower edges of scales of the 1st dorsal scale row, extends from the neck to the vent.

The tail is green as the body anteriorly, its upper surface and sides becoming quickly covered with irregular rusty brown or reddish brown blotches, some faintly darker above but not forming defined crossbands., These blotches progressively fused posteriorly making the tail entirely reddish brown.

The venter is pale greenish yellow, uniform anteriorly up to about midbody; on the posterior half of the body length, the tips and outer parts of the ventral plates become progressively stippled with dark greyish green dots. The ventral surface of the tail is greenish yellow, slightly stippled with dark greyish green dots anteriorly, turning in a short distance to rusty brown, irregularly and more strongly stippled with the same dark dots.

Description of the paratypes. A summary of morphological and meristic data of the paratypes is given in Table 3. None of the paratypes significantly differs from the description given for the holotype.

Species description and variation. The maximal confirmed total length known is 1,138 mm (SVL 965 mm, TaL 173 mm; ZMA.RENA 21754, female; holotype). The second largest of our specimens has a total length of 1,008 mm (SVL 855 mm, TaL 153 mm; RMNH 5656A, female). In our sample of seven specimens, we cannot prove a difference of size between males and females, but it is likely (see below, sexual dimorphism). As described for the holotype, with the following variation for major characters: internasals separate by one large scale in all specimens; 2–3 small postoculars, in contact with first temporals or followed by 2–3 small scales between postoculars and first temporals; 1 large, elongate, subtriangular supraocular on each side, 2.0–2.4 times as long as wide, 1.5–1.8 times wider than the corresponding internasal, more or less strongly indented by adjacent cephalic scales; 4–5 scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of eyes, those of the first row between the large scale separating the internasal scales distinctly enlarged, other barely enlarged, smooth and juxtaposed; 6–8 cephalic scales (6: 1/7 specimens; 7: 5/7 specimens; 8: 1/7) on a line between supraoculars, smaller than upper snout scales, smooth, flat and juxtaposed; occipital scales not enlarged and smooth (in 3 specimens) or slightly keeled; (4 specimens); temporal scales smooth, large, subequal, in 2 to 4 rows; 9–12 supralabials (9: 1/14 occurrences; 10: 5/14; 11: 6/14;

Table 3. Morphological characters of the paratypes of *Trimeresurus kirscheyi* sp. nov.; M: male, F: female. For other abbreviations see Appendix I.

Collection No.	Sex	SVL (mm)	TaL (mm)	TaL/ TL	VEN	SC	SL	SL touch orbit	Cep	IL	DSR
RMNH 5174	M	521	148	0,221	183	82	11/10	2	7	13/13	21
RMNH 5175	M	585	157	0,212	180	81	10/9	2	6	12/13	21
RMNH 5656A	F	855	153	0.152	184	65	10/11	2	7	13/12	21
RMNH.5656B	F	485	87	0,152	184	68	11/10	2	7	12/12	21
RMNH 5656C	F	805	inc.	inc.	184	inc.	10/10	2	7	14/13	21
RMNH 5656D	F	306	52	0,145	185	64	11/11	2	7	14/14	21

12: 1/14); only the third supralabials are in contact with subocular in all specimens; 4th and 5th supralabials always separated from the subocular by a relatively large scale; 1st SL always separated from nasal by a complete, deep suture; 2nd SL tall, entirely bordering the anterior margin of the loreal pit, always in contact with the nasal; 3rd SL longest and highest, 1.2–1.5 times longer than high; 4th SL usually higher than long; 5th SL as long as tall, not narrow; 12–14 IL (12 in 4/14 occurrences; 13 in 7/14; 14 in 3/14); scales of the 1st pair longitudinally in contact; first three, exceptionally two pairs of infralabials in contact with anterior chin shields; 6–8 rows of smooth gular scales; throat shields irregularly arranged.

The body is robust but elongate in both males and in females. In the six adult specimens, the snout is 23.5–27.5% as long as the head or 1.5–2.3 times longer than the diameter of the eye with an important sexual dimorphism: in two males: 1.50–1.70 times; in four adult females: 2.05–2.58 times. Eye average or large, amounting for 0.7–1.2 times the distance eye–lower edge of the lip in both sexes, with also a sexual dimorphism making males with proportionally larger eyes: in two males: 1.10–1.18 times; in four adult females: 0.70–0.80 times; in a juvenile female: 1.30. Ratio TaL/TL: 0.145–0.221, with a sexual dimorphism (see below). DSR: (21–23)-21-15, distinctly keeled, smooth on 1st DSR; VEN: 180–187 (plus 0–2 preventrals), with a sexual dimorphism (see below); SC: 64–82, all paired, with a strong sexual dimorphism (see below); anal entire. In our sample of seven specimens, only two have 23 DSR on the neck, all others have 21 rows. Furthermore, all specimens have 21 rows at midbody and 15 rows before vent.

Coloration. We indicate the coloration and pattern of specimens in preservative as we could not find any photographs of a living specimen or any freshly killed animals. The head is in the same hues of green as the body above and on its sides, somewhat darker on the cephalic region, distinctly paler on the sides of the snout and supralabials which are pale yellowish green or pale bluish green; rostral, scales of the upper snout surface, preoculars, supraoculars, cephalic, occipital and temporal scales are uniform; no postocular streak in all known specimens. Chin, mental, infralabials and throat are cream, pale greenish yellow, or pale yellowish green, uniform or with infralabials irregularly and faintly marbled with darker greenish yellow or green.

The body is uniform dark bluish green, dark sea green, dark emerald green or dark green, distinctly paler in shades of green on the lower part of the sides, or, depending on the conditions of preservation, dark brown or even blackish brown; no dark crossbands, even faint; some scales narrowly edged with black on their anterior part, not forming any regular pattern; a cream ventrolateral stripe extends from the neck to the vent on the scales of the 1st DSR; it is edged below on the lower part of scales of the 1st DSR with black, producing a more or less visible dark lower ventrolateral stripe. The tail is in the same shades of green anteriorly, its upper surface and sides becoming quickly covered with 4 or 5 large, irregular rusty brown or reddish brown blotches, barely separated and progressively fused posteriorly making the tail entirely rusty brown, mottled with darker areas; a black, narrow and irregular ventrolateral stripe is present at the limit between the subcaudals and scales of the first row of dorsal scales of the tail; the white ventrolateral stripe does not extend along the green lower part of the tail.

The venter is uniform pale greenish yellow; posterior outer parts of each ventral marbled with bluish grey or bluish green, darker than the background colour of the venter; outer tips of each ventral narrowly edged with black. The under surface of the tail is greenish yellow anteriorly, slightly stippled with dark greyish green dots, along a variable distance which may reach at least half of the tail length, not edged with shades of rust, then turning posteriorly to rusty red or rusty brown more strongly stippled with dark dots.

Hemipenis. Unknown.

Sexual dimorphism. Males and females differ in the relative length of the tail, and in the number of ventrals and subcaudals and perhaps in the total length: (1) Strong difference in the ratio TaL/TL: 0.212–0.221 ($\bar{x}$ = 0.216) in 2 males vs. 0.145–0.152 ($\bar{x}$ = 0.149) in 4 females. (3) Differences in the number of ventrals: 180–183 ($\bar{x}$ = 181.5) in 2 males vs. 184–187 ($\bar{x}$ = 184.8) in 5 females. (3) Differences in the number of subcaudals: 81–82 ($\bar{x}$ = 81.5) in 2 males vs. 64–68 ($\bar{x}$ = 65.8) in 4 females.

The largest three specimens are females. Obviously, the sample is too small to show a dimorphism in total length, but as in other members of the group and as can be judged from

our data, females are also larger in this species. Moreover, as shown above, there is a sexual-related difference in the proportional size of the eyes, which are larger than in females.

According to our sample, we cannot judge about a sexual difference in the coloration and pattern of the body, as the species is not known alive, and one of the two males is decoloured. The eye colour in life is unknown.

Etymology. The specific nomen is dedicated to Mr. Tom Kirschey, a conservationist and naturalist from Germany currently working for NABU organization. He has worked on the survey and conservation of the wildlife of Sumatra and Java. He is also the author of several books about herpetology and wildlife. Suggested common names: English: Simeulue Pitviper. Bahasa Indonesia: Ular Hijau Simeulue. Simeulue: Bĭrĭt tiu. French: Trimérésure de Simeulue. German: Simeulue Grubenotter.

Distribution. Indonesia. *Simeulue Island* (Province of Aceh). This species is endemic to this island located about 150 km off the north-west coast of Sumatra.

Natural history. Nothing is known on the natural history of this species, but it might be similar to the other species of this group living on the Mentawai Islands.

Trimeresurus whitteni sp. nov.
[urn:lsid:zoobank.org:act: 8020A7A4-DDA9-44C1-AA15-B1BA506D5242]
(Figs. 8, 9, 11, 12B; Tables 1, 4)

Trimeresurus hageni — Sanders *et al*. 2002: 109 [*partim*], 2004: 729 [*partim*]

Holotype. MZB.OPHI.2310, adult male, Saibi Samukop, Siberut Island, Kepulauan Mentawai, Sumatera Barat Province, Indonesia, collected by Irvan Sidik and M. Toha in June 1994.

Paratypes (6 specimens). CAS SUR 8318, BMNH 1977.1237, RMNH 5517 (all males), BMNH 1979.267–269 (females), all from Siberut Island.

Diagnosis. A large species of pitviper of the genus *Trimeresurus*, characterized by the combination of (1) body elongate, head long and massive in adults; (2) an overall green coloration, with irregular areas interstitial skin black and many scales irregularly edged with black producing faint, poorly contrasted crossbands; (3) a white or white and black ventrolateral stripe; (4) a dark postocular streak in most specimens, black and black and red; (5) 21 DSR at midbody; (6) 1st supralabial totally separated from nasal scale; (7) large internasals, always in contact in all examined specimens; (8) 10–11 supralabials, 4th or 4th–5th SL in contact with subocular; (9) supraoculars large but elongate, separated by 7–8 cephalic scales; (10) tail long, with a ratio TaL/TL between 0.191 and 0.209 in males and 0.144 and 0.151 in females; (11) 178–191 VEN; (12) 63–77 SC (males: 74–77; females: 63–67); (13) eye copper to greenish copper in life; (14) cephalic scales not edged with black; (15) a red or grey postocular streak; (16) venter green, uniform; and (17) tail green as the body anteriorly, with greyish red, salmon, rusty brown or reddish brown blotches, progressively fused posteriorly making the tail entirely red or salmon.

Comparison. The main characters separating *Trimeresurus whitteni* sp. nov. from other taxa of the *T. sumatranus* and *T. hageni* groups are summarized in Table 1. *Trimeresurus whitteni* sp. nov. mainly differs from *T. sumatranus* by (1) a lower number of SC in males (74–77, $\bar{x}$ = 75.5 vs. 66–72, $\bar{x}$ = 68.8); (2) a higher value of the ratio TaL/TL in males (0.191–0.209, $\bar{x}$ = 0.203 vs. 0.144–0.169, $\bar{x}$ = 0.160); (3) the internasals always in contact vs. usually separate; (4) 2–4 supralabials touching the subocular ($\bar{x}$ = 2.75) vs. 5–7 ($\bar{x}$ = 5.95); (5) number of cephalic scales between the supraoculars usually 8, sometimes 7, $\bar{x}$ = 7.71 vs. 4–7 ($\bar{x}$ = 5.62); (6) bands on body absent vs. present; (7) supralabials and cephalic no black borders vs. scales strongly and broadly edged with black.

T. whitteni sp. nov. differs from *T. hageni* by (1) by the temporal streak which is in males of *T. whitteni* sp. nov. thin and brown vs. always white to light pink in *T. hageni* whereas it is in females of *T. whitteni* sp. nov. dark vs. white to light pink in *T. hageni;* (2) by the missing white dorsolateral dots which are present in 13 of the 14 males of *T. hageni* and in about two third of the females; (3) by the colour of the upper labials of the females, which are light green in *T. whitteni* sp. nov. vs. bluish white in *T. hageni;* (4) by the number of cephalic scales which are usually 8 in *T. whitteni* sp. nov. and usually 7 in *T. hageni* ($\bar{x}$ = 7.1 vs. $\bar{x}$ = 6.8; z = -2.75, P <0.01); (5) by the eye colour which is bright orange, salmon or pale rusty red in *T. whitteni* sp. nov. vs. grey, pale yellow or usually yellowish green in *T. hageni*; (6) by faint and

irregular dark crossbands in *T. whitteni* sp. nov. vs. an unbanded pattern in *T. hageni*; (7) *T. whitteni* sp. nov. has a robust head and bulky body, unlike *T. hageni* that has slenderer, longer head shape and a more slender body.

T. whitteni sp. nov. differs from *T. gunaleni* mainly by (1) a higher number of VEN in males (178–182, $\bar{x}$ = 180.3 vs. 162–179, $\bar{x}$ = 168.4) and females (185–191, $\bar{x}$ = 187.3 vs. 164–174, $\bar{x}$ = 169.5); (2) a higher of SC in males (74–77, $\bar{x}$ = 75.5 vs. 71–72, $\bar{x}$ = 71.5) and with some overlap also in females (63–67, $\bar{x}$ = 64.3 vs. 58–66, $\bar{x}$ = 60.5); (3) Number of cephalic scales between the supraoculars usually 8, sometimes 7, $\bar{x}$ = 7.71 vs. 5–7 ($\bar{x}$ = 6.22); (4) the internasals in contact vs. separate; (5) 2–4 supralabials touching the subocular ($\bar{x}$ = 2.75) vs. 6, rarely 7 ($\bar{x}$ = 6.11); (6) the number of infralabials (12–15, $\bar{x}$ = 13.0 vs. 10–11, $\bar{x}$ = 10.9); (7) supralabials and cephalic no black borders vs. scales strongly and broadly edged with black.

T. whitteni sp. nov. differs from *T. kirscheyi* sp. nov. (see below) by (1) a lower number of SC in males (74–77, $\bar{x}$ = 75.5 vs. 81–82, $\bar{x}$ = 81.5); (2) a lower value of the ratio TaL/TL in males (0.191–0.209, $\bar{x}$ = 0.203, vs. 0.212–0.221, $\bar{x}$ = 0.217); (3) the internasals in contact vs. separate; (4) by the relation of the size of the supraoculars compared to the internasals (1.0–1.2 vs. 1.6–1.8 times wider) (5) by the lateral line, which is broad vs. weak; (6) by the temporal streak, which may be present in *T. whitteni* sp. nov. but is always missing in *T. kirscheyi* sp. nov. There might also be differences in live colouration or eye colour, but as there are no live data for *T. kirscheyi* sp. nov., it cannot be compared at this time.

We provided the list of characters separating *T. whitteni* sp. nov. from *T. calamitas* under the account of this latter species.

Description of the holotype. Rostral barely visible from above, triangular, much broader than high; nasals pentagonal, barely divided by a shallow furrow above the nostril; on each side, 1 large, subrectangular, elongate internasal; internasals in broad contact above the rostral; on each side, 2 / 2 canthal scales bordering the *canthus rostralis*, not larger or barely larger than the adjacent snout scales; 1 elongate, triangular loreal scale between nasal and the upper preocular; 2 / 2 preoculars above the loreal pit, the upper one largest and visible from above, both scales elongate and in contact with loreal; lower preocular forming the lower margin of loreal pit; 1/1 thin, elongate, crescent-like subocular; 2/3 small postoculars, followed by a series of 3/3 small scales between postoculars and first temporals; on each side, 1 large, elongate supraocular, rectangular at left, subtriangular at right, 2.8/2.5 times as long as wide respectively, 0.7/0.9 times as wide as internasal, not indented by adjacent cephalic scales; 4 scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of eyes, distinctly enlarged, smooth and juxtaposed; 8 cephalic scales on a line between supraoculars, smaller than upper snout scales, smooth, flat and juxtaposed; occipital scales not larger than cephalic scales, obtusely keeled; temporal scales smooth, large, subequal, arranged along 3 rows anteriorly, 4 rows posteriorly; 10/10 supralabials, 3rd and 4th SL in contact with subocular, 5th separated from subocular by 1 large scale; 1st SL entirely separated from nasal; 2nd SL tall, entirely bordering the anterior margin of the loreal pit, in contact with nasal; 3rd SL longest and highest, 1.4/1.2 times longer than high; 4th SL tall and narrow, 1.3/1.5 times higher than long, as high as 3rd SL; 5th SL relatively narrow; 13/12 IL; scales of the 1st pair longitudinally in contact; first three pairs of infralabials in contact with anterior chin shields; 7 rows of smooth gular scales; throat shields irregularly arranged.

Body elongate, laterally compressed; head elongate, subtriangular, wide at its base, clearly distinct from the neck, slightly flattened anteriorly, thick posteriorly, 1.5 times as long as wide; snout average, round when seen from above, moderately obliquely truncated when seen from the side, with a moderate canthus rostralis, amounting for 27.9 % of head length and 1.8 times as long as diameter of eye; a large oval, vertically elongate nostril piercing in the middle of nasal scale; distance nostril-loreal pit about 0.5 times the distance between the nostril and the eye; eye average, amounting for 0.55 times the distance between the lower margin of eye and upper lip border; tail long, thick anteriorly then tapering and prehensile. SVL 638 mm, TaL 160 mm, TL 798 mm; largest head width 35.0 mm; ratio TaL/TL 0.201. DSR: 22-21-15 scales, rhomboid, distinctly keeled with the exception of scales of 1st DSR which are smooth; 178 VEN (+ 3 preventrals); 74 SC, all paired; anal entire.

***Coloration*.** The head is uniform dark brownish grey, without dark edges on cephalic or snout scales; scales of the sides of the snout and anterior supralabials somewhat paler; supralabials not or very slightly edged with black; postoculars and temporals narrowly edged with brownish black, producing a very faint postocular streak extending from eye to corner of the mouth, barely visible at left. Chin and throat pinkish brown; mental and infralabials dark brownish grey; posterior gular strongly mottled with dark brown.

The body is uniform dark brownish grey, somewhat paler and more bluish grey on the lower part of the sides; many dorsolateral scales edged posteriorly with black, especially in the posterior half of the body, producing very faint and incomplete vertical crossbars; no pale dorsal blotches or spots; a narrow, discontinuous ventrolateral stripe, made of pale areas on scales of the 1st dorsal scale row (scales not entirely white), extends from the neck to the vent. The tail is brownish grey above and on its sides with 7 large, pinkish cream blotches, contrasting abruptly with the dorsal colour at the level of the vent, forming incomplete rings anteriorly, progressively merging together and leaving the tail pinkish cream with some faint, irregular brown markings posteriorly.

The venter is uniform pale pinkish brown anteriorly, becoming progressively darker and turning to reddish brown then to dark lead grey after the first quarter of the body, with the posterior edge of each ventral pale bluish grey, distinctly paler than the background colour of the venter. The tail is entirely pinkish cream, irregularly mottled with dark brown, without definite rings.

Description of the paratypes. A summary of morphological and meristic data of the paratypes is given in Table 4. None of the paratypes significantly differs from the description given for the holotype.

Species description and variation. The maximal confirmed total length known is 1,031 mm (SVL 875 mm, TaL 156 mm; BMNH 1979.267, female). The second largest of our specimens has a length of 844 mm (SVL 668 mm, TaL 176 mm; CAS SUR 8318, male). In our sample of 7 specimens, we cannot prove a difference of size between males and females, but it is likely (see below, sexual dimorphism).

As described for the holotype, with the following variation for major characters: internasals in contact in all specimens; 2–3 small postoculars, in contact with first temporals or followed by 2–3 small scales between postoculars and first temporals; 1 large, elongate, subtriangular supraocular on each side, 2.0–2.4 times as long as wide, 1.0– 1.2 times as wide as internasal, not indented by adjacent cephalic scales; 3–5 enlarged scales on upper snout surface on a line between the scale separating the internasals and a line connecting the anterior margins of the eyes, smooth and juxtaposed; 7–8 cephalic scales (7: 2/7 specimens; 8: 5/7) on a line between supraoculars, smaller than upper snout scales, smooth, flat and juxtaposed; occipital scales not enlarged and smooth (in 3 specimens) or slightly keeled; (4 specimens); temporal scales smooth, large, subequal, in 2 to 4 rows; 10–11 supralabials (10: 6/14 occurrences; 11: 8/14); 3rd SL or 3rd–4th SL in contact with subocular, 3rd SL in contact in all specimens, 4th SL in contact in only 3/14 occurrences, separated by 1 scale in other occurrences, 5th SL always separated by a relatively large scale; 1st SL always separated from nasal; 2nd SL tall, entirely bordering the anterior margin of the loreal pit, always in contact with nasal; 3rd SL longest and highest, 1.2–1.7 times as long as high; 4th SL higher than

Table 4. Morphological characters of the paratypes of *Trimeresurus whitteni* sp. nov.; M: male, F: female. For other abbreviations see Appendix I.

Collection No.	Sex	SVL (mm)	TaL (mm)	TaL/ TL	VEN	SC	SL	SL touch orbit	Cep	IL	DSR
CAS SUR 8318	M	668	176	0,209	182	77	10/10	2	6	12/13	21
BMNH 1977.1237	M	470	111	0,191	181	76	11/10	2	6	13/13	21
RMNH 5517	M	632	167	0.209	182	75	10/11	4	6	15/14	21
BMNH 1979.267	F	875	156	0,151	185	63	11/11	4	6	13/13	21
BMNH 1979.268	F	505	90	0,151	186	63	11/11	2	6	14/15	21
BMNH 1979.266	F	238	40	0,144	191	67	11/11	2	7	14/ 13	21

long; 5th SL tall and narrow; 12–15 IL (12 in 2/14 occurrences; 13 in 7/14; 14 in 3/14; 15 in 2/14); scales of the 1st pair longitudinally in contact; first three pairs of infralabials in contact with anterior chin shields; 5–8 rows of smooth gular scales; throat shields irregularly arranged.

The body is robust but elongate in both males and in females. In adults, the snout is 23.5–28.0 % as long as the head or 1.8–2.3 times as long as the diameter of the eye. Eye average, amounting to 0.7–0.9 times the distance eye–lower edge of the lip in both sexes. Ratio TaL/TL: 0.144–0.209, with a sexual dimorphism (see below). DSR: (21–23)-21-15, distinctly keeled, smooth on 1st DSR; VEN: 178–191 (plus 1–3 preventrals), with a sexual dimorphism (see below); SC: 63–77, all paired, with a strong sexual dimorphism (see below); anal entire. In our sample of 7 specimens, only one specimen has 23 DSR and another 22 DSR on the neck, all others have 21 rows. Furthermore, all specimens have 21 rows at midbody and 15 rows before vent.

***Coloration*.** In life, the head is in the same hues of green as the body above and on its sides, somewhat darker on the cephalic region, often paler on the sides of the snout and supralabials which are rather bright greenish yellow or pale yellowish green; rostral, scales of the upper snout surface, preoculars, supraoculars, cephalic, occipital and temporal scales either nearly uniform or, more usually, narrowly and irregularly edged with black, at least along one or two of their margins but without producing a conspicuous pattern of black streaks; in some specimens, some upper snout scales and cephalic scales broadly edged with black or with rather large spots or irregular black areas on the snout, producing a somewhat confuse, "dirty" pattern on the upper head surface; supraoculars usually uniform but sometimes marbled with black; an irregular, broad, entire or sometimes faint or irregularly interrupted, postocular streak extending from eye to corner of the mouth on the 2nd row of temporals, progressively descending on 1st row, usually black or irregularly mixed rusty-red and black (often dark grey, or dark brown in preservative, or barely visible if the head background colour is brown), the red colour being sometimes reduced to a few dot; usually 1st–3rd anterior supralabials, sometimes also 4th–6th SL, narrowly edged or with a small black spot on their anterior edge, or 3rd SL and following more or less marbled with black. Chin and throat are pale greenish yellow, yellowish-green or pale bluish green (often cream in preservative); mental and infralabials are greenish yellow or pale yellowish green with infralabials uniform or irregularly edged with black or with a black spot; other infralabials and gular scales more or less marbled with darker greenish yellow or green. In life, the eye colour is bright orange, salmon or pale rusty red, sometimes ochre red.

The body is deep green, grass green, emerald green, yellowish green or pale olive green, somewhat paler green or paler yellowish green on the lower part of the sides (sometimes the same colours are retained in preservative but often turning to greyish brown, brown or dark grey); many dorsal scales narrowly edged with black on their anterior part, usually more strongly on the forepart of the body, from the 1st or 2nd DSR up to the vertebral row, forming faint and irregular, poorly contrasted dark crossbands, either nearly straight or W- or jigsaw-shaped, either present throughout the body or most conspicuous and extensive on the hinder part of the body, usually longitudinally separated each from the other by 2–4 dorsal scales, or in contact on the vertebral region; in some specimens, these crossbands become broader and "solid" on the posterior part of the body and form a series of dark dorsolateral blotches; a narrow ventrolateral stripe, white, cream, pale green or pale bluish green (same in preservative), usually extends from the neck to the vent on the upper half or most of the scales of the 1st DSR, sometimes on the lower edge of scales of the 2nd DSR, or lower half of scales of the 1st DSR often black, contrasting with the white upper area and producing a dark lower ventrolateral stripe fused with the dark tips of ventrals; the white stripe may be absent in some specimens, leaving the black stripe alone. The tail is in the same hues of green anteriorly with 5–8 (usually 6 or 7) large blotches, salmon, bright red, dirty or greyish red, rusty brown or reddish brown, progressively fused posteriorly making the tail entirely in these shades of red or salmon, mottled with darker areas; a white, rather broad ventrolateral stripe often extends along the green part of the tail but is absent in some specimens; a black ventrolateral stripe is often present below the white one or, when this latter one is absent, below its position.

The venter is pale green or yellowish green in life (greenish white or greenish yellow in preservative), with the posterior edge of each ventral or nearly the whole of the central area of

each ventral marbled with pale bluish grey or pale greyish green, paler than the background colour of the venter; outer tips of each ventral edged with black, more broadly on the posterior half of the body, sometimes producing a dark, discontinuous stripe below the white ventrolateral stripe when this latter one is present. The under surface of the tail is green anteriorly along a distance varying from the first subcaudals to the middle of the tail, broadly edged with salmon, bright red, dirty or greyish red, rusty brown or reddish brown, depending on the colour of the dorsal blotches, which broaden up to leave the green colour only as a stripe in the central third or quarter of the subcaudals; the "red" colour is irregularly and broadly edged with the white colour of the ventrolateral stripe; posteriorly to about the middle of the tail its under surface is entirely in the same hues of red than its upper surface.

***Hemipenis*.** Unknown.

***Sexual dimorphism*.** Males and females differ in the relative length of the tail, and in the number of ventrals and subcaudals and perhaps in total length: (1) Strong difference in the ratio TaL/TL: 0.191–0.209 ($\bar{x}$ = 0.202) in 4 males vs. 0.144–0.151 ($\bar{x}$ = 0.149) in 3 females. (2) Differences in the number of ventrals: 178–182 ($\bar{x}$ = 180.8) in 4 males vs. 185–191 ($\bar{x}$ = 187.3) in 3 females. (3) Differences in the number of subcaudals: 74–77 ($\bar{x}$ = 75.5) in 4 males vs. 63–67 ($\bar{x}$ = 64.3) in 3 females.

The largest known specimen is a female (TL 1,031 mm) but the next three specimens in length are males (largest male: TL 844 mm). Obviously, the sample is too small to show a dimorphism in total length, but as in other members of the group and as can be judged from live pictures, females are also larger in this species.

According to our sample, there is no sexual difference in the coloration and pattern of the body. At best, the white ventrolateral stripe may be more green than white, and thus less visible, in some large females. Although the colour of the eye is variable in this species, there is no difference between males and females.

Etymology. The specific nomen is dedicated to Mr. Tony Whitten (10 April 1953–29 November 2017), a leading conservationist and naturalist in Indonesia who extensively

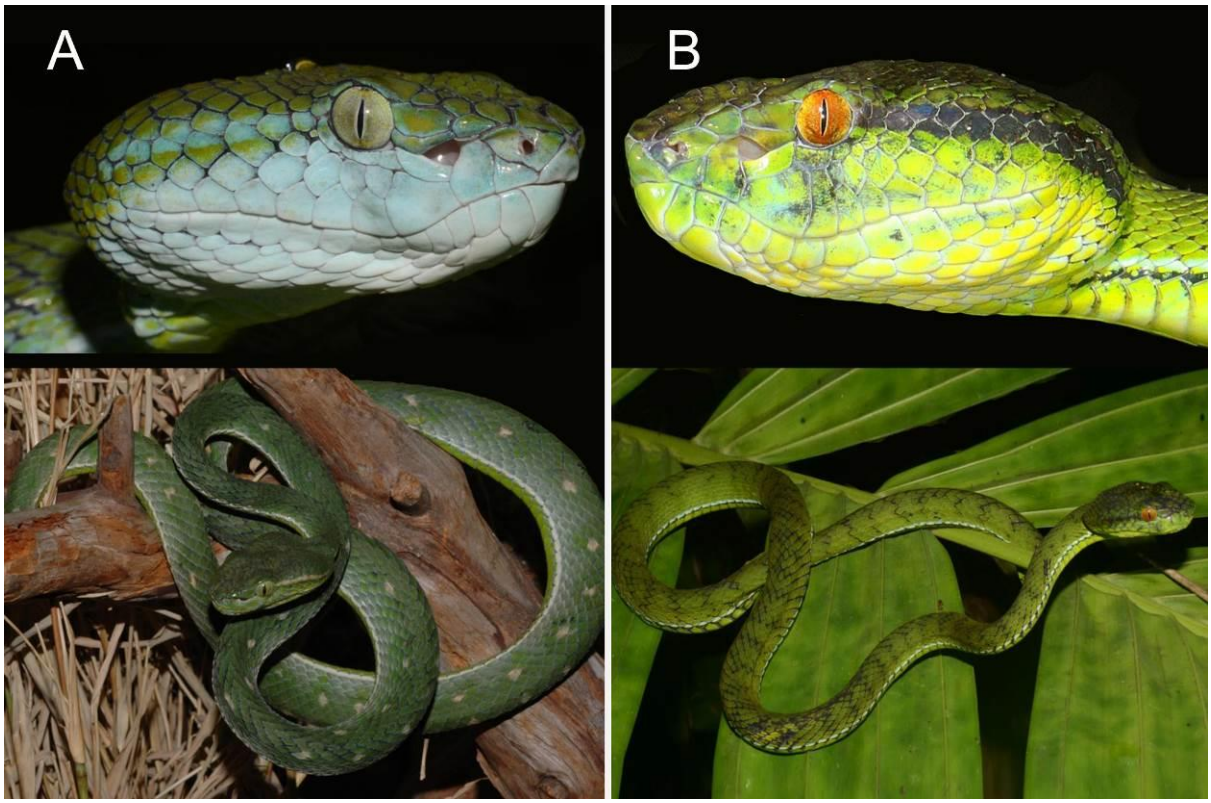

Figure 12. A comparison of the heads of adult females (above) and the body coloration of adult males (below) between (A) *Trimeresurus hageni* and (B) *Trimeresurus whitteni* sp. nov. © Photo: Gernot Vogel & Tomáš Bublík

worked in the region of Sumatra, especially on Siberut Island. He published and acted as editor of numerous publications, of which we may cite here the major work on the ecology of Sumatra and adjacent islands (Whitten *et al*. 2000) and the most recent paper about the reptile fauna of the Mentawai and other islands off the west coast of Sumatra (Dring *et al*. 1990). At the time of his death, he was senior adviser at *Flora & Fauna International*, and had recently established a specialist group on karst habitats for *International Union for Conservation of Nature*. Before this present paper, 11 species of invertebrates and vertebrates had been named after him. A more complete obituary of T. Whitten was published by Watts (2017). Suggested common names: English: Siberut Pitviper. Bahasa Indonesia: Ular Mati Ekor. Siberut: Ulou Bopai pai. French: Trimérésure de Siberut. German: Siberut Grubenotter.

Distribution. Indonesia. *Siberut Island* (West Sumatra Province). Endemic to this island located about 150 km off the west coast of Sumatra. The species might also live on Sipora Island, just south of Siberut, from where Dring *et al*. (1990) reported a pitviper under the name *T. sumatranus*.

Natural history. *Trimeresurus whitteni* sp. nov. inhabits regions typically covered with tropical moist and humid forests. Males usually were found during the night close to streams, where they often rest on low vegetation hanging above the water. One male was observed eating a frog (Tomáš Bublík, pers comm.; photographed). Females are much larger and seem to be less depending on water bodies and were found deeper inside the forest. One specimen regurgitated a bat. In the forests on Siberut, a forest rat was found to be very common and might serve as food (Tomáš Bublík pers. comm.; unpublished observations).

Populations of unresolved status

We briefly mention here specimens originating from two other populations present on islands off the west coast of Sumatra, for which the taxonomic status cannot be resolved at the present time.

Population of Batu Island: *Trimeresurus* cf. *whitteni* "Batu Island". We examined only two specimens (one adult male and one adult female) from this small island, located just north of Siberut. This snake bears some similarities with *Trimeresurus whitteni* sp. nov. but these specimens differ from that species by the following characters: (1) tail short, with ratio TaL/TL = 0.179 vs. 0.191–0.209 in four males of *T. whitteni* and 0.169 in the females vs. 0.144–0.151 in the three females of *T. whitteni*; (2) cephalic scales much enlarged, with only 5–6 scales between each supraocular (vs. 7–8 in *T. whitteni*); (3) 83 subcaudals vs. 74–77 in 4 males of *T. whitteni*; (4) occipital scales smooth vs. keeled in most specimens of *T. whitteni*.

As we have only two preserved specimens and no data and description of a living animal, we refrain from taking any taxonomic action, in spite of the morphological differences with the new species described here, *T. whitteni*, *T. calamitas* and *T. kirscheyi*.

Discussion

The Mentawai Islands are relatively close to the west coast of Sumatra. However, they are well-known for their large percentage of endemic species, an endemism which has been known for a long time for primates, with four endemic species (Roos *et al*, 2003), mammals in general (Wilting *et al*. 2012) and recently was also shown for lizards (Das 2005, Das & Lim 2009, Iskandar *et al*. 2017). Wilting *et al*. (2012) even showed that the closest relatives of several mammal species were not living on Sumatra but on the more distant Borneo, Java and Peninsular Malaysia. They concluded that the relationships represent traces of species historically distributed throughout the Sunda Region that became extinct in Sumatra during the Pleistocene.

Veron *et al*. (2017) tried to clarify the relationships of the species within the subfamily Hemigalinae of the civets (Mammalia). For the banded civet *Hemigalus derbyanus* (Gray, 1837), the examined individual from Siberut Island was genetically very distant from the populations from both Sumatra and Borneo (for both mitochondrial Cytb and nuclear FGB genes), but closer to Sumatran individuals. In contrast, the Mentawai population of the common palm civet (*Paradoxurus philippinensis lignicolor* Miller, 1903) was found to be closer to those from Borneo and the Philippines (*Paradoxurus philippinensis* Jourdan, 1837) than to the nearby Sumatran populations (*Paradoxurus musangus* [Raffles 1821]) (Patou *et al*. 2010; Veron *et al*. 2015).

However, there are hardly any investigations of the snake fauna of these islands. The latest work on the snakes of the Mentawai Archipelago and other islands off the west coast of Sumatra was published more than 30 years

ago as a by-product of a primate research project (Dring *et al*. 1990). Detailed comparisons with Sumatran or other Indonesian Islands are missing. In the last work on the snakes of Sumatra, the Mentawai Islands were not covered (David & Vogel, 1996).

Thus, as far as mammals are concerned, there is very limited genetic exchange between the Mentawai Islands and Sumatra, which at the closest distance is little more than 100 km away. The Mentawai islands have been separated since the mid-Pleistocene (Batchelor 1979, Wilting *et al*. 2012, Whitten *et al*. 2000, Karin *et al*. 2017) by the 1,500 meter-deep Mentawai Basin. It is not known when they were connected to the Sumatran landmass but, with the exception of Nias and Batu, all other islands have remained separated from Sumatra even during the period which showed the greatest area of land exposed in the last two million years (Whitten *et al*. 2000). The hypothesis of a land bridge between Siberut and Sumatra that would have involved the Batu Islands (Voris 2000) is not mentioned by Whitten *et al*. (2000). However, the stretch of water between Batu Islands and Siberut, the closest Mentawai Island, is deeper than the approximate maximum sea-level drop (< 125 m) during Pleistocene glacial maxima (Rohling *et al*. 1998, Voris 2000, Wilting *et al*. 2012, Whitten *et al*. 2000). The evolutionary divergence time estimates (1–3 My) of some endemic Mentawaian taxa relative to Sumatran and other Sundaic populations also contradicts a land bridge (Wilting *et al*. 2012). In contrast, the islands east of Sumatra (Bangka, Belitung, etc.) show comparatively little endemism as they were part of the Sunda shelf (Voris, 2000, Whitten *et al*. 2000, Inger & Voris 2001). However, endemic species can be found even here (Riyanto *et al*. 2017).

Trimeresurus calamitas nov. sp. is the more striking of the three new species. It bears characters of both *T. sumatranus* and *T. hageni*. Whereas the colouration is similar to *T. sumatranus*, other characters, as scale counts or relative tail length, are close to *T. hageni*. It is therefore not surprising that it was often misidentified as *T. sumatranus*, for example by De Rooij (1917). This brings us to the idea that somewhere in the past both species might have occurred on the Island of Nias. However, we leave this question open until fresh material is collected and molecular studies can be done.

The populations from Siberut and Simeulue are quite different in morphology from *T. calamitas*. Their colouration is more or less uniform green, or with diffuse black crossbars in *T. whitteni* of Siberut, as we can find in so many of the species of the genus *Trimeresurus*. The white or pinkish white dorsolateral dots and temporal streak of *T. hageni* are missing in specimens of the Simeulue population previously identified as *T. sumatranus* by De Rooij (1922). Specimens of the populations of Siberut and Simeulue are quite similar on a morphological basis, as stated above. However, there are constant differences in pholidosis.

The status of the population of Batu Islands is not fixed. We have only one male and one female specimen of this complex available from these Islands, which were mentioned by Brongersma (1933b). These specimens are currently not assignable to any of the populations discussed above. They have some peculiar characters, as stated above. Especially the very large head scales and an extremely short tail. Both characters are more common with *T. sumatranus* but are even outside of the range of this species. We suppose that the Batu population is another unnamed species but as only two specimens are available, we cannot formally name it; we refer it here as *Trimeresurus* cf. *whitteni* "Batu Island".

We examined one specimen from the Pagai Islands. Despite some differences (large white dots posterior before the tail, and a low number of 72 subcaudals), we regard it as *T. hageni* but did not include it into the variation given for that species.

Lastly, Boulenger (1894) also mentions a specimen of *T. sumatranus* from Sipora. We could not examine that specimen and if a population exists on that island we suggest naming this population *T. whitteni* until it can be examined in detail. We here describe only three new species out of the four populations that might deserve a full species rank: we regard this as the first step of the investigations on the pitvipers on the Mentawai Islands. With the three species formally described in the present paper, and the recently described species *T. gunaleni*, the number of the species known in the subgenus *Parias* rises to ten (David & Vogel 2015), with one or two potential additional species not yet described. The last species described before these three recently recognized species was *Trimeresurus* (*Parias*) *malcolmi* Loveridge, 1938. Thus, the number of taxa in this group has been constant for 80 years. Considering that these snakes belong to large

and venomous species, this fact seems to be quite surprising. This is even more so, as most specimens were available in collections for about 100 years and no molecular data was used for the descriptions. Obviously, Sumatra and the surrounding islands are still very incompletely known.

Meanwhile, and unfortunately, a large part of Nias Island has been deforested (Collins *et al*. 1991, Loucks & Whitten 2001, Tampubolon *et al*. 2017). Whereas *T. calamitas* sp. nov. was quite commonly collected about a century ago (Modigliani 1889), we could not locate any recent specimens in collections or traces of live specimens on the internet or literature except the picture of a single specimen published on the website *iNaturalist* (www.inaturalist.org; last accessed on 21 September 2022). This individual was found by an expedition of the Museum of Vertebrate Zoology, Berkeley, on Nias Island. *T. calamitas* sp. nov. was also found in grassland (Modigliani 1889), which might have been replaced by palm oil or other commercial plantations. It is therefore important to protect not only the last tracts of primary forests, but also the grasslands on Nias to ensure the survival of the species.

The situation on Siberut seems to be much better, as the island is still covered with extensive tracts of primary lowland rainforest. *Trimeresurus whitteni* sp. nov. was easily found along streams and therefore seems to be a species of lesser conservation concern. Finally, it should be considered that the islands west of Sumatra also harbour some limestone areas, habitats that are well known for endemic reptile species (Clements *et al*. 2006, Grismer *et al*. 2016) that have not yet been examined. Detailed inventories of these underexplored islands are needed.

We do not have recent information about the ecological situation of Simeulue Island. Recent satellite photographs suggest that parts of the tropical humid lowland forest remain in the centre of the island but Vogel & Iskandar (2012), in the assessment of another pitviper inhabiting Simeulue, *Trimeresurus brongersmai* Hoge, 1969, stated that forest is nearly gone due to forest fires, agricultural development and, especially, logging activities. Lastly, we do not have ecological data about the Batu Islands, a small archipelago located between the islands of Nias and Siberut, off the west coast of Sumatra, belonging to North Sumatra province. This archipelago of about 1,200 km², comprising three main islands and seventy-five smaller islands, is crossed by the equator.

A map for the species of this group is given in Fig. 13.

Key to the complexes of *Trimeresurus sumatranus / Trimeresurus hageni*

1. (a) Internasals separate 2

   (b) Internasals fused 4

2. (a) Less than 4 supralabials touching the suboculars on both sides; endemic to Simeulue Island ..... *T. kirscheyi* sp. nov.

   (b) More than 4 supraoculars touching the subocular on both sides 3

3. (a) More than 178 ventrals in males, more than 175 ventrals in females, relative tail length less than 0.169 in males, less than 0.161 in females; dorsal surface strongly banded with black crossbands ..... *T. sumatranus*

   (b) 178 or less than 178 ventrals in males, less than 175 ventrals in females, relative tail length more than 0.200 in males, more than 0.144 in females; dorsal surface not banded .... *T. gunaleni*

4. (a) Cephalic scales with thick, dark margins 5

   (b) Cephalic scales without thick dark margins 6

5. (a) Less than 73 subcaudals in males, usually 6 supralabials touching the suboculars, no dorsolateral white spots on the body, tail posterior red ..... *T. sumatranus*

   (b) More than 73 subcaudals in males, usually less than 6 supralabials touching the subocular, dorsolateral white spots on the body might be present, tail marbeled posteriorly ..... *T. calamitas* sp. nov.

6. (a) A row of white or cream dorsolateral spots on each side; eye colour grey, pale yellow or usually yellowish green; upper labials of the females bluish-white or bluish green; no dark crossbands on the scales of the body but interstitial skin with darker areas ..... *T. hageni*

   (b) No dorsolateral spots; eye colour bright orange, salmon or pale rusty-red; upper labials of the females light green; faint and irregular dark dorsal crossbands ..... *T. whitteni* sp. nov.

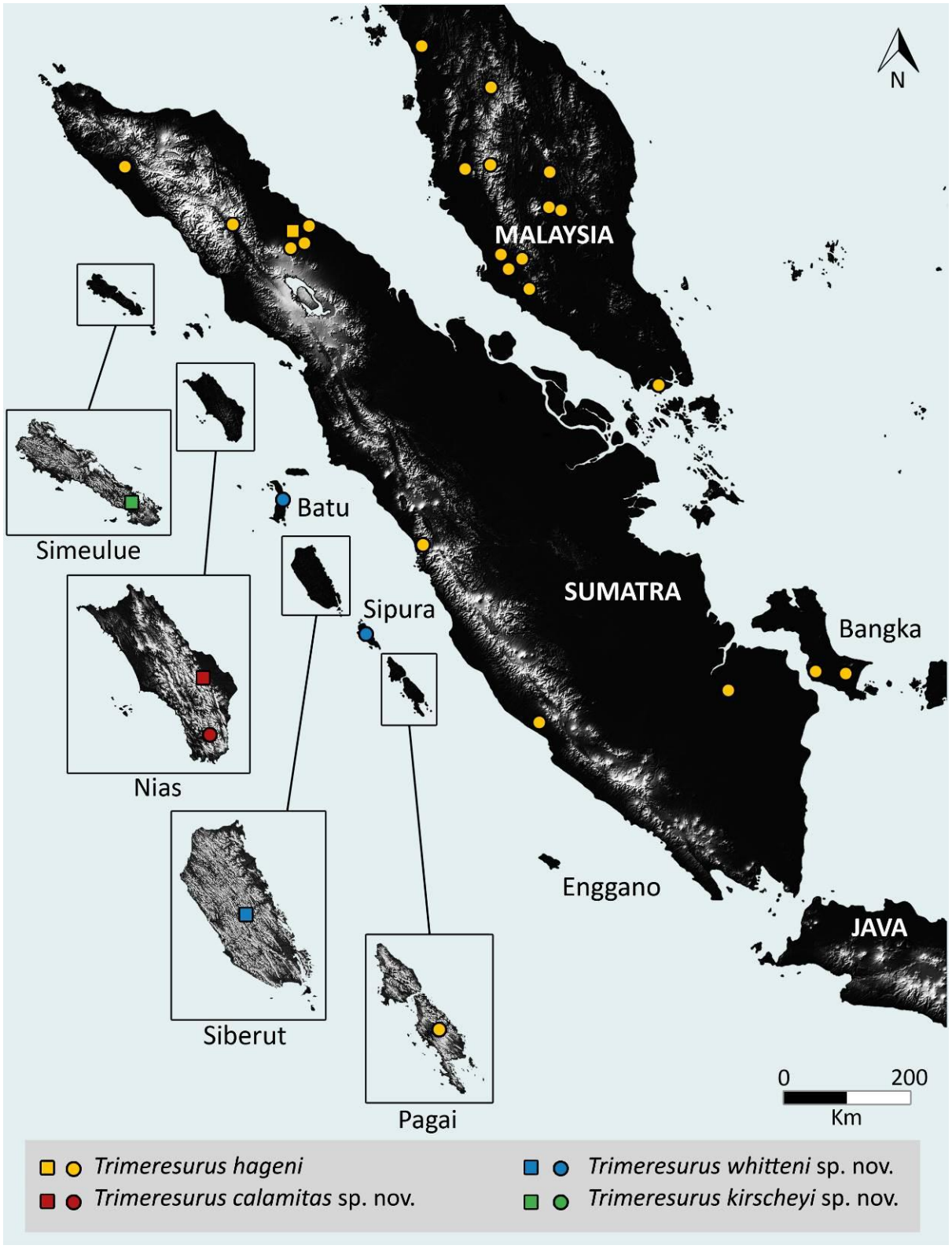

Figure 13. Current distribution map of *Trimeresurus hageni* group; the type localities are indicated in squares

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Appendix I. List of morphological characters and variables used in this study and their abbreviations

Number	Abbreviation	Character
Morphometry		
1	SVL	Snout-vent length
2	TaL	Tail length
3	TL	Total length
4	TaL/TL	Ratio tail length/Total length
Scalation		
5	DSR	Number of dorsal scale rows
6	MSR	Number of dorsal scale rows at midbody
7	PSR	Number of dorsal scale rows one head length before vent
8	VEN	Number of ventral plates
9	SC	Number of subcaudal plates
10	Cep	Cephalic scales (scales on a line between the middle of supraoculars)
11	InN	Number of Internasal scale(s)
12	InN sep	Internasal scales touching each other
13		Keeling of the occipital scales
14	SL	Supralabial scales
15		Number of scales between 3rd supralabial and subocular
16		Number of scales between 4th supralabial and subocular
17		Number of scales between 5th supralabial and subocular
18	C_{tot}SL	Total number of supralabials touching subocular
19	IL	Infralabials
Pattern		
20		Presence of black margins on dorsal scales of the head
21		Upper labials being lighter than other parts of the head
22		Ventrals with dark margins
23		Subcaudals with dark margins
24		Presence of bands on the body
25		Presence of dorsolateral light spots on the body
26		Presence of a ventrolateral stripe
27		Coloration of the ventrolateral stripe
28		Presence of a temporal streak
29		Colour of the temporal streak
30		Colour of eyes in life
31		Posterior part of the tail reddish
32		Large light blotches before tail

Appendix II. Additional specimens examined

Trimeresurus gunaleni* (*n*=9)**. **Indonesia**. ***Sumatra. MZB.OPHI 5452, Mt. Sibayak, ca. 1,500–2,200 m a.s.l., west of Brastagi (Berastagi), Karo Regency, Sumatera Utara Province (holotype); NMW 28159:1, ZMB 29642, NMW 23909:4, NMW 28159:2, "Padang, Sumatra;" NHMB 2599, "Solok, Sumatra;" SMF 52844, "Padang Mountains, Sumatra, 1,700 m," all from Sumatera Barat Province (all paratypes). Two live male specimens from Mt. Singkut, 1,600 m a.s.l., Karo Regency, Sumatra Utara Province.

Trimeresurus sumatranus* (*n*=60)**. **Indonesia**. ***Sumatra. Bengkulu Province. MZB.OPHI 1035, Gunung Gadang; MZB.OPHI 2180, "Muara Aman, North Bengkulu"; MZB.OPHI 3718, ZMB 66177–8; ZFMK 76340 (Neotype of *Coluber sumatranus* Raffles, 1822), ZMB 70490, "Bengkulu"; ZMH R06936, Lebong-Tandai (3°01'S, 101°5'E). Jambi Province. MZB.OPHI 457, "Jambi". Lampung Province. MZB.OPHI 2166, Dirgahayu Rimba, Lampung; MZB.OPHI 2219, Air Putih, Muara Aman, North Bengkulu. Sumatera Barat Province. OMNH R2135–6, Kambot, Ulu Gadut, Mt. Gadut, ca. 800 m; MZB.OPHI 2443, MZB.OPHI 2445, Anai River; RMNH 1583 (Holotype of *Trigonocephalus formosus* Müller & Schlegel, 1842), "Aan de westkust van het eiland Sumatra, in de omstreken van het dorp Limomanis, eenige uren beoosten Padang…", i.e. 'On the west coast of Sumatra Island, in the vicinity of Limomanis, a few hours east of Padang', now near Limau Manis. ***Borneo (Kalimantan)***. Kalimantan Barat Province. MZB.OPHI 1052, Sungai Mentawir, Paser Utara, Kalimantan Timur; ZSM 283/1977-1–2, Landak River; MZB.OPHI 2138a–b, Tanjung Lokang, Kapuas Hulu Regency. Kalimantan Tengah Province. MZB.OPHI 2647, Maruwai. Kalimantan Timur Province. MZB.OPHI 1340, Nyapa, Kelai River, Berau, Kalimantan Timur. Unidentified locality. MZB.OPHI 2424, Ange, Betung Kerihun, Kalimantan Barat. **Federation of Malaysia**. ***Borneo***. State of Sabah. FMNH 230063–064, Danum Valley Research Center, 5°12'N-117°50'E, Lahad Datu District; FMNH 239947–948, Marak Parak, 6°18'N 116°42'E, Kota Marudu District; FMNH 239949–958, Purulon camp, Area I, 5°13'N 115°57'E, Crocker Range National Park, Tenom District; FMNH 243943, FMNH 239959, watershed, 4°54'N-115°45'E, Mendolong camp, Sipitang District; FMNH 249756, Tawau Hills Park, 4°37'N 117°54'E, Tawau District. State of Sarawak. BMNH 91.8.29.33, Mt. Dulit, Miri District, Miri Division; BMNH 1978.1879, Gunung Mulu National Park, Miri District, Miri Division; FMNH 71643, Pa Brayong, Lawas District, Limbang Division; FMNH 76326, Mt. Matang, 1°35'N-110°14'E, Kuching District, Kuching Division; FMNH 138687–690, FMNH 148829–830, Nanga Tekalit camp, 1°38'N-113°34'E, Mengiong River, Kapit District, Kapit Division; FMNH 158671, Bintulu, Bintulu Division; FMNH 273627, Bukit Kana, 2°39'N 112°54'E, Bintulu Division. ***West Malaysia***. State of Johore. BMNH 1971.1532, Panti Forest Reserve, South Johore. State of Pahang. ZRC 2.2929, Kuala Tahan; ZMB 69982, "Pahang". State of Trengganu. BMNH 1974.5001–3, Gunong Lawit. **Thailand**. Yala Province. BMNH 1936.9.12.3–4, "Betong, Pattani".

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