ON *TRIMERESURUS FASCIATUS* (BOULENGER, 1896) (SERPENTES: CROTALIDAE), WITH A DISCUSSION ON ITS RELATIONSHIPS BASED ON MORPHOLOGICAL AND MOLECULAR DATA

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ABSTRACT. – The Indonesian species, *Trimeresurus fasciatus* (Boulenger, 1896) was up to now known only from the holotype. A few specimens of recently imported pitvipers represent the first recorded specimens of *T. fasciatus* since its original description. We report on variation of the morphological characters of this species on the basis of five new specimens. The relationships of *T. fasciatus* with other taxa of the genus *Trimeresurus*, especially *T. albolabris* and *T. insularis*, are inferred from mtDNA data. *Trimeresurus insularis* and *T. fasciatus* are shown to be closest relatives. The biogeography of these Indonesian pitvipers is briefly discussed.

KEY WORDS. – Indonesia, Tanahjampea Island, Serpentes, *Trimeresurus fasciatus*, *Trimeresurus insularis*, biogeography.

INTRODUCTION

The poor knowledge of the biodiversity of snakes in equatorial regions can be exemplified by the case of *Trimeresurus fasciatus*. Boulenger (1896: 63) described, as *Lachesis fasciatus*, a new species of pitviper on the basis of a single specimen (BMNH 96.4.29.46, female) collected from "Jampea Island", now Tanahjampea Island, Province of Sulawesi Selatan, a small island about 155 km south off Sulawesi Island, Indonesia. This island is about 20 km long and 12 km wide, and culminates at 521 m a.s.l. Since the original description, no specimen of this species has been reported on, nor has the herpetology of the island been investigated. There is no other known specimen in Western museums, and none seems to be present in zoological collections of the Bogor Museum (D. T. Iskandar, pers. comm., July 1998).

During 1999-2000, about ten specimens of an unusual brown pitviper were imported in Europe from Indonesia through the pet trade. Their origin was stated to be indeed Tanahjampea, although it was not possible to have the definitive proof of the collecting locality. A close inspection proved them to have characters very similar to those given by Boulenger (1896) for *Lachesis fasciatus*. These animals are the first known specimens of this rare species since its original discovery more than a century ago. We here expand the description of this species on the basis of data from three preserved specimens and the shed skin of two other specimens still alive at the time of writing. Biological observations on these captive specimens are detailed. On the basis of morphological and molecular analyses, we compare *T. fasciatus* with *T. albolabris* and *T. insularis* Kramer, 1977, and with *T. puniceus*, an Indonesian species also showing a brown background colour.

MATERIALS AND METHODS

Morphological study. – This study is based on the examination of six specimens of *Trimeresurus fasciatus*, namely the holotype, three recently imported specimens subsequently preserved (all males), and the shed skins of two females identified below as Specimen 1 and Specimen

2, respectively, still alive at the time that this paper was written (see Appendix). Upon death, both females will be deposited in the collections of the ZMFK (Bonn, Germany). Comparisons are based on the examination of 25 specimens of *T. albolabris* and five specimens of *T. insularis*, which are listed in the Appendix.

We retained standard morphological characters used by previous authors, such as Pope & Pope (1933) and Regenass & Kramer (1981), along with other morphometrical and meristic characters adapted from How et al. (1996). Measurements (all in millimeters), except body and tail lengths, were taken with a slide-calliper to the nearest 0.1 mm; all measures on body were measured at the nearest millimetre. Ventral scales were counted according to Dowling (1951). The terminal scute is excluded from the number of subcaudals. The number of dorsal scale rows is given at one head length behind head, at midbody (i.e. at the level of the ventral plate corresponding to half of the total ventral number), and at one head length before vent, respectively. Values for symmetric head characters are given in left/right order.

Main abbreviations used in text are: SVL: snout-vent length. - TaL: tail length. - TL: total length. - TaL/TL: ratio tail length / total length.

Molecular study. – Tissue sample (liver) of *Trimeresurus fasciatus* was obtained from specimen MNHN 2000.0401. Other specimens of which the mtDNA was investigated are *T. insularis* (MNHN 2000.0402; Wetar, Indonesia; liver) and *T. puniceus* (a living captive specimen imported from Java; shed skin). DNA extraction followed protocols previously described (Vidal et al., 1997). Amplification of a 642 bp portion of the cytochrome b gene was performed using the following set of primers: L14724, 5'-TGA-CTT-GAA-GAA-CCA-CCG-TTG-3' (Palumbi et al., 1991) and HVN650, 5'-TAT-GGG-TGG-AAK-GGG-ATT-TT-3' (original). Both strands of the PCR products were sequenced using the CEQ cycle sequencing kit (Beckman) in the CEQ-2000 DNA Analysis System (Beckman). The two strands obtained for each sequence were aligned using the BioEdit Sequence Alignment Editor program (Hall, 1999).

The following sequences were retrieved from *GenBank*: *T. albolabris* (Hong Kong, Accession Number AF171884; Northeast Thailand, AF171893; Southeast Thailand, AF171885 & AF171895; West Java, AF171886 & AF171891; North Thailand, AF171920, AF171910 & AF171908; South Thailand, AF171923 & AF171894; West Thailand, AF171921); *T. andersoni* (Andaman Islands, AF171922); *T. cantori* (Nicobar Islands, AF171899); *T. erythrurus* (Myanmar, AF171900); *T. insularis* (Flores Island, AF171883; East Java, AF171887 & AF171892; Komodo Island, AF171924; Alor Island, AF171882; Pantar Island, AF171881); *T. purpureomaculatus* (West Malaysia, AF171889); *T. septentrionalis* (Nepal, AF171909); *T. trigonocephalus* (Sri Lanka, AF171890); *T. venustus* (South Thailand, AF171914); and *Protobothrops tokarensis* (Japan, AF038884).

Sequence entry and alignment were performed manually with the MUST2000 software (Philippe, 1993). Alignment was straightforward as there were no indels. The sequences will be deposited in *GenBank* upon publication. For phylogenetic analyses, we followed the approach outlined by Hassanin et al. (1998). The consistency index (CI) excluding uninformative sites was calculated for each type of substitution and each position of codon using PAUP 3.1.1 (Swofford, 1993), resulting in 18 CI values which were used to design step matrices in PAUP 3.1.1. A heuristic weighted parsimony search was then performed with the following option: tree bisection-reconnection (TBR) branch swapping with 100 random addition replications. Support for nodes was estimated using the bootstrap technique (Felsenstein, 1985), with 1000 replicates (TBR branch swapping, closest option).

Museum abbreviations. – BMNH: The Natural History Museum, London, United Kingdom; MNHN: Muséum National d'Histoire Naturelle, Paris, France; SMF: Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, Germany; ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; ZRC: Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.

RESULTS

The most significant morphological and meristical characters obtained from the five new available specimens are reported in Tables 1 and 2, which also include data from the holotype of *Trimeresurus fasciatus*. Based on these data, the conspecificity of these five new specimens with the holotype of *T. fasciatus* cannot be doubted. There are only minor differences, such as supraoculars partly divided in the holotype, or a darker background colour in specimen MNHN 1999.9071.

Expanded description and variation (Figs. 1-4). – Compared with Boulenger's (1896) original description, the

Fig. 1. *Trimeresurus fasciatus*. Holotype (BMNH 96.4.29.46). General view. Photograph by Jean-Christophe de Massary.

Table 1. Main morphological characters (body and head) of available specimens of *Trimeresurus fasciatus*. Abbreviations: TL: total length. - SVL: snout-vent length. - TaL: tail length. - TaL/TL: ratio tail length / total length. - SnL/HL: ratio snout length (distance between the snout tip and a line connecting anterior margin of the eyes) / head length. - VEN: ventrals. - SC: subcaudals. - SR: number of dorsal scale rows at midbody. - KSR: dorsal scale rows at midbody keeled: 0 smooth, + weakly keeled, ++ strongly keeled. - IIN: number of scales separating the internasals. - Can: number of canthal scales. - SL: supralabials. - 1st SL/Nas: separation of 1st SpL and nasal: 0: united, 1 partly separated, 2: separated. - 4th SL / SOc: number of scales between the 4th SL and the subocular. - SOc/IN: ratio width of supraocular/width of internasal. - Cep: cephalic scales on the shortest line separating the middle of supraoculars. - IL: infralabials.

SPECIMEN	Sex	TL	SVL	TaL	TaL/TL	SnL/HL	VEN	SC	MSR	KSR	IIN	Can	SL	1st SL/Nas	4th SL/SOc	SOc/IN	Cep	IL
BMNH 96.4.29.46	F	459	375	84	0.183	25.2	159	61	21	+	1	4/4	9/10	1/1	1/1	1.08/1.05	6	11/11
MNHN 1999.9071	M	505	399	106	0.210	25.6	160	65	21	+	1	4/4	10/9	1/1	1/1	0.95/0.88	9	10/10
MNHN 2000.0401	M	509	406	103	0.202	26.3	159	63	21	+/++	1	4/4	9/9	0-1/1	2/1	0.88/1.00	8	11/11
ZRC.2.5620	M	494	396	98	0.198	26.0	158	64	21	+/++	1	4/4	11/10	1/1	1/1	0.83/0.88	9	11/10
Specimen 1 (shed skin)	F	—	—	—	—	—	163	—	21	++	1	5/5	10/10	—	2/2	—	10	11/11
Specimen 2 (shed skin)	F	—	—	—	—	—	163	—	21	++	1	4/4	10/10	—	2/2	—	10	11/11

Table 2. Main coloration and pattern characters of available specimens of *Trimeresurus fasciatus*. Abbreviations: TBB: presence of dark transversal bands of the body: 0 absent, 1 present, 2 strongly distinct. STBB: shape of the dark transversal bands of the body: 0 entire, 1 divided on vertebral line. - NTBB: number of dark transversal bands of the body. - HI.col: difference in coloration of supralabials and upper head surface: 0: similar or just slightly paler, 1: distinctly paler. - PoS: postocular streak: 0 absent, 1 present. Note: (1): based on data recorded on the specimen alive.

SPECIMEN	Background color	TBB	STBB	NTBB	HLcol	PoS	Venter
BMNH 96.4.29.46	brownish-grey	2	1	60	1	0	pale greyish-brown
MNHN 1999.9071	brown	2	1	55	1	0	pale brown
MNHN 2000.0401	brownish-grey	2	1	56	0	0	pale greyish-brown
ZRC.2.5620	brownish-grey	2	1	53	1	0	pale greyish-brown
Specimen 1 (shed skin)	brownish-grey (1)	2 (1)	1 (1)	54 (1)	1 (1)	0 (1)	pale brown (1)
Specimen 2 (shed skin)	brownish-grey (1)	2 (1)	1 (1)	—	1 (1)	0 (1)	pale brown (1)

description of *Trimeresurus fasciatus* can be expanded as follows:

Body rather elongated, somewhat laterally compressed; head triangular, flattened, rather short, 1.4-1.8 times as long as wide, clearly distinct from a thin neck; snout elongated, accounting for 24-26% of total head length and 1.7-2.1 times as long as diameter of eye, flattened, rounded seen from above, projecting, flat or slightly turned up, obliquely truncated when seen from the side, with a sharp *canthus rostralis*; eye rather large, with the eye diameter/distance eye-upper lip border ratio equal to 0.8-1.0; tail cylindrical and prehensile.

Maximum known total length: TL 509 mm (SVL 406 mm, TaL 103 mm) for a male (MNHN 2000.0401).
It is obvious that this species reaches a larger size, at least 80 cm, as we measured the shed skin of a female (Specimen 2) which is greater than 90cm (SVL about 78 cm, TaL > 13 cm).

Ratio TaL / TL: 0.183-0.210 (3 males: 0.198-0.210; 1 female: 0.183.).

Ventrals: 158-163 (plus 2 or 3 preventrals); subcaudals: 61-65, all paired; anal shield entire.
Dorsal scale rows: 21(23)-21-15, moderately or strongly keeled at midbody on the upper half of the body, weakly keeled ventrolaterally, smooth on the first outer row.

Rostral triangular, about 1.5 times broader than high; nasal rectangular, 1.6-1.8 times as long as high, undivided, with nostril in its middle; one pair of enlarged, subrectangular internasals, 1.3-1.5 times as wide as deep, distinctly larger than adjacent upper snout scales, separated by one small triangular scale in all specimens; 4 or 5 subequal canthal scales bordering the *canthus rostralis* between internasal and corresponding supraocular, barely larger than adjacent snout scales; one comparatively large triangular loreal between upper preocular and nasal; 2 or 3 postoculars; one large and wide supraocular on each side, entire or partly divided, usually indented by upper head scales, about 1.8 times as long as wide, much wider than the adjacent upper head scales, and about 0.8-1.1 times as wide as the internasals; scales on upper surface of head and snout relatively large, smooth, juxtaposed, irregular, slightly larger on snout than in frontal-parietal region, abruptly much smaller immediately behind

Fig. 2. *Trimeresurus fasciatus*, adult male in life. Photograph by Gernot Vogel.

Fig. 3. *Trimeresurus fasciatus*, adult female in life. Photograph by Gernot Vogel.

Fig. 4. *Trimeresurus fasciatus*, juvenile in life. Photograph by Gernot Vogel.

a line connecting the back of supraoculars, progressively slightly keeled backwards on occipital region; 6-10 cephalic scales on a line between supraoculars; temporals unequal, large, in 3 or 4 rows, obtusely keeled backwards; one elongated subocular; 9-10 supralabials; 1st supralabial small, partly fused with nasal but distinctly separated by a groove; 2nd supralabial high, forming the anterior border of loreal pit, in contact with nasal; 3rd supralabial largest, pentagonal, about 1.4 times as long as high, usually separated from subocular by one scale (in contact in a single case out of ten); 4th supralabial much lower than third one, separated from subocular by one scale nearly as large than the supralabial; 5th and other posterior supralabials slightly smaller than 4th one, separated from subocular by one or two rows of scales of similar size; 10-11 infralabials, first pair in contact with each other, first, second and third pairs in contact with chin shields; 6-8 rows of smooth gular scales; chin shields irregularly arranged.

Hemipenes: in situ (based on MNHN 2000.0401), hemipenes are very long and slender, reaching 25th subcaudal and forked at the level of the 5th subcaudal. The three quarters of the distal part are smooth, covered with calyces, the remaining part being covered with papillae. The sulcus spermaticus is not prominent.

Dorsal and upper tail surfaces brownish-grey, ochre brown or chesnust brown, with about 55-60 well-defined greyish-brown, olivaceous brown or dark brown crossbands on the back, about 3-4 dorsal scales long, reaching ventrally the midlateral region, usually divided on the vertebral line, with their two parts confluent or set off, sometimes nearly totally alternating; an irregular dark brown blotch more or less defined on lower part of flank under a corresponding dorsal band, more conspicuous on foremost part of body. This pattern may be much subdued in large females, which look rather uniformly brown (see Fig. 3). Venter pale greyish-brown or brown, heavily speckled with dark brown, anterior part and tip of ventrals nearly totally dark brown. Upper head surface and temporal regions olivaceous brown or dark brown, variegated with very diffuse darker markings; region of supralabials and snout pale greyish-brown or pale brown, irregularly variegated or speckled with dark brown; no postocolar streak; mental and infralabials pale greyish-brown like venter, with irregular scattered dark brown spots. The coloration and pattern of juvenile snakes are similar to adults, with a upper head surface dark lead-grey (Fig. 4).

Molecular data. – Our molecular dataset includes 504 bp for 29 taxa (174 variable sites, 117 of which are informative for parsimony). The CI values used to design step matrices are the following : AG1 (first position of codon): 0.571, AG2 (second position of codon): 1, AG3 (third position of codon): 0.586, CT1: 0.5, CT2: 1, CT3: 0.376, AT1: 1, AT2: 1, AT3: 0.778, AC1: 0.75, AC2: 1, AC3: 0.583, CG1: 1, CG2: 1, CG3: 0.6, GT1: 1, GT2: 1, GT3: 1. The resulting heuristic search produced two equally parsimonious trees, the strict consensus of which is shown on Fig. 5.

Trimeresurus puniceus from Java does not belong to the *T. albolabris* complex which comprises *T. albolabris, T. andersoni, T. cantori, T. erythrurus, T. fasciatus, T. insularis, T. purpureomaculatus* and *T. septentrionalis* (bootstrap value: 90%). Within this complex, four main lineages are distinguished: one comprising the various populations of *T. albolabris* from Thailand, Hong Kong and West Java (bootstrap value below 50%); one comprising *T. andersoni, T. cantori, T. erythrurus* and *T. purpureomaculatus* from Andaman Islands, Nicobar Islands, Myanmar and West Malaysia respectively (bootstrap value: 59%); one comprising *T. septentrionalis* from Nepal; and one comprising the insular species *T. insularis* and *T. fasciatus* from Lesser Sunda Islands (Alor, Flores, Komodo, Pantar, Tanahjampea and Wetar Islands) and East Java (bootstrap value: 67%). Within the latter lineage, *T. fasciatus* is the sister-group to the various populations of *T. insularis* (bootstrap value: 60%). *Trimeresurus insularis* from Flores Island is the sister-group to the remaining populations of *T. insularis* (bootstrap value: 76%) which comprise two clades: one from East Java (bootstrap value: 69%) and one from Alor, Komodo, Pantar and Wetar Islands (bootstrap value: 56%).

DISCUSSION

Taxonomy. – The status of *Trimeresurus fasciatus* has, quite surprisingly, received some attention from herpetologists, although this species has variously be regarded as valid or as a synonym of *T. albolabris* (Gray, 1842) (for example, by Auffenberg, 1980). This confused taxonomical history will be presented elsewhere (David et al., in prep.) Recent authors, like Golay et al. (1993), David & Ineich (1999) and McDiarmid et al. (1999) have regarded *T. fasciatus* as valid.

Trimeresurus albolabris is largely present in Indonesia. In order to accommodate specimens from eastern Java and islands located further east, Kramer (1977: 755) described *T. albolabris insularis* (type locality: Soe, Timor Island, Indonesia). According to Regenass & Kramer (1981), the main differences between these taxa bear on: (1) colour of the lips clearly distinct from dorsal head surface in *albolabris*, not so different in *insularis*, (2) temporals highly keeled in *insularis*, smooth or weakly keeled in *albolabris*, (3) Ventral scales 148-173 in *T. albolabris* vs. 156-167 in *T. insularis*, and on some other minor scalation characters. Malhotra & Thorpe (1996, 2000) and Giannasi et al. (2001a) showed, based on mtDNA data, that the molecular phylogeny among *T. albolabris* populations did not correlate with the morphological variation. Accordingly, these authors refuted the currently accepted subspecific division of this species as defined in Regenass & Kramer (1981). The problem was partly clarified by Giannasi et al. (2001b), who elevated to full species status *T. albolabris insularis*, as well as *T. albolabris septentrionalis* Kramer, 1977, a taxon known from Nepal and northern India.

According to Regenass & Kramer (1981), David & Vogel

(1996), How et al. (1996), Malhotra & Thorpe (1996), and How & Kitchener (1997), members of the *T. albolabris* complex have been reported from the following Indonesian islands (from west to east): (1) *T. albolabris*: Sumatra (David & Vogel, 2000), Bangka, Western Java, and Madura; (2) *T. insularis*: Eastern Java, and the islands of Bali, Lombok, Sumbawa, Sumba, Komodo, Rinca, Flores, Adonara, Lembata, Pantar, Alor, Roti, Semau, Timor, Wetar, Kisar and Romang. The presence of *T. albolabris* on Sulawesi Island, cited by Regenass & Kramer (1981: 170) on the basis of a single specimen, is doubtful.

Our molecular results strongly support the distinct specific status of the taxa *T. fasciatus* and *T. insularis* with respect to *T. albolabris* sensu stricto. Giannasi et al. (2001b) showed both the monophyly of the clade corresponding to *T. insularis*, and its important molecular difference with *T. albolabris* from the Asian mainland and western Java. However, these authors did not have at hand the mtDNA sequence of *T. fasciatus*, which has been investigated in the present paper. According to our molecular results (see Fig.

5), *T. fasciatus* and *T. insularis* are closest relatives. Moreover, this clade may be divided into four subclades: (1) *fasciatus*; (2) *insularis* populations from Flores Island; (3) *insularis* populations from East Java and (4) *insularis* populations from Wetar, Komodo, Alor and Pantar. The yellow-coloured morph occurring on Wetar Island unambiguously roots within the clade of *insularis*, and does not warrant any distinct taxonomical status. Besides the overall yellow or greenish-yellow colour of the body, there is seemingly no morphological difference between the morph of Wetar and other populations of *T. insularis*.

Comparison. – We investigated the main morphological differences between *Trimeresurus fasciatus* and *T. insularis* (data for this latter species originate from Kramer [1977], Regenass & Kramer [1981] and How et al. [1996], supplemented by values obtained from five examined specimens). The taxa *fasciatus* and *insularis* share the following diagnostic characters: (1) long, smooth hemipenes; (2) first supralabial partly united to nasal; and (3) a pattern largely composed of darker crossbands, although they are
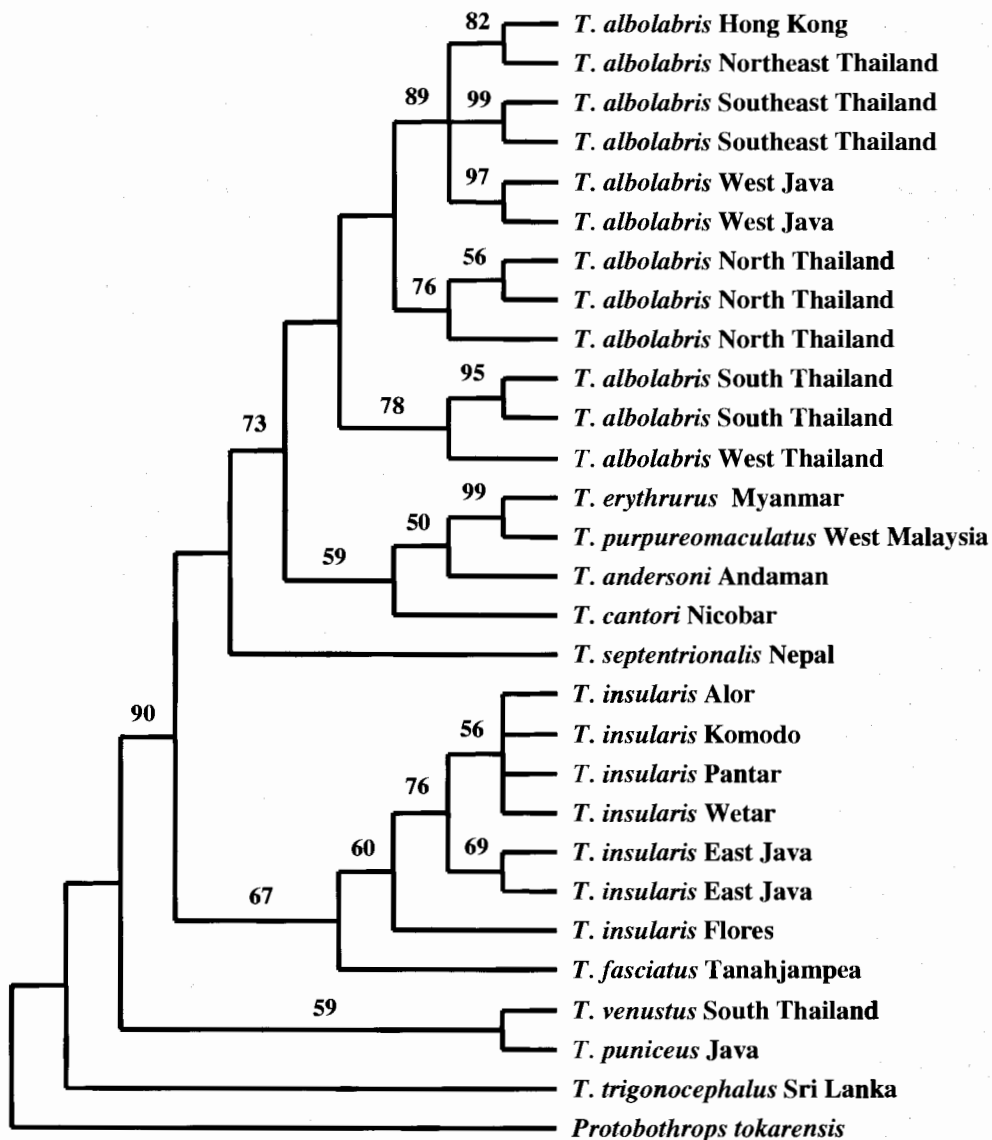

Fig. 5. Strict consensus MP tree. Values above branches are boostrap proportions (1000 replicates).

much subdued in *insularis*, strongly defined in *fasciatus*. To the contrary, these species differ by: (1) the background colour, usually green or greenish-blue (or yellow) in *insularis*; (2) the ratio TaL/TL, higher in males of *insularis* (0.214-0.224 vs. 0.198-0.210 in *fasciatus*) but lower in females (0.157-0.159 vs. 0.183 in *fasciatus*); (3) a shorter snout in *fasciatus*, expressed by the ratio distance eye-nostril/ head length (x 100) (19.5-21.1 [mean 20.3 ± 0.7] in *fasciatus* vs. 21.2-24.2 [mean 23.1 ± 1.3] in *insularis*); (4) the relative width of supraoculars compared with internasal width, greater in *fasciatus* (0.85-1.05 [mean 0.94 ± 0.09]) than in *insularis* (0.40-0.65 [mean 0.57 ± 0.10]); (5) internasals separated by one scale in *fasciatus*, in contact in *insularis*; (6) the number of cephalic scales, lower in *fasciatus* (6-10) than in *insularis* (9-13); (7) the 3rd supralabial usually in contact with the subocular in *fasciatus*, separated in *insularis*; and (8) a lower number of infralabials in *fasciatus* (10-11) than in *insularis* (11-13).

Lastly, there is another brown species in the Indonesian region, *T. puniceus* (Kuhl, 1824). Our molecular results show that it definitely does not belong to the *T. albolabris* complex. Morphologically, it differs from *T. fasciatus* by (1) a much different coloration and dorsal pattern (see Hoge & De Lemos Romano, 1974); (2) uplifted, multiple supraoculars; and (3) a short second supralabial, which does not border the anterior margin of the loreal pit and is topped by a prefoveal bordering the pit. The shape of the head is also quite different, with the snout more elongated in *T. puniceus*.

Biogeographical implications. – The occurrence of two species of the *albolabris* complex on Java and the distribution of *Trimeresurus fasciatus* and *T. insularis* raise potential biogeographical issues. *Trimeresurus albolabris* has long been recorded in West Java and some adjacent islands; elsewhere, it occurs widely on the Asian mainland, except West Malaysia, and is also known from south-western Sumatra (David & Vogel, 2000; Giannasi et al., 2001b). On the other hand, recent studies by Malhotra & Thorpe (2000) and Giannisi et al. (2001b) have shown that the populations from East Java should be referred to *T. insularis*.

The geological and palaeoclimatical events which affected Southeast Asia are now quite well understood (see Heaney, 1991; Holloway & Hall, 1998; Inger, 1999; Inger & Voris, 2001), and give some clues on the biogeography of snakes in this region. According to these authors, even at the maximum lowering of sea level which occurred during the mid-Pleistocene epoch, the modern Lesser Sunda Islands were by no way connected to the exposed Sunda Shelf and Java, with the exception of Bali. Furthermore, during the early Pliocene, about three million years before this glaciation, the Sunda Islands were limited to a few scattered and disjunct islands (Inger, 1999; Inger & Voris, 2001). If modern parts of Southeast Asia and the western Indonesian islands were alternately aggregated or fragmented, according to the level of the oceans, it is largely accepted that land composing the Lesser Sunda Islands has not been in direct connection with the Sunda Shelf since the Oligocene (about 30 m.y.b.p.). This long differentiation led Inger (1999: 452)

to class these two large areas into two different biogeographic regions, namely the Sunda Region and the Lesser Sunda Region respectively, with the separation extending between Java and Bali.

Our molecular data show a basal split between the *T. fasciatus* / *T. insularis* clade on the one hand and the remaining species of the *T. albolabris* complex on the other hand. In accordance with available geological data, the *T. fasciatus* / *T. insularis* lineage must therefore have been isolated early in the exposed land of the future Lesser Sunda Islands. The derived position of the east Javanese *insularis* populations within the *T. fasciatus* / *T. insularis* clade supports this hypothesis. *Trimeresurus insularis* should therefore be regarded as a former endemic of the Lesser Sundas, and its presence in eastern Java may be satisfactorily explained by a recent and limited colonization from one of the islands lying at the western edge of the Lesser Sunda Islands. In western Java, durably connected to the Sunda Shelf, the presence of *T. albolabris* can be explained by the former presence of this species in most of the modern Indochinese and Malay peninsulas, and western Sunda Shelf when the climate was dryer than nowadays. Indeed, *T. albolabris* is now absent from Southeast Asian areas affected by the equatorial climate, namely a climate without marked dry seasons. It has persisted only in the dryer areas of the Sunda Region, especially in western Java and south-western Sumatra. These areas receive comparatively moderate rainfall and are affected by a dry season lasting at least two months. Further north, *T. albolabris* is again present in southern Thailand, which also undergoes a two month-long dry season. There is no definite record of *T. albolabris* from West Malaysia, much of Sumatra and Borneo (David & Vogel, 2000).

Present climatic conditions prevailing on western and eastern Java are quite different. Eastern Java, inhabited by *T. insularis*, but not by *T. albolabris*, is much dryer than western Java. With a five-month long dry season, eastern Java shows a dry, highly seasonal tropical climate very similar to the one present in Lesser Sunda Islands, where *T. insularis* is widespread on several islands.

CONCLUSION

The investigation of fresh specimens of *Trimeresurus fasciatus* led us to ascertain its relationships with *T. insularis*, named for the eastern Indonesian populations of the *T. albolabris* complex and only recently raised to full species status. The precise taxonomic status of populations of this latter species, spread over a large number of islands, is still not established. The examination of further specimens will allow us to ascertain more accurately meristic variation of *T. insularis*. Although a part of the veil surrounding the systematic identity of *T. fasciatus* has been lifted after over 100 years of its description, this species remains a fascinating example of our poor knowledge of Southeast Asia herpetofauna. If the herpetofauna of larger islands of

Indonesia is still poorly known, it is even nearly totally unknown for several of the smaller islands of the Lesser Sunda Islands.

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APPENDIX

MATERIAL EXAMINED

Trimeresurus albolabris (n = 25). – **Cambodia**: MNHN 1970.588-590 (three males), MNHN 1970.595-596 (two males), MNHN 1970.598 (male), MNHN 1987.1091 (male), MNHN 1988.3980 (male), MNHN 1995.9449 (male), without precise locality; **Indonesia**: MNHN 1939.205 (female), Jakarta, Java Island; SMF 37833-34 (two males), Lake Ranau (Danau Ranau), on the border between provinces of Sumatera Selatan and Lampung, Sumatra; **Laos**: MNHN 1897.432 (female), Ban Taxeng, Kas' Country; **Myanmar**: MNHN 1893.415 (female), 1893.416 (male), Bhamo, Kachin State; **Thailand**: MNHN 1986.1503 (male), no locality, through the pet trade; MNHN 1998.0569-70 (females), Ban Salakern, Ban Lat, Petchaburi Province; **Vietnam**: MNHN 1904.404-405 (two females), Cao Bang Province; MNHN 1911.103 (male), "Cochinchine", now southern Vietnam; MNHN 1937.29 (female), 29A (female), 29B (male), 29C (male), vicinity of Bien Hoa, South Vietnam; MNHN 1974.1350 (male), Ha Tinh Province.

Trimeresurus fasciatus (n = 4). – **Indonesia**: BMNH 96.4.29.46, "Jampea Island", now Tanahjampea, Province of Sulawesi Selatan (holotype; female); MNHN 1999.9071 (male), MNHN 2000.0401 (male), ZRC.2.5620 (male), Tanahjampea, Province of Sulawesi Selatan (all through the pet trade).

Trimeresurus insularis (n = 5). – **Indonesia**: MNHN 4056 (male), Timor Island; MNHN 4057 (male), "Indes Orientales"; MNHN 2000.0402, Wetar Island (female); SMF 76352 (female), 76353 (male), Flores Island.