ON TRIMERESURUS FASCIATUS (BOULENGER, 1896) (Serpentes; Crotalidae), WITH A DISCUSSION ON ITS RELATIONSHIPS BASED ON MORPHOLOGICAL AND MOLECULAR DATA

Patrick David  
Département Evolution et Systématique, USM 602 Taxinomie-Collections Reptiles & Amphibiens, Muséum National d'Histoire Naturelle  
25, rue Cuvier, F-75005 Paris, France  
Email: patrick@mnHN.fr

Gernot Vogel  
Staatliches Museum für Naturkunde (SNM), Kreuzgraben 1, D-69115 Heidelberg, Germany  
Email: Gernot.Vogel@online.de

Nicolas Vidal  
Service de Systématique Moléculaire (CNRS/IN 154), Muséum National d'Histoire Naturelle, 43 rue Cuvier, F-75005 Paris, France  
Email: vidal@mnHN.fr

ABSTRACT. – The Indonesian species, Trimeresurus fasciatus (Boulenger, 1896) was up to now known only from the holotype. A few specimens of recently imported pipisipers 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 pipisipers is briefly discussed.

KEY WORDS. – Indonesia, Tanahjampea Island, Sengentes, 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: 65) described, as Laeocis fasciatus, a new species of pipisiper on the basis of a single specimen (BMNH 96.4.29.46, female) collected from "Jampa Island", now Tanahjampea Island, Province of South Sulawesi, Sulawesi, 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 species 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 pipisiper were imported 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 Laeocis 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 Kreuger, 1977, and with T. paniceus, 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 I 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 ZMPK (Bonn, Germany). Comparisons are based on the examination of 25 specimens of T. albolabiata 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 Regensass & Kramer (1981), along with other morphometric and meristic characters adopted 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 behind vent, respectively. Values for symmetric head characters are given in leftright order.

Main abbreviations used in text are: SVL: snout-vent length, TdL: tail length, TL: total length, Ta/L: tail length/total length.

Molecular study. – Tissue sample (live) of Trimeresurus fasciatus was obtained from specimen MNHN 2000.0402. Other specimens of which the mtDNA was investigated are T. insularis (MNHN 2000.0402; Watar, Indonesia; live) and T. puniceus (living captive specimens 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-GCA-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. albolabiata (Hong Kong, Accession Number AF171884; Northeast Thailand, AF171893; Southeast Thailand, AF171885 & AF171895; West Java, AF171886 & AF171891; North Thailand, AF171900 & AF171900; South Thailand, AF171923 & AF171894; West Thailand, AF171921; T. andersoni (Andaman Islands, AF171922); T. cantori (Nicobar Islands, AF171899); T. erythraeus (Myanmar, AF171900); T. insularis (Flores Island, AF171883; East Java, AF171887 & AF171892; Komodo Island, AF171924; Aior Island, AF171882; Pantar Island, AF171881); T. purpureomaculatus (West Malaysia, AF18899); T. serpentiniens (Nepal, AF19109); T. trigonocephalus (Sr Lanka, AF171900); T. venustus (South Thailand, AF171914); and Protothomastes tokarevski (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).


RESULTS

The most significant morphological and meristic 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 conspicuousness of five new specimens with the holotype of T. fasciatus cannot be doubted. There are only minor differences, such as supracocialpartly 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.

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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 ventral line. - NTBB: number of dark transversal bands of the body. - HLC: color 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.

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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, Tail 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 90 cm (SVL about 78 cm, Tail > 33 cm).

**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.

Ratio TL/TL: 0.183-0.210 (7 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, 1.5-2.1 times as long as high, undivided, with nostril in its middle; one pair of enlarged, subrectangular internasals, 1.5-1.5 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 bounding 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, mostly indented by upper head scales, about 1.5 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
a line connecting the back of supracoculars, progressively slightly keeled backwards on occipital region; 6-10 cephalic scales on a line between supraoculars; temporalis unequal, large in 3 or 4 rows, obliquely 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 nasals; 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 16); 4th supralabial much lower than third, separated from subocular by one scale nearly as large as 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; 10-14 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 chestnut brown, with about 55-60 well-defined greyish-brown, obliquous brown bands. Brown cross-bands 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 set off, sometimes nearly usually 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 ventral nearly totally dark brown. Upper head surface and temporal regions obliquous 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 postocular streak; mental and infralabials pale greyish-brown like tenter, 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 paniculatus from Java does not belong to the T. albolabris complex which comprises T. albolabris, T. andersoni, T. cantori, T. eythrophus, 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. eythrophus 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 Sundas Islands (Alor, Flores, Komodo, Pantar, Tanahaljuma and Weat Islands) and East Java (bootstrap value: 76%). Within the later 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 Weat Islands (bootstrap value: 56%).

DISCUSSION

Taxonomy. – The status of Trimeresurus fasciatus has, quite surprisingly, received some attention from herpetologists, although this species has variously been regarded as valid or as a synonym of T. albolabris (Gray, 1842) (for example, by Aufenberg, 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 McDermott 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 distinctly different 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 148-176 in T. albolabris, 156-171 in T. insularis; and on some other minor scalation characters. Malhotra & Thorpe (1996, 2000) and Giannini 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 Giannini 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
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 Westar, 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 Trimereutes fasciatus and T. insularis (data for this latter species originate from Krauer [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 bootstrap proportions (1000 replicates).](image-url)
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 (0.214-0.244 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-nasal/nose 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 interocular 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 supraocular 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) splintered, multiple supraoculars; and (3) a short second supraocular, which does not border the anterior margin of the loreal pit and is topped by a preocular 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 in 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; Giannini et al., 2001b). On the other hand, recent studies by Malhotra & Thorpe (2000) and Giannini et al. (2001b) have shown that the populations from East Java should be referred to T. insularis.

The geological and palaeoclimatic 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 Miocene, 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 biogeographical 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, darably 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 Indo-Chinese 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 drier 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 east Javanese 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 variations 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 Sundas Islands.

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LITERATURE CITED


APPENDIX

MATERIAL EXAMINED


Trimeresurus fasciatus (n = 4). – Indonesia: BMNH 96.4.29-46, “Jampoa Island”, now Tanahjampea, Province of Solawesi Selatan (holotype; female); MNHN 1999.9071 (male), MNHN 2000.0401 (male); ZRC 2.5629 (male), Tanahjampea, Province of Solawesi Selatan (all through the pet trade).

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

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