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Revision of the *Tropidolaemus wagleri*-complex (Serpentes: Viperidae: Crotalinae). I. Definition of included taxa and redescription of *Tropidolaemus wagleri* (Boie, 1827)

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ABSTRACT

In this first paper of a series of three, the taxonomy of the Asian pitvipers of the genus *Tropidolaemus* is re-evaluated on the basis of morphological analyses. Variation in morphological characters was investigated on the basis of specimens from the whole range of the pitviper currently known as *Tropidolaemus wagleri* (Boie, 1827). Our results, based on morphological univariate and multivariate analyses, define three clusters of populations that are morphologically diagnosable and which are here considered to represent distinct species following the Biological Species Concept and the Phylogenetic Species Concept. After a review of available names among the list of synonyms created during the confused taxonomical history of the genus *Tropidolaemus*, it appears that *Tropidolaemus wagleri* (Boie, 1827) is the valid name of the first cluster which includes populations inhabiting Southern Thailand, West Malaysia, Sumatra, Nias, Mentawei Archipelago and Bangka Island (but not Belitung). In order to stabilize the binomen, we select and describe a neotype for *Tropidolaemus wagleri*. A second cluster, for which the binomen *Tropidolaemus subannulatus* (Gray, 1842) is

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available, includes in this preliminary step populations from Borneo, Sulawesi, Sulu Archipelago and the Philippines. Its detailed taxonomy will be addressed in the second paper of the series. Lastly, the third cluster includes specimens from Mindanao Island, Philippines, recognized here as *Tropidolaemus philippensis* (Gray, 1842).

KEY WORDS: Indonesia, Thailand, West Malaysia, Sumatra, Borneo, Sulawesi, Philippines, Serpentes, Viperidae, *Tropidolaemus*, *Tropidolaemus wagleri*, *Tropidolaemus subannulatus*, *Tropidolaemus philippensis*, *Tropidolaemus laticinctus*, *Tropidolaemus huttoni*, taxonomy, neotype

INTRODUCTION

Among pitvipers of tropical Asia, members of the genus *Tropidolaemus* Wagler, 1830 are among the most widespread and often commonly encountered venomous snakes in many islands of the Indo-Malayan Archipelago. Long regarded as a synonym or a subgenus of *Trimeresurus* (see, for example, Brattstrom, 1964), the genus *Tropidolaemus* was resurrected by Burger (1971) to then accommodate the sole species formerly called *Trimeresurus wagleri*. The validity of the genus is accepted by all recent authors. This genus is characterized by the absence of a nasal pore, upper surfaces of the snout and head covered with distinctly keeled small scales, strongly keeled gular scales, second supralabial not bordering the anterior margin of the loreal pit and topped by a prefoveal, and a green coloration in juveniles which may or may not change with growth. For long, *Tropidolaemus wagleri* was the sole species included in the monotypic genus, but David & Vogel (1998) showed that the Indian species *Trimeresurus huttoni* Smith, 1949 was clearly a member of this genus.

In this first paper of a series of three, we address the rather confused nomenclatural history and taxonomy of *Tropidolaemus wagleri* (Boie, 1827) sensu auctorum (see, for example, David & Ineich, 1999; McDiarmid et al., 1999; Gumprecht et al., 2004). Members of this species complex are widespread throughout the Indo-Malayan part of Asia, with an isolated population in Southern Vietnam. Besides this latter country, it is distributed from southern Thailand to the Philippines and Sulawesi Island, including West Malaysia, and the islands of Sumatra, Borneo, Bangka, Nias, the Mentawai Archipelago, and Belitung. Although a common and conspicuous, very variable species, few authors tried to investigate its taxonomy, most probably following Boulenger (1896) who synonymised the various names under the sole specific name *Lachesis wagleri*. Nevertheless, Taylor (1917, 1922) examined Philippine populations and recognized three subspecies, of which two were considered endemic to the Philippine islands, *Tropidolaemus wagleri alboviridis* (Taylor, 1917) and *T. wagleri subannulatus* (Gray, 1842). This position was not accepted by Leviton (1964), who investigated the taxonomy of the Philippine populations and considered again *Tropidolaemus wagleri* to be monotypic. However, Leviton added: “The exact status of the nominal species and subspecies I have placed into the synonymy of *T. wagleri* cannot be settled until the type specimens and additional material from scattered localities can be examined.”

The monotypic status of *Tropidolaemus wagleri* was accepted by subsequent authors (Harding & Welch, 1980; Hoge & Romano-Hoge, 1981; Alcala, 1986; Welch, 1988; Golay et al., 1993; David & Vogel, 1996, Manthey & Grossmann, 1997; McDiarmid et al., 1999), although some noted that the taxonomy of the species was unsatisfactory (David & Ineich, 1999). David & Vogel (1998) discussed the taxon described as *Trimesurus philippensis* Gray, 1842, regarded as valid by Taylor (1922) and Maslin (1942) as *Trimeresurus philippinensis*, but placed in the synonymy of *Tropidolaemus wagleri* by Leviton (1964), who, however, seemingly did not examine its holotype. David & Vogel (1998) examined two specimens, namely the holotypes of *Trimeresurus philippensis* Gray, 1842 and *Tropidolaemus hombronii* Jacquinot & Guichenot, 1848, clearly a synonym of the former one. David & Vogel (1998) and David & Ineich (1999) noted that both specimens displayed notable morphological differences (scalation of head and body and coloration) with *Tropidolaemus wagleri*.

Nevertheless, the taxonomy of *Tropidolaemus wagleri* had yet to be investigated, in spite of obvious positive relationships between colour morphs and geographical ranges. Iskandar & Colijn (2001: 160–161) introduced a new taxonomy based only on verbal communications with U. Kuch & N. Vidal. Without further explanation, they divided *Tropidolaemus wagleri* auctorum into five subspecies: *Tropidolaemus w. wagleri* Wagler, 1830 (Thailand, Peninsular Malaysia, Sumatra, Nias, Mentawei Islands, Riau Islands Bangka and Belitung), *T. w. alboviridis* (Philippines: Negros Island), *T. w. celebensis* (Sulawesi, Buton and Sangihe Islands), *T. w. philippensis* (Philippine Islands: Sibutu, Basilan, Jolo, Leyte, Samar, Dinagat, Luzon and Mindanao) and *T. w. schlegelii* Bleeker, 1857 (Borneo, Natuna and Karinata Islands, and the Philippine islands of Palawan and Balabac). This taxonomy was adopted by Aulya (2006). However, it clearly resulted from very early and partial results and was not based on any serious analysis of morphological variation.

During the frame of our investigations on Asian pitvipers, we undertook a thorough analysis of morphological variation of the "*wagleri* complex". First, preliminary results were mentioned in Vogel (2006), who accepted three full species, *T. wagleri*, *T. subannulatus* (Gray, 1842) and *T. philippensis*. Within *T. subannulatus*, Vogel (2006) differentiated four populations. Lastly, Kuch et al. (2007) briefly described as *Tropidolaemus laticinctus* one of these populations from Sulawesi island (already identified in Vogel [2006] as "*celebensis* morph 2"), but merely copied the taxa boundaries suggested by Vogel (2006) and failed to mention some major differences between the taxa that they "recognized" in their paper.

In this first paper, we firstly address the nomenclatural history and ascertain the validity of specific names proposed since Boie (1827). We redefine the general taxonomy of *Tropidolaemus wagleri* sensu lato, based only on morphological characters. In order to stabilize the binomen, we select and describe a neotype for *Tropidolaemus wagleri*. We will not discuss furthermore the validity of *Tropidolaemus huttoni*, although information then not available to David & Vogel (1998), such as a bright red snout in both living specimens, reinforces the distinct specific status of this taxon (Hutton & David, in prep.). This paper is a first step in a general revision of the genus *Tropidolaemus*.

MATERIAL AND METHODS

The present paper is based on 107 preserved specimens examined by us from the entire range of *Tropidolaemus wagleri* sensu lato. We could not examine specimens of the taxon subsequently described as *Tropidolaemus laticinctus*, as specimens deposited in major collections were on loan for several years. We also considered specimens depicted in the literature, and many specimens of the complex alive at the time of writing this paper. Preserved specimens examined are listed under each relevant taxon. Living specimens used for this paper will be deposited in the collections of the MNHN and ZFMK upon their death.

Selection of morphological characters.—We retained standard morphological characters previously used by David & Vogel (1998), Vogel et al. (2004) and David et al. (2006), including morphometrical characters adapted from How et al. (1996). A total of 98 morphological characters or values were recorded for each specimen, but only 52 morphometrical and meristic characters were retained in our analyses, either standing on their own or derived from the raw characters. Others proved to be of no value for this group of pitvipers. Characters retained for this study are listed in Table 1. Not all variables listed in this table proved to be useful to separate at least one population of the *Tropidolaemus wagleri* complex from the others, but all were investigated and used in combinations of characters and/or were used in univariate and multivariate analyses. Special attention was given to the ontogenetic and sexually related variation in coloration and pattern of the head and body. Obviously some populations do have several colour phases during their live span. The colour of the eyes is not a diagnostic character in this first analysis.

Measurements, except body and tail lengths, were taken with a slide-caliper to the nearest 0.1 mm; all measures on body were taken to the nearest millimetre. Ventral scales were counted according to Dowling (1951). The terminal scute is excluded from the number of subcaudals. The numbers of dorsal scale rows are given at one head length behind head, at midbody (i.e. at the level of the ventral plate corresponding to half of the total number of ventrals) and at one head length before vent respectively. Values for symmetric head characters are given in left / right order. The real coloration of body and eyes were observed only on living animals or very freshly preserved specimens.

TABLE 1. 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	HL	Head length
5	SnL	Snout length (from the tip of rostral to a line connecting the anterior eye margins)
6	ED	Eye diameter (vertical)
7	DEL	Distance lower eye margin–edge of the lip
8	D E-nostril	Distance between the anterior eye margin and the nostril
9	D E-pit	Distance between the anterior eye margin and the loreal pit
10	W-In	Width of internasals (means)
11	L-SpOc	Length of supraoculars
12	W-SpOc	Width of supraoculars
13	L-3SL	Length of 3rd supralabial
14	H-3SL	Height of 3rd supralabial
15	H-4SL	Height of 4th supralabial
16	TaL/TL	Ratio tail length/Total length
17	SnL/HL	Ratio snout length/head length
18	HL/SVL	Ratio head length / snout-vent length
19	D E-pit/HL	Ratio distance eye–pit/head length
20	D E-nostril/HL	Ratio distance eye–nostril/head length
21	D E-pit/D E-nostril	Ratio distance eye–pit/distance eye–nostril
22	SnL/ED	Ratio snout length / eye diameter
23	W-In/W-SpOc	Ratio width of internasals/width of supraoculars
24	L-3SL/HL	Ratio length of 3rd supralabial/head length
25	L-3SL/H-3SL	Ratio length of 3rd supralabial / height of 3rd supralabial
26	H-4SL/H-3SL	Ratio height of 4th supralabial / heigth of 3rd supralabial
27	ED/DEL	Ratio: vertical eye diameter/distance eye margin–edge of the lip
28	L-SpOc/W-SpOc	Ratio of the length of supraocular/width of the supraoculars
Scalation		
29	ASR	Dorsal scale rows at neck
30	DSR	Dorsal scale rows at midbody

...... continued

TABLE 1 (continued)

Number	Abbreviation	Character
31	MSR	Dorsal scale rows at midbody
32	VEN	Ventral plates
33	SC	Subcaudal plates
34	SL	Supralabial scales
35	HeSc	Head scales (scales on a longitudinal row between the internasals and the limit of the neck)
36	SnSc	Snout scales (scales on a line between the internasals and a line connecting the anterior margin of eye)
37	Nli	Number of linguals (scales between IL and preventrals, on one side)
38	Cep	Cephalic scales (scales on a line between the middle of supraoculars)
39	K-Tem	Keeling of temporal scales
40	IL	Infralabials
41	KSR	Keeling of dorsal scale rows at midbody
42	C3SL/SubOc	Number of scales between 3rd SL and subocular
43	C4SL/SubOc	Number of scales between 4th SL and subocular
44	C45SL/SubOc	Number of scales between 4th and 5th SL and subocular
45	K-Occ	Keeling of the occipital scales
46	IN-sep	Number of scale(s) between the internasals
47	SC/SpOc	Number of scales directly in contact with supraocular
48	N-SupOC	Number of supraoculars
Pattern		
49	Body colour	Body colour
50	Dor-bands	Colour of dorsal bands
51	COLPOcStr	Colour of postocular streak
52	Col Venter	Colour of the belly

Selection of analytical units. —According to the morphology of specimens and their origin and following the method adopted by Wüster & Thorpe (1992), we divided the general distribution of *Tropidolaemus wagleri* sensu lato into 9 OTUs (Operational taxonomic units), based both on geographical distribution and a preliminary analysis of their coloration and pattern in adult specimens. A preliminary investigation showed morphological homogeneity between members of some of these populations, but constant differences with others. These OTUs are defined as follows: OTU 1 (6 ♂, 21 ♀): Sumatra Island. – OTU 2 (1 ♂, 5 ♀): West-Malaysia and Singapore. – OTU 3 (4 ♀): southern Thailand. – OTU 4 (1 ♀): Belitung Island. – OTU 5 (9 ♂, 15 ♀): Borneo Island, from both West Malaysia and Indonesia. – OTU 6 (2 ♂, 8 ♀): Sulawesi and adjacent islands. – OTU 7 (3 ♂, 22 ♀): Philippines, all islands including Palawan. – OTU 8 (1 ♂): Natuna Island. – OTU 9 (4 ♂, 1 ♀): Philippines (Mindanao Island; for conspicuously, distinctly patterned, blotched specimens).

Analyses of morphological data. —Data were analysed in using both univariate and multivariate analyses. All ratios involving measures of any part of head were considered only in adult specimens in order to cope with ontogenetic variation. On the basis of mean values of TL observed in our sample, we arbitrarily fixed as 300 mm in males and 400 mm in females (TL) the lower size limit to regard examined specimens as adult.

Abbreviations are: *n*: number of specimens. – *x*: mean value. – *s*: standard deviation. – *P*: probability of occurrence of a value as extreme as or more extreme than the observed value. –

Multivariate analyses.—A multivariate ANCOVA (Maxwell & Delaney, 1990; Norusis & SPSS, 1993) was performed to select those quantitative characters that showed significant overall differences between the OTU's. OTU and sex were included as factors and SVL was included as covariate. The relevance of the qualitative characters was determined by means of Chi-square. Subsequent multivariate analyses were restricted to the selected characters.

Growth-stage related characters were adjusted to a common SVL (e.g. Thorpe, 1975, 1983; Turan, 1999) to correct for potential ontogenetic variation between the various samples. Whether a character was related to growth-stage was determined by establishing the correlation with SVL. The following allometric equation was applied: $X_{adj} = X - \beta(SVL - SVL_{mean})$ where X_{adj} is the adjusted value of the morphometric variable; X is the original value; SVL is the snout-vent length; SVL_{mean} is the overall mean snout-vent length; β is the coefficient of the linear regression of X against SVL. The adequacy of the procedure was assessed by testing the significance of the correlation between the adjusted variables and SVL (e.g. Turan, 1999).

A linear PCA (e.g. Cramer, 2003) was carried out to check the homogeneity of the initial OTU's (e.g. Wüster & Thorpe, 1992; Turan, 1999; Wüster et al., 2001). Only quantitative morphological characters were included.

Following validation of the initial OTU's, discriminant analyses were performed. Nonlinear discriminant analysis was used to analyse quantitative and qualitative characters simultaneously. This technique uses optimal scaling (e.g. De Geer, 1988; Shen and Lai, 1998) to quantify the categories of qualitative characters. Thus, characters pertaining to coloration and degree of keeling of the dorsal scales were included. Nonlinear discriminant analysis was carried out with OVERALS (e.g. Meulman et al., 1999; Michailidis & De Leeuw, 1998). Qualitative variables regarding degree of keeling of the dorsal scales were specified as ordinal variables, qualitative variables regarding coloration were specified as single nominal variables and quantitative variables regarding various aspects of morphology were specified as numeric. Linear discriminant analysis (e.g. Cramer, 2003) was used to analyse quantitative characters, which pertained solely to morphology. Both nonlinear and linear discriminant analyses were primarily used as exploratory tools by plotting the resulting object scores to visualize the separation between the OTU's. However, linear discriminant analysis is capable of establishing multivariate significance-levels and was thus also used for this purpose.

All statistical analyses were carried out with the software SPSS (2003; SPSS for Windows. Release 11.5.2.1. Standard Version. SPSS Inc., Chicago).

Museum abbreviations. —BMNH: The Natural History Museum, London, UK. —CAS: California Academy of Sciences, San Francisco, USA. —FMNH: Field Museum of Natural History, Chicago, USA. — MHLCLFE: Muséum d'Histoire Naturelle Henri Lecoq, Clermont-Ferrand, France. - MNHN: Muséum national d'Histoire naturelle, Paris, France. —RMNH: Nationaal Natuurhistorisch Museum (Naturalis), Leiden, The Netherlands. —ZIH: Zoologisches Institut der Universität Heidelberg, Heidelberg, Germany. — ZMA: Zoological Museum, University of Amsterdam, Amsterdam, the Netherlands. —ZMH: Zoologisches Institut und Museum, Universität Hamburg, Hamburg, Germany.

HISTORICAL ANALYSIS

As a prelude to any revision, we consider that the nomenclatural evaluation and definition of all specific names which appeared in the literature is mandatory. *Tropidolaemus wagleri* (Boie, 1827) was one of the first described Asian pitvipers, so it is understandable that such a wide ranging and morphologically variable complex of populations incited ancient authors to name a good number of "new" taxa. Others, such as Boulenger, went into the rightly opposed direction in regarding these new taxa as synonyms. The problem is further intricate by the fact that many taxa were named well before the establishment of rules in zoological taxonomy. The best example is given by the name-bearing types of *Tropidolaemus wagleri* itself, which are discussed below. All names of specific level related to *Tropidolaemus wagleri* sensu lato (but excluding *Tropidolaemus huttoni*) are discussed in chronological order. Only synonyms are considered, not chresonyms.

"*Trigonocephalus wagleri*" Schlegel, 1826

Trigonocephalus wagleri Schlegel, 1826: 239.—Type locality. None mentioned.

Comments. Schlegel credited the specific nomen to H. Boie, most probably on the basis of the unpublished manuscript of this latter author "Erpétologie de Java".

Status. A nomen nudum, as Schlegel cited the specific nomen in the list of species of the genus *Trigonocephalus* and did not provide any description.

"*Cophias wagleri*" Schlegel, 1827

Trigonocephalus wagleri Schlegel, 1827: col. 293. —Type locality. None mentioned.

Comments. Schlegel again credited the specific nomen to H. Boie.

Status. A nomen nudum, as Schlegel cited the specific nomen in the list of species of the genus *Cophias* and did not provide any description.

***Cophias wagleri* Boie, 1827**

Cophias wagleri Boie, 1827: col. 561. —Type locality. Not given. —Types. Two secondary syntypes, both unlocated, can be inferred from the original text, see below.

Comments. F. Boie, who published the notes of his late brother H. Boie, did not provide any description, but based this taxon upon three sources:

(1) "H. Boie *Erp. de Java*". Here F. Boie (1827) referred to the unpublished manuscript of his brother H. Boie (Boie, n.d.). This manuscript does not constitute a publication in the meaning of the International Code of Zoological Nomenclature (ICZN, 1999). Nevertheless, at least two specimens were described in this manuscript (Boie, n.d.). They were described as: "a bright green postorbital streak, body and tail above with black and yellow, black-edged, parallel crossbars, below yellowish-green, sides dotted with green." Although their locality was not indicated by Boie, by all evidence they belong to the western populations (defined above as OTU 1 to OTU 3). This pattern of yellow crossbars separated by dark green of black crossbars with light green or yellow dots is known only in adult females from Thailand, West Malaysia and Sumatra (and adjacent islands). As these specimens appeared in an invalid publication, we do not consider them syntypes.

(2) "*Col. sumatranus* Raffles". For some reason, Boie confused his *Cophias wagleri* with *Coluber sumatranus* Raffles, 1822, a totally different taxon, still valid and now known as *Trimeresurus sumatranus* or *Parias sumatranus* depending on authors' classification of Asian pitvipers (see, for example Malhotra & Thorpe, 2004; Vogel, 2006). Such confusion between these two species occurred as late as Ouwens (1916: Figs. 22 & 22a), as explained in David (2007). Raffles (1822) based his description on a single specimen, which also becomes a secondary syntype of *Tropidolaemus wagleri* (see Dubois & Ohler, 1996).

(3) "Seba T. II tab. 68 fig. 4". Boie here referred to a specimen depicted on a plate of Seba (1735: Pl. 68). Although the drawing is rather fair, the depicted snake is indeed either a juvenile or a male of *Tropidolaemus wagleri* sensu lato, and definitely not a *Coluber sumatranus* Raffles, 1822. His banded pattern suggests a juvenile member of the genus *Tropidolaemus*, although it is unclear whether it belongs to the western populations of *T. wagleri*. This specimen is regarded as the second syntype of *Cophias wagleri* Boie, 1827.

As a consequence, we here designate the specimen depicted in Seba (1735: Fig. 68), the sole correctly identified valid syntype of *Cophias wagleri*, as the lectotype of *Cophias wagleri* Boie, 1827. This specimen being now untraced, we describe below a neotype of *Cophias wagleri* Boie, 1827.

Status. A valid taxon, as *Tropidolaemus wagleri*. Indeed, although Boie (1827) did not provide any description, the binomen *Cophias wagleri* Boie, 1827 is valid on the basis of Art. 12.1 and 12.2 of the *Code*, which allow a description by "indication" for names published before 1931. Art. 12.2.1 states that a bibliographic reference to a previously published description or definition (...) constitutes such an indication. Boie's (1827) description should hence considered valid. As pointed in McDiarmid et al. (1999), this is due only to the existence of the indication referring to Seba's plate. This fact was overlooked by David & Vogel (1996) who erroneously credited the first valid description to Wagler (1830), also on the basis of an indication. Wagler gave a short description of the genus that included the single species *Cophias wagleri* H. Boie, 1827. Of course, all these authors who credited the authorship of the taxon to Schlegel (1837) (for example Hoge & Romano Hoge, 1981; Golay et al., 1993) or to Boie *in* Schlegel (1837) (Leviton, 1964), also overlooked the validity of *Cophias wagleri* Boie, 1827.

Description of Neotype. Schlegel (1837: 542) had at hand two adult and six juvenile specimens, all from Sumatra. Possibly the adults were those seen by Boie and described in his unpublished manuscript. Golay et al. (1993) stated that six (or seven) specimens deposited in the RMNH (Leyden) were syntypes of *Trigonocephalus wagleri* Schlegel, 1837. This combination is merely a chresonym of *Cophias wagleri* Boie, 1827, so these specimens are by no means syntypes of *Cophias wagleri*. Furthermore, the two adults described in Boie's manuscript cannot be regarded as syntypes, as the source in which they were cited does not constitute a publication in the sense of the *Code*. Lastly, the citation of specimens from Sumatra by Schlegel (1837) cannot be regarded as a type locality restriction, in contrast to the opinion of some authors (see, for example, Orlov et al., 2002).

The sole valid syntype is the specimen depicted on Seba's plate. As the whereabouts of this specimen are unknown, in order to stabilize the specific nomen *wagleri* and in agreement with Dubois & Ohler (1996), we here design a neotype for *Cophias wagleri* Boie, 1827. As, by all available evidence, (1) possibly Seba (1735) but definitely Boie (n.d.) had at hand specimens from the western populations, and (2) the subspecific nomen *wagleri* has ever been attached to western populations, for purpose of stability, we select and describe a neotype from the western populations, as follows:

Neotype (Figs. 4–7): MNHN 1879.0708 (ex MNHN 5784), an adult female from "Deli: rivière de Bedagneh (Est de Sumatra)", now Bedagai River (about 3°30'N, 99°13'E), Sumatera Barat Province, Sumatra, Indonesia. Collected by Mr. Rochet.

Body moderately stout, laterally compressed; head distinctly triangular, wide at its base, clearly distinct from the neck (at least twice as broad as the neck), thick when seen from the side, average, 1.2 times as long as wide and amounting for 6.5 % of SVL; snout obliquely truncated when seen from the side, with a distinct canthus rostralis, rounded seen from above, rather long, amounting for 25.6 % of HL or 2.3 times as long as diameter of eye; nostrils small, piercing in the middle of the nasal; eye small, amounting for 0.7 time of the distance eye–lip; tail average, tapering and strongly prehensile.

SVL: 591 mm; TaL: 112 mm; TL: 703 mm; HL: 38.7 mm; ratio TaL/TL: 0.159.

VEN: 137 (+ 2 preventrals); SC: 51, paired, plus one terminal scale; anal shield entire.

DSR: 27 – 25 – 21 scales, rhomboid, strongly keeled.

Rostral visible from above, about 1.2 times broader than high, triangular; nasals subrectangular, entire; no nasal pore; 1 internasal on each side, elongated, narrow, slightly bent, 2 times as long as wide; internasals in contact; 5 / 5 canthal scales, not larger than adjacent snout scales, bordering the *canthus rostralis*; 1 elongate triangular loreal scale between upper preocular and the nasal; 2 elongate upper preoculars above the loreal pit; lower preocular forming the lower margin of loreal pit; 2 / 2 small postoculars; 1 small, narrow, flat supraocular on each side, 2.7 times as long as wide on both sides, 0.5 time as wide as the internasals, irregularly bordered on their inner margins by the upper head scales; 7 slightly enlarged scales on upper snout surface on a line between the scales separating the internasals and a line connecting the anterior margins of eyes, strongly keeled, imbricate, rhomboid; 14 cephalic scales on a line between the supraoculars, small, strongly keeled, flat and imbricate; occipital scales not larger than cephalic scales, strongly keeled; temporal scales small, irregular in size, in 3 rows, all strongly keeled; 2 / 1 small, thin, elongated, suboculars; 10 / 10 SL; 1st SL rather short, entirely separated from nasal; 2nd SL short, not bordering the anterior margin of the loreal pit, topped by a prefoveal scale which borders the pit and is separated from the nasal by 4 / 4 minute scales; 3rd SL longest and highest, 1.5 / 1.6 times as long as high, separated from the subocular by 1 / 1 small scale; 4th SL 1.0 / 0.9 times as long as high, 0.7 time as high as 3rd SL, separated from the subocular by 2 scales on each side; 5th SL smaller than 4th one, separated from subocular by 2 scale rows of similar size; 13 / 12 IL, showing some keeling; scales of the 1st pair longitudinally in contact, first 3 or 4 pairs in contact with anterior chin shields; 8 / 8 rows of strongly keeled gular scales.

In preservative, this specimen shows the typical complex "speckled" coloration of females of the western population. Body deep black, with 26 irregular bright yellow crossbars, on the body 2 or 3 scale wide, separated by 5-7 scales; many scales of black areas with a yellow or yellowish green centre, this colour becoming broader and more green on the lower side of the sides; tail also deep black, irregularly marked with very irregular bright yellow blotches, the first ones forming incomplete crossbands, the others reduced to elongated blotches; tip of tail black.

The dorsal head surface is deep black with small irregular yellow blotches; a wide, bright yellow postocular streak, narrowly edged below with white, extending from eye to behind the corner of the mouth in widening posteriorly; lower half of rostral and supralabials ochre yellow, narrowly edged with black; area between the posterior supralabials and the postocular streak deep black, the lower half of this area speckled with pale yellowish green, the upper part more or less entirely black, producing a distinct black stripe bordering below the postocular streak.

Venter yellow, the posterior edge of ventrals black; chin and throat yellow, the infralabials narrowly edged with black; some greenish-yellow, black edged blotches on the chin near the posterior infralabials.

Trimesurus maculatus Gray, 1842

Trimesurus maculatus Gray, 1842: 48. —Type locality. "Singapore". - Syntypes. Not indicated. Lectotype (implicitly designated by Boulenger, 1896: 563): BMNH 1946.1.17.69, from "Singapore". Coll. by General Hardwicke.

Gray recognized a "Var. 1", unnamed but stated as inhabiting the Philippine Islands. Such specimens mentioned as variety are not regarded as syntypes according to the Code.

Comments. The description of Gray is confusing. This author indeed described this new species from specimen(s) from Singapore, but also recognized a "Variety 1" inhabiting the Philippine Islands. This variety has no specific name, and has hence no nomenclatural status. *Trimesurus maculatus* Gray, 1842 was synonymised with *Trimeresurus wagleri* by Günther (1864: 388).

Status. A subjective synonym of *Tropidolaemus wagleri* (Boie, 1827).

Trimesurus subannulatus Gray, 1842

Trimesurus subannulatus Gray, 1842: 48. —Type locality. "The Philippines". - Syntypes. BMNH 1946.1.19.32-33 (female and young). Coll. by H. Cuming.

Comments. *Trimesurus subannulatus* Gray, 1842 was synonymised with *Trimeresurus wagleri* by Günther (1864: 388). It is however the oldest available name for populations of the Philippines and conspecific populations.

Status. A valid name; recognized here as *Tropidolaemus subannulatus*, the valid specific name of Philippine populations (at the possible exception of Negros, and excluding those referred to *Tropidolaemus philippensis*) and populations of Borneo, Sulawesi and adjacent islands (excepted the form referred to *Tropidolaemus laticinctus* Kuch, Gumprecht & Melaun, 2007) if these latter ones proved to be conspecific with Philippine populations. The specific taxon *subannulatus* is the oldest available name for the oriental clade of the *Tropidolaemus wagleri* complex.

Trimesurus philippensis Gray, 1842

Trimesurus philippensis Gray, 1842: 48. —Type locality. "The Philippines". —Syntypes. BMNH 1946.1.17.67 (female). Coll. by H. Cuming.

Comments. *Trimeresurus philippensis* (Gray, 1842) was synonymised with *Lachesis wagleri* by Boulenger (1896: 562). It was regarded as valid by Taylor (1922), Maslin (1942) as *Trimeresurus philippinensis* and David & Ineich (1999), but placed in the synonymy of *Tropidolaemus wagleri* by Leviton (1964). It is here regarded as a valid species.

Peters (1861: 691) cited this species as *Tropidolaemus philippinensis* Gray, an unjustified emendation.

Status. Recognized here as a distinct, valid species, *Tropidolaemus philippensis*.

Tropidolaemus hombronii Jacquinot & Guichenot, 1848

Tropidolaemus hombronii Jacquinot & Guichenot, 1848: Pl. 2 (Reptiles Ophidiens): Fig. 2; Text (dated 1853): 23. —Type locality. "Samboangan, île Mindanao (archipel des Philippines)", now Zamboanga, Mindanao Island, Philippines. —Holotype. MNHN 4064.

Comments. Plate 2 of the section "Reptiles Ophidiens" is dated of 1848, whereas the volume of the text did not appear before 1853. This taxon was synonymised with *Lachesis wagleri* by Boulenger (1896: 562).

Status. A subjective synonym of *Tropidolaemus philippensis* (Gray, 1842).

Trigonocephalus wagleri var. *celebensis* Gray, 1849

Trigonocephalus wagleri, var. *celebensis* Gray, 1849: 9. Name appearing in the synonymy of *Trimesurus subannulatus* Gray, 1842, as a name provided or written on a label by the Leyden Museum. —Type locality. "Celebes", now Sulawesi. —Holotype. BMNH 49.3.2.38 (female).

Comments. Gray (1849) cited this taxon in the list of available material of *Trimesurus subannulatus* Gray, 1842, stating that the relevant specimen or name, or both originating from the Leyden Museum. Was this binomen regarded by Gray as a valid subspecies or a synonym of *Trimeresurus subannulatus*? Both interpretations are possible, but the sole fact that Gray (1849) cited this taxon under the genus *Trigonocephalus*, and not under the genus *Trimesurus*, makes clear that Gray merely copied the name as received from Leyden and regarded it at once as a synonym of *Trimesurus subannulatus*.

The combination *Trigonocephalus wagleri*, var. *celebensis* was mentioned for specimen "d.", as the name attached to this specimen that was sent to the collections of the British Museum of Natural History by the Museum of Leyden. Whether the binomen was written on the label or on any other document is unclear to us. The catalogue of the BMNH includes only one specimen from Sulawesi donated by the Leyden Museum, which should be the specimen cited by Gray (1849).

According to Art. 11.6.1 of the Code, a name described as a junior synonym should be considered to be available if it was subsequently but before 1961 treated as an available name and adopted as the name of a taxon. This was the case in, at least, Peters (1872b: 584), who cited *Tropidolaemus subannulatus* Gray var. *celebensis* and thus made the name available.

Status. Taxon here regarded as a subjective synonym of *Tropidolaemus subannulatus* (Gray, 1842), but available, as *Tropidolaemus* (*subannulatus*) *celebensis*, for populations inhabiting Sulawesi which would prove to be distinct from both *Tropidolaemus subannulatus* and *Tropidolaemus laticinctus*.

"*Trigonocephalus wagleri* var. *sumatrenis* Gray, 1849"

Trigonocephalus wagleri, var. *Sumatrenis* Gray, 1849: 9. Name appearing in the synonymy of *Trimesurus subannulatus* Gray, 1842, as a name provided or written on a label by the Leyden Museum. —Type locality. Sumatra. —Holotype. BMNH 1.2.6.e (female).

Comments. As for *Trigonocephalus wagleri*, var. *celebensis*, Gray (1849) cited this taxon in the list of available material of *Trimesurus subannulatus* Gray, 1842. It thus should also be considered a synonym of *Trimesurus subannulatus*.

Gray used the spelling "*sumatrenis*", and not *sumatrensis* as cited by McDiarmid et al. (1999).

The combination *Trigonocephalus wagleri*, var. *Sumatrenis* was mentioned for specimen "e.". The catalogue of the BMNH includes only one specimen from Sumatra donated by the Leyden Museum, which should be the specimen cited by Gray (1849).

However, we could not locate any instance in which this combination was regarded as valid before 1961. Therefore, according to Art. 11.6.1 of the Code, this name, although resulting from a valid description, was not made available. According to Dubois (2000), it is here considered to be an anoplonym.

Status. An unavailable name; subjective synonym of *Tropidolaemus wagleri* (Boie, 1827).

"*Tropidolaemus schlegelii* Bleeker, 1857"

Tropidolaemus schlegelii Bleeker, 1857: 6. No description. —Type locality. "Sinkawang", now Singkawang, Kalimantan Barat (West Kalimantan), Indonesia. —Holotype. BMNH 63.12.4.128. Coll. by Dr. Bleeker.

Comments. This combination appeared in a list of snakes known from Borneo. It was mentioned also by Bleeker (1859: 436, 440–441), who synonymised it with *Trimesurus subannulatus* Gray, 1842. Günther (1864: 389) synonymised *Tropidolaemus schlegelii* Bleeker, 1857 with *Trimeresurus wagleri* Schlegel.

Status. A nomen nudum; subjective synonym of *Tropidolaemus subannulatus* (Gray, 1842).

***Trimeresurus subannulatus immaculatus* Peters, 1872**

Trimeresurus subannulatus Gray var. *immaculatus* Peters, 1872a: 42.—Type locality. Not explicitly given, "Sarawack auf Borneo", by implication based on the title of the paper, now State of Sarawak, Borneo, Federation of Malaysia. —Syntypes in Genova Museum.

Comments. This taxon was synonymised with *Lachesis wagleri* by Boulenger (1896: 562).

Status. Taxon here regarded as a subjective synonym of *Tropidolaemus subannulatus* (Gray, 1842), but available, as *Tropidolaemus* (*subannulatus*) *immaculatus*, for any population inhabiting Borneo which would prove to be potentially distinct from *Tropidolaemus subannulatus*.

***Trimeresurus wagleri alboviridis* Taylor, 1917**

Trimeresurus wagleri alboviridis Taylor, 1917: 366. - Type locality. "Isabela, Occidental Negros", now Isabela, Negros Occidental Province, Negros Island, Philippines. - Holotype. CM R2433, Coll. by E. H. Taylor, September 12, 1915.

Comments. This taxon was synonymised with *Trimeresurus wagleri* by Leviton (1964).

Status. Taxon here regarded as a subjective synonym of *Tropidolaemus subannulatus* (Gray, 1842), but available, as *Tropidolaemus (subannulatus) alboviridis* for a potentially distinct population inhabiting Negros Island and adjacent islands which would prove to be distinct from *Tropidolaemus subannulatus*.

***Tropidolaemus laticinctus* Kuch, Gumprecht & Melaun, 2007**

Tropidolaemus laticinctus Kuch, Gumprecht & Melaun, 2007: 3, Figs. 1-6, 7A–B, 8A–B, 9–10, 11A–B. —Type locality. "Between L. Posso and Tomini Bay, Celebes", now between Lake Poso and Tomini Bay, Province of Sulawesi Tengah, Indonesia.—Holotype. BMNH 96.12.9.80 (subadult or adult male). Coll. by P. & F. Sarasin.

Comments. This taxon, briefly described while the present paper was in preparation, was named to accommodate populations identified either as *Lachesis wagleri* variety E by Boulenger (1896), *Tropidolaemus wagleri*, "red form" by de Lang & Vogel (2005), or *Tropidolaemus subannulatus* (*celebensis* morph 2) by Vogel (2006).

Status. A valid species, which includes populations from Sulawesi not conspecific with *Tropidolaemus subannulatus*.

Besides these specific names, several chresonyms resulting from misidentifications were applied to members of the *Tropidolaemus wagleri* complex:

Trimesurus sumatranus (nec *Coluber sumatranus* Raffles, 1822, now *Trimeresurus sumatranus* or *Parias sumatranus*, a valid species): Gray (1842: 48; 1849: 10).

Trigonocephalus formosus (nec *Trigonocephalus formosus* Müller & Schlegel, 1842; see Leviton [1964: 267]): Gray (1849: 10).

To summarize, the available specific epithets currently available are as follows:

- ***Tropidolaemus wagleri*** **(Boie, 1827)**: valid combination for western populations, namely Thailand, West Malaysia, Sumatra, Bangka and Mentawei Archipelago.
- ***Tropidolaemus subannulatus*** **(Gray, 1842)**: valid combination for populations of the Philippine Islands and any, or all of the eastern populations which might be conspecific with Philippine populations, at the exception of *Tropidolaemus philippensis* and *Tropidolaemus laticinctus* Kuch, Gumprecht and Melaun, 2007.
- ***Tropidolaemus philippensis*** **(Gray, 1842)**: valid combination for some populations of southern and western Mindanao Island, Philippines.
- ***Tropidolaemus celebensis*** **(Gray, 1849)**: available name for any population inhabiting Sulawesi which would prove to be distinct from *Tropidolaemus subannulatus* as defined here and from *Tropidolaemus laticinctus*.
- ***Tropidolaemus immaculatus*** **(Peters, 1872)**: available name for any population inhabiting Borneo which would prove to be distinct from *Tropidolaemus subannulatus* as defined here.
- ***Tropidolaemus alboviridis*** **(Taylor, 1917)**: available name for any population inhabiting Negros and adjacent islands, which would prove to be distinct from *Tropidolaemus subannulatus* as defined here.
- ***Tropidolaemus laticinctus*** **Kuch, Gumprecht & Melaun, 2007**: valid combination for some populations of Sulawesi, not conspecific with *Tropidolaemus subannulatus* as defined here.

The splitting of *Tropidolaemus wagleri* into five subspecies proposed by Iskandar & Collijn (2001) was both premature and unsupported, and partly based on unavailable names. The taxonomy of the *Tropidolaemus wagleri* complex is now addressed.

TAXONOMIC RESULTS

Multivariate ANCOVA demonstrated the existence of highly significant overall differences between OTU's ($p<0.0000001$). Characters exhibiting significant overall differences between OTU's were selected for further multivariate analyses. Growth stage related characters were adjusted to a common SVL of 458 mm. In PCA, the maximum number of characters was included, thus eliminating specimens with many missing values. A plot of the object scores corresponding to the first two principal components is shown in Figure 1. A strong sexual dimorphism is demonstrated but phenetic subclusters suggesting taxonomic heterogeneity of the initial

OTU's are not in evidence. Noticeable is the strong separation of OTU 9 which overlaps geographically with OTU 7. This result underlines the usefulness of PCA as a means to check the homogeneity of initial OTU's.

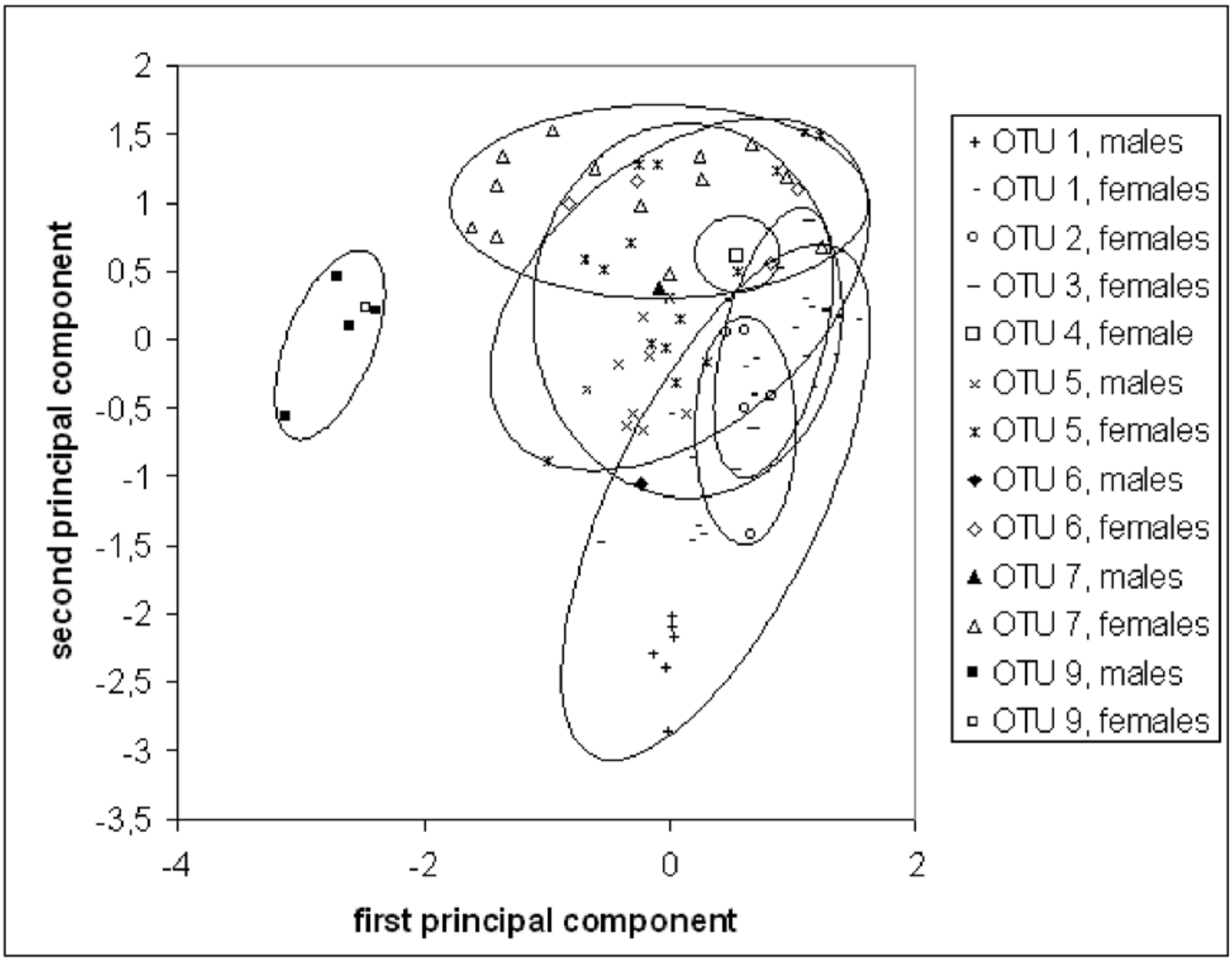

FIGURE 1. Ordination of the OTU's along the first two principal components based on PCA of quantitative morphological characters.

In nonlinear discriminant analysis, variables with many missing values were excluded in order to maximize the number of specimens in the analysis. Each OTU was included as separate *a priori* group. A plot of the object scores corresponding to the first two canonical variates is shown in Figure 2 and correlations between characters and the first two canonical variates are given in Table 2. The plot demonstrates the existence of three clearly defined clusters of the original OTU's, which are grouped into three distinct, higher-order OTUs (see Wüster and Thorpe, 1992), named here as OTU I to OTU III. OTU I comprises the populations of Thailand, West Malaysia + Singapore, Sumatra and Natuna Island. The second OTU comprises the populations of Borneo, Belitung, Sulawesi and the Philippines (OTU II). Lastly, the third OTU consists only of the population occurring in southern Mindanao, Philippines, composed of conspicuously distinctly patterned specimens (OTU III).

Subsequently, a linear discriminant analysis was performed. The three clusters, defined on the basis of figure 2, were used as *a priori* groups. The maximum number of quantitative morphological characters was included, thus eliminating specimens with many missing values. A plot of the object scores corresponding to the first two canonical variates is shown in Figure 3 and correlations between characters and the first two canonical variates are given in Table 3. Both canonical variates were highly significant based on Wilk's lambda ($P<0.0000001$).

TABLE 2. Correlations between characters and the first two canonical variates (I).

Characters	Correlation with first canonical variate	Correlation with second canonical variate
Body colour	0.44	0.83
Dor-bands	0.81	-0.42
COLPOcStr	-0.14	0.44
Col Venter	0.54	-0.34
K-Occ	-0.13	-0.55
KSR	-0.42	-0.43
Ven	-0.30	-0.30
Sc	-0.46	-0.28
IN-sep	0.91	-0.20
Sn-SC	-0.44	-0.37
TaL	-0.28	-0.17
MSR	-0.39	-0.49
DSR	-0.30	-0.43
Σ SL	0.12	-0.60
CEP	-0.58	-0.38

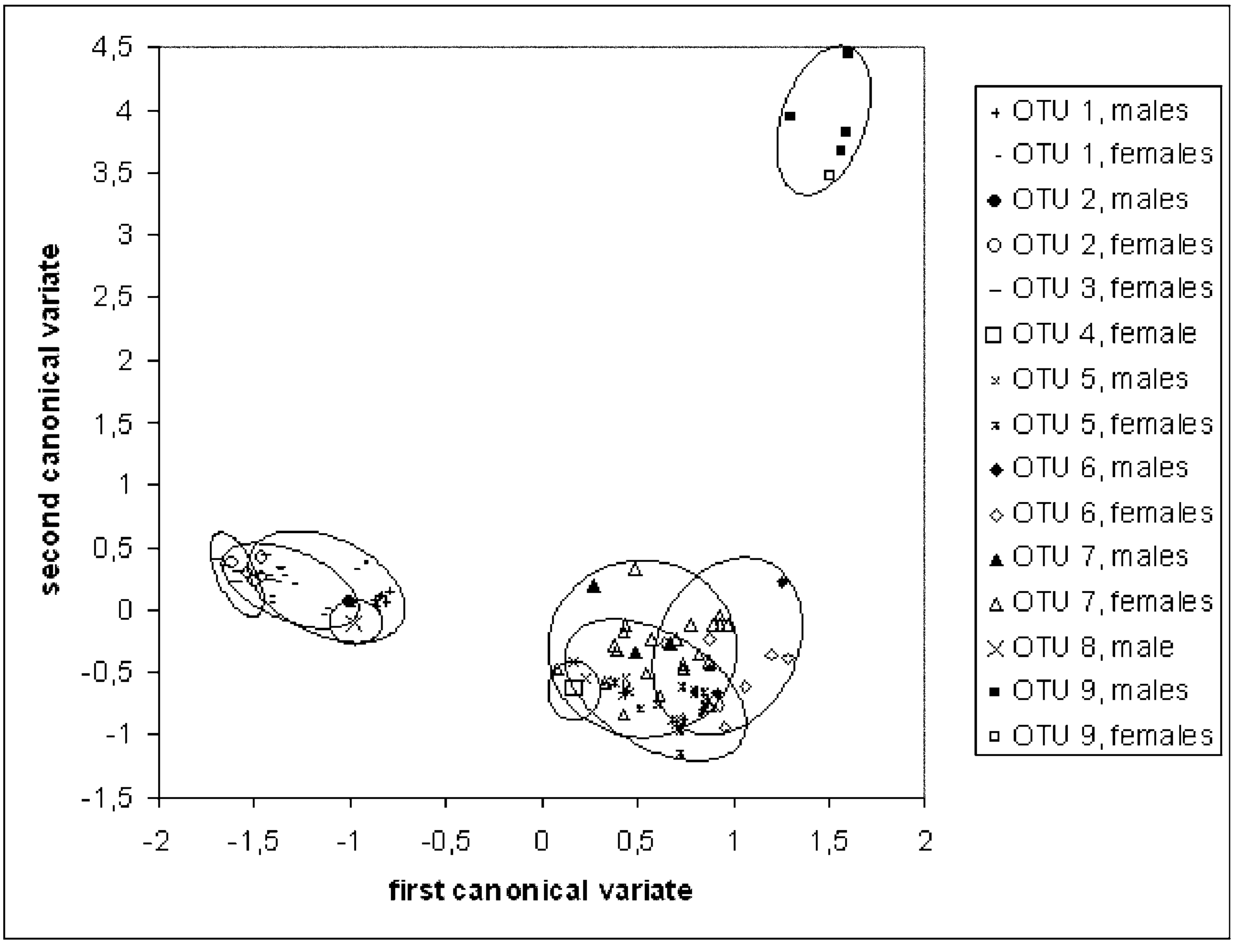

FIGURE 2. Ordination of the OTU's along the first two canonical variates based on nonlinear discriminant analysis of morphological and coloration characters.

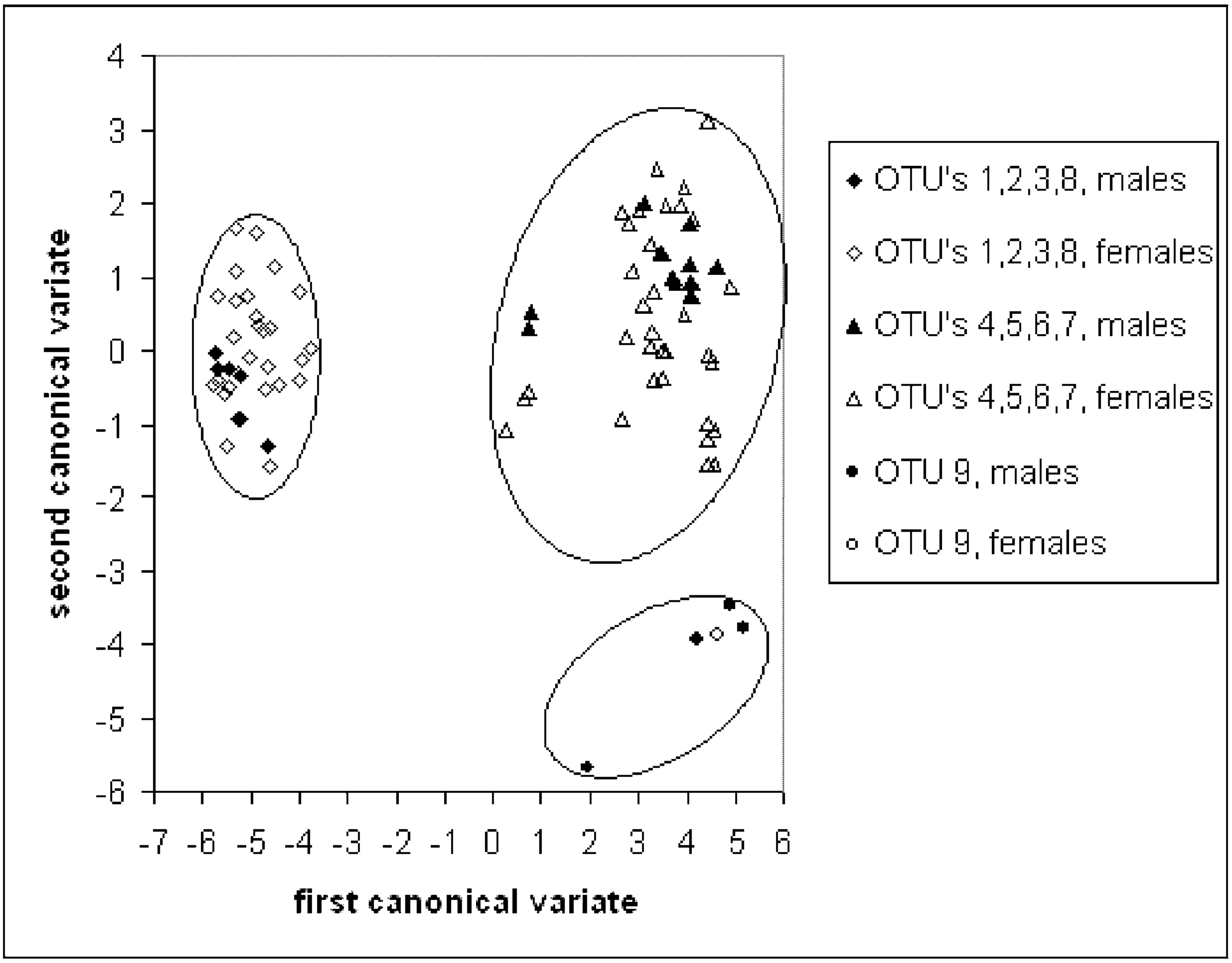

FIGURE 3. Ordination of the three clusters along the first two canonical variates based on linear discriminant analysis of morphological characters.

TABLE 3. Correlations between each character and the first two canonical variates (II).

Characters	Correlation with first canonical variate	Correlation with second canonical variate
IN-sep	0.83	0.22
CEP	-0.21	0.55
ASR	0.01	0.52
MSR	-0.15	0.54
He-SC	-0.08	0.54
DSR	-0.14	0.52
NLI	-0.07	0.57
W-SpOc	0.03	-0.37
Σ IL	-0.12	0.51
C3SL/SubOc	0.08	0.51
Σ SL	0.04	0.51
Sn-SC	-0.10	0.49
C4SL/SubOc	-0.04	0.36
Ven	-0.08	0.35

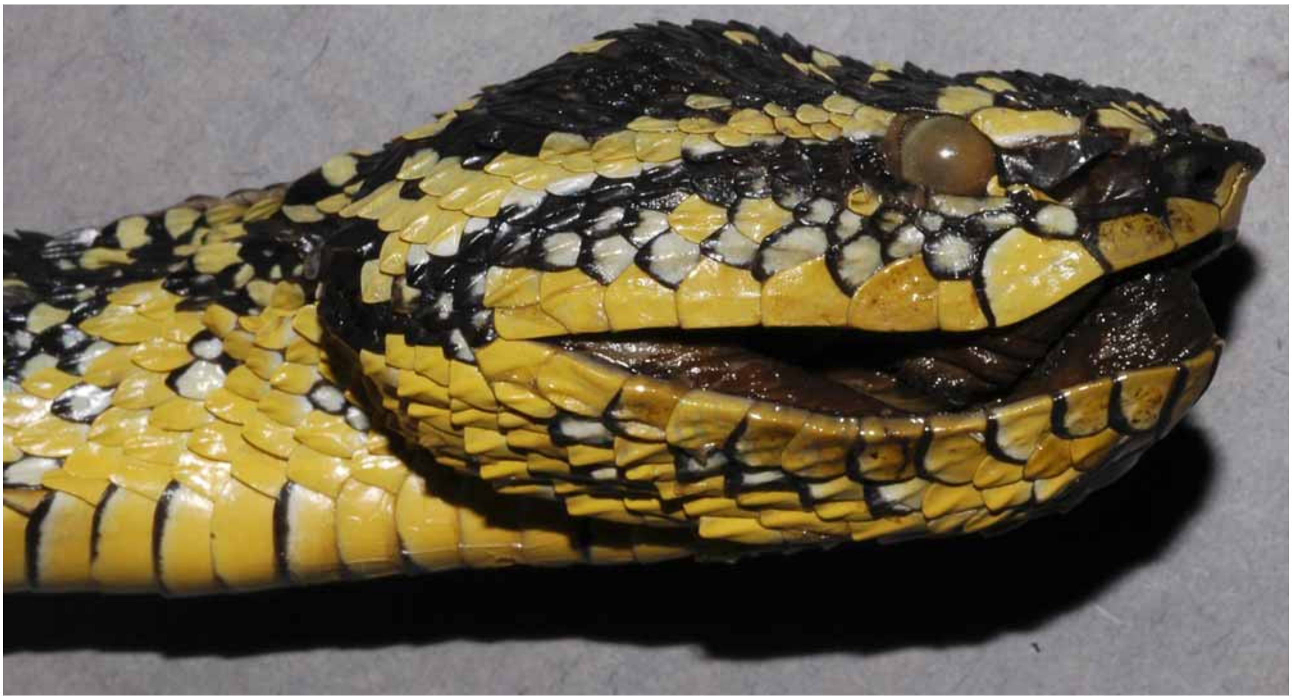

FIGURE 4. Neotype of *Tropidolaemus wagleri* (MNHN 5784). Lateral view of the head, right side. Photograph by Gernot Vogel.

FIGURE 5. Neotype of *Tropidolaemus wagleri* (MNHN 5784). Lateral view of the head, left side. Photograph by Gernot Vogel.

FIGURE 6. Neotype of *Tropidolaemus wagleri* (MNHN 5784). Dorsal view of the head. Photograph by Gernot Vogel.

FIGURE 7. Neotype of *Tropidolaemus wagleri* (MNHN 5784). General view. Photograph by Gernot Vogel.

On the basis of our results, we consider these three OTUs as three different taxa deserving a specific level according to the Phylogenetic Species Concept (PSC) (see Vogel et al., 2004, and David et al. (2006) for the discussion and a summary of references on this concept). All three OTUs defined here are diagnosable by the combination of a limited number of morphological characters. This falls into the basic definition of the PSC.

For these three species or complex, the following names are available:

OTU I: *Tropidolaemus wagleri* (Boie, 1827)
OTU II: *Tropidolaemus subannulatus* (Gray, 1842)
OTU III: *Tropidolaemus philippensis* (Gray, 1842)
OTU II, recognized here as a species, will probably be further split into other taxa in a forthcoming paper based both on morphological and molecular analyses. We regard it as a complex of taxa, of which all of them will differ from T. *wagleri* and *T. philippensis* at the species level. For the sake of convenience, we merely name it in this paper as *Tropidolaemus subannulatus*, the first available name.

Tropidolaemus wagleri **(Boie, 1827)**
(Figs. 8–11)

Diagnosis.—A species of the genus *Tropidolaemus*, characterized by (1) internasals always in contact; (2) a strong ontogenetic variation of the background body colour: black (never green) in adult females, whereas males and juveniles retain a vividly green background colour; (3) a strong ontogenetic variation of the pattern: yellow crossbands around the body in adult females, white spots in adult and juvenile males, white crossbars in juvenile females; (4) a black postocular stripe in adult females and a white and red one in males and juveniles of both sexes; (5) a banded belly in adult females and a uniform belly in males and juveniles; (6) 21–23 DSR at midbody in males and 23–27 in females, usually feebly keeled in males and distinctly keeled in females; (7) 143–152 VEN in males and 134–147 VEN in females; (8) 50–55 SC in males and 45–54 in females. Other characters appear in the Description below.

FIGURE 8. *Tropidolaemus wagleri*. Living adult female from Jambi Province, Sumatra, Indonesia. Photograph by Gernot Vogel.

FIGURE 9. *Tropidolaemus wagleri*. Living adult female from Pahang, West-Malaysia. Photograph by Dick Visser.

Description and variation.—The maximal total length among our sample is 920 mm (SVL 770 mm, TaL 150 mm) for a female from Thailand (MNHN 1996.0291). Our largest male is 522 mm long (SVL 435 mm, TaL 87 mm; BMNH 95.5.1.56; Natuna Islands).

Body laterally compressed, slender in males, thick and stout in females. Head strongly triangular, wide at its base, clearly distinct from the neck (at least twice as broad as the neck), average in length, amounting for 6.1–7.6% of SVL (x = 7.0 %) in males, 5.6–7.8% of SVL (x = 6.9 %) in females, wide at its base, a bit flattened in males, very thick in females when seen from the side. Snout obliquely truncated when seen from the side, with a distinct canthus rostralis, rather massive, rounded when seen from above, amounting for 25–30 % (x = 27 %) of HL in males and 21–30 % (x = 25 %) of HL in females, or 1.4–2.0 (x = 1.6) times as long as diameter of eye in males and 1.4–3.2 (x = 2.2) in females. Nostrils small, piercing in the middle of the nasal. Eye small, amounting for 0.6–1.6 (x = 1.0) times in males and 0.6–1.5 (x = 0.8) times in females of the distance eye–lip. Tail tapering progressively and prehensile.

Ratio TaL/TL: 0.139–0.196, with a strong sexual dimorphism (see below).

This species exhibits quite an unusual ontogenetic variation in the ratio TaL/TL, a character that we had not observed in any species of the other pitvipers. If we consider males and females with a SVL below 250 mm and above 300 mm respectively, we obtain the values given in Table 4.

TABLE 4. Ontogenetic variation in ratio TaL/TL in Tropidolaemus wagleri.

SVL Ratio TaL/TL	Males	Females
< 250 mm	0.179-0.196	0.176-0.186
> 300 mm	0.167	0.139-0.163

FIGURE 10. *Tropidolaemus wagleri*. Living adult male from South Thailand. Photograph by Gernot Vogel.

DSR: (21) 23-27 – 21-25 (27 in 1 specimen) – 17-21, weekly keeled or smooth in males, more or less strongly keeled in females.

VEN: 134–152 (plus 1–2 preventrals); SC: 45–55, all paired. Anal shield entire.

Rostral visible from above, about 1.2–1.3 times broader than high, triangular; nasals subrectangular, entire; 1 (rarely 2, in only 3/38 specimens) internasals, elongated, narrow, slightly bent, about 2 times as long as wide; internasals in contact in all examined specimens; on each side, 4-5 canthal scales, not or barely larger than adjacent snout scales, bordering the *canthus rostralis*; 1 elongate triangular loreal scale between upper preocular and the nasal; 2 elongate upper preoculars above the loreal pit; lower preocular forming the lower margin of loreal pit; 2 (rarely 3, in 2/76 occurrences)) postoculars; 1 (rarely 2, in only 2/76 occurrences) small, narrow, flat supraocular on each side, 2.0–3.2 (x = 2.4) times as long as wide, 0.4–0.7 (x = 0.6) times as wide as the internasals, irregularly bordered on their inner margins by the upper head scales; 5–9 (x = 6.8, s = 0.9) slightly enlarged scales on upper snout surface on a line between the scales separating the internasals and a line connecting the anterior margins of eyes, rhomboid, strongly keeled and imbricate; 12–17 (x = 13.8; s =

1.5) cephalic scales between the middle of the supraoculars, small, strongly keeled, flat and imbricate; occipital scales not larger than cephalic scales, strongly keeled; temporal scales small, irregular in size, in 3 rows, all strongly keeled; 1 or 2 small, thin, elongated, suboculars; 8–11 SL (x = 9.4; s = 0.5) on each side, total number 16–21 (x = 18.9; s = 1.1); 1st SL rather short, entirely separated from nasal; 2nd SL short, not bordering the anterior margin of the loreal pit, topped by a prefoveal scale which borders the pit and is separated from the nasal by 2–4 minute scales; 3rd SL longest and usually highest, 1.2–1.9 (x = 1.65; s = 0.20) times as long as high, either in contact (20 / 76 occurrences) with the subocular(s), or usually separated by 1 (54 / 76 occurrences) or 2 (2/76) small scales(s), with a sexual dimorphism; 4th SL nearly as long as high, 0.7–1.1 (x = 0.9; s = 0.1) times as high as 3rd SL, either in contact (7 / 76 occurrences, all males) with the subocular(s), or separated by 1 (23 / 76 occurrences), 2 (45 / 76) or 3 (1 / 76) small scales(s); 10–13 IL (x = 11.4; s = 1.0) on each side, total number 20–28 (x = 23.1; s = 1.7), strongly keeled; scales of the 1st pair longitudinally in contact, first four pairs in contact with anterior chin shields; 7–10 rows of strongly keeled gular scales.

In life and in preservative, this species shows both strong sexual and ontogenetic dimorphisms.

FIGURE 11. Holotype of *Trimesurus maculatus* (BMNH 1.2.5a = BMNH 1946.1.17.69). Adult male, Singapore. General view. Photograph by Gernot Vogel.

Adult females: they display the typical and complex “speckled” black and yellow coloration. Body deep glossy black, with 25-30 irregular bright yellow vertical crossbars, 2 or 3 scale wide, separated by 5-7 scales; many scales of the black areas with yellow or yellowish green centre, this colour becoming broader and more green on the lower side of the sides; tail also deep black, irregularly marked with very irregular bright yellow blotches, the first ones forming incomplete crossbands, the others reduced to elongated blotches; tip of tail entirely black.

The dorsal head surface is deep black with small irregular yellow blotches; a wide, bright yellow postocular streak, narrowly edged below with white, extending from eye to behind the corner of the mouth in widening posteriorly; lower half of rostral and supralabials ochre yellow, narrowly edged with black; area between the posterior supralabials and the postocular streak deep black, the lower half of this area speckled with pale yellowish green, the upper part more or less entirely black, producing a distinct black stripe bordering below the postocular streak.

Venter yellow, the posterior edge of ventrals black; chin and throat yellow, the infralabials narrowly edged with black giving dark crossbands; some greenish-yellow, black edged blotches on the chin near the posterior infralabials.

Adult and juvenile males: body bright or deep green, lateral a bit lighter, with small dorsolateral dots, anterior red, posterior white. These continue to the tail, tip of the tail mottled with brown. A loreal streak running from the nasal to the ankle of the mouth, ventrally red and dorsally white coloured. Belly and underside of the head light, uniform.

Juvenile females: as in males, but the white (cream or pink in life) and red rounded, dorsolateral, spots are replaced by vertical crossbars of the same colour, reaching about the limit of the upper third of the sides.

Sexual dimorphism.—It is clearly marked in the total length, in the ratio TaL/TL, the pattern, the keeling of the dorsal rows and in other several other characters as listed below. Several scale values are higher for females probably due to their larger size.

The most important characters are as follows:

(1) Difference in the ratio TaL/TL:
0.157–0.196 (x = 0.183; s = 0.010) in males, vs. 0.139–0.178 (x = 0.157; s = 0.011) in females.

(2) Differences in the mean number of ventrals:
143–152 (x = 146.9; s = 2.9) in males vs. 134-147 (x = 139.5; s = 3.2) in females.

(3) Differences in the number of number of scale-rows at midbody:
21–23 (x = 22.3; s = 1.0) in males vs. 23 – 27 (x = 24.9; s = 0.6) in females.

(4) Differences in the total number of SL:
16–18 (x = 16.7; s = 1.2) in males vs. 17–20 (x = 18.9; s = 1.1) in females.

(5) Differences in the number of cephalic scales:
12–13 (x = 12.7; s = 0.5) in males vs. 13–15 (x = 14.6; s = 1.3) in females.

(6) Differences in the total number of infralabials:
19 – 28 (x = 23.1; s = 1.7) in males vs. 17–20 (x = 20.7; s = 1.5) in females.

(7) Differences in the number of scales between 3rd SL and subocular in males:
0 in all in males vs. 0-2 (x = 0.9) in females.

(8) Scale-rows at midbody less strongly keeled in males than in females.

(9) Pattern: see above. Males generally show no ontogenetic shift in colouration, whereas the colouration in females strongly varies. This is evident for the pattern, the postocular streak, the ground colour and the ventral colour. For details, see Table 5.

TABLE 5. Comparison of colouration characters in the *Tropidolaemus wagleri* group.

TAXON	**Ground colour**		**Dorsal markings**		**COLPOcStr**		**Pattern of venter**	
	Males	Females	Males	Females	Males	Females	Males	Females
Tropidolaemus wagleri	green n = 8	black + yellow n = 24	red dots n = 8	yellow bands n = 24	white and red n = 8	black n = 24	uniform n = 8	banded n = 24
Tropidolaemus subannulatus	green n = 11	green or green and blue n = 39	white spots or blue + red n = 11	blue + white, red + white, blue n = 39	white and red n = 11	variable n = 39	uniform or with red dots n = 11	uniform or blotched with blue or red n = 39
Tropidolaemus philippensis	turquoise n = 4	more or less green n = 2	black net n = 4	black net n=2	black or white n = 4	black n = 2	uniform n = 4	uniform n=2

Remarks.—only adult specimens are considered.

Range.—Vietnam. Known from the southern provinces of Minh Hai and Song Be (Orlov et al., 2003). —Thailand. Known only from the South: it has been recorded from the provinces of Phang Nga, Pattani, Surat Thani, Nakhon Si Tammarat, Narathiwat, and Yala (Nabhitabhata et al., 2004). —Federation of Malaysia. West Malaysia. Probably distributed throughout the Peninsula. —Singapore. —Indonesia. Recorded from the islands of Sumatra, Bangka, Mentawei Archipelago, Natuna Islands, Nias, and Riau Archipelago.

Materials (38 specimens). Indonesia. Natuna Islands. BMNH 95.5.1.56, "Sirhassen, Natuna Islands", now Serasan Island, Natuna Archipelago. —Riau Archipelago. ZMA 17718, "Doeriam", now Durian Island, Province of Riau. —Sumatra. MHLCLFE 206-207, vicinity of Lubuksao, between Lubukbasung and Muko-muko, on the northwestern shore of Lake Maninjau, Province of Sumatera Barat. - MNHN 1879.0708, "Bedagneh River, Deli", now Bedagai River, Province of Sumatera Utara; MNHN 4063, MNHN 7767, MNHN 1880.0043, MNHN 1998.0479, "Sumatra"; MNHN 1998.0480, MNHN 1999.6577-6578, Jambi Province; MNHN 2000.4274-84, Lake Maninjau, Province of Sumatera Barat. - ZIH No number (1)-(3), "Sumatra". - ZMH R-07440, Padang District, Province of Sumatera Barat; ZMH R-07448-450, Sungei Lalak (0°27'S, 102°59'E), Province of Indragiri. - **Federation of Malaysia**. West Malaysia. MNHN 1884.0160-0161, "Malaya"; MNHN 2006.0422, "West Malaysia (from the pet trade). —**Thailand**. MNHN 1990.4250, MNHN 1990.4287, MNHN 1996.0291-0292, MNHN 2006.0417-0418, "Thailand" (from the pet trade).

***Tropidolaemus subannulatus* (Gray, 1842)**

(Figs. 12–25)

Diagnosis. —A species of the genus *Tropidolaemus*, characterized by (1) the internasals separated by 2 (rarely 1) scales, never in contact; (2) a background colour in the shades of green, namely green, blue or green and blue ground in females, green (blue in some Negros populations) in males and juveniles; (3) crossbands around the body blue and white, red and white, blue, blue and red or white in adult females, white parts can be light blue in life, white spots or white and red spots in males and juveniles; (4) a variable postocular stripe in adult females and a white and red one in juveniles and males; (5) in adult females the belly is uniform or blotched with blue or red, never banded, in males and juveniles the belly is uniform or with red dots; (6) 128–148 VEN in males and 127–147 in females, SC: 45–53 in males and 40–54 in females; (7) 21–23 MSR in males and 21–29 in females, keeling variable in both sexes; (9) 4–7 scales on the snout at males and 5 – 8 in females; (10) 3rd SL nearly always (87 / 90 occurrences) separated from the subocular by 1 scale or 2 scales, without sexual dimorphism; (10) tail long in males, with a ratio TaL/TL between 0.146 and 0.182, moderate to long in females, 0.139–0.183; (11) occipital scales distinctly keeled in males.

Description and variation. —The maximal TL among our sample is 963 mm (SVL 820 mm, TaL 143 mm) for a female from "Siau, Sangi Islands", now Sangihe Islands (BMNH not registered). Our largest male is 463 mm long (SVL 384 mm, TaL 79 mm; FMNH 222869 from Borneo).

We refrain from giving a more detailed description here, as the variation among this species or complex of species will be discussed in the next and forthcoming paper of the series. A splitting into several taxa seems to be likely.

Range. —Brunei. See Das (2007). – Federation of Malaysia. States of Sabah and Sarawak on Borneo (Stuebing & Inger, 1999; Malkmus et al., 2002). – Indonesia. Known from the islands of Belitung, Borneo (Kalimantan), Buton, Kalimantan, Sangihe Archipelago, and Sulawesi. – Philippines. Recorded from the islands of Balabac, Basilan, Bohol, Dinagat, Jolo, Leyte, Luzon, Mindanao, Negros, Palawan, Panay, Samar, Sibutu, and Tumindao (Alcala, 1986).

FIGURE 12. Syntypes of *Tropidolaemus subannulatus* (BMNH 1946.1.19.33). Philippines. General view. Photograph by Gernot Vogel.

FIGURE 13. Syntypes of *Tropidolaemus subannulatus* (BMNH 1946.1.19.33). Philippines. General ventral view. Photograph by Gernot Vogel.

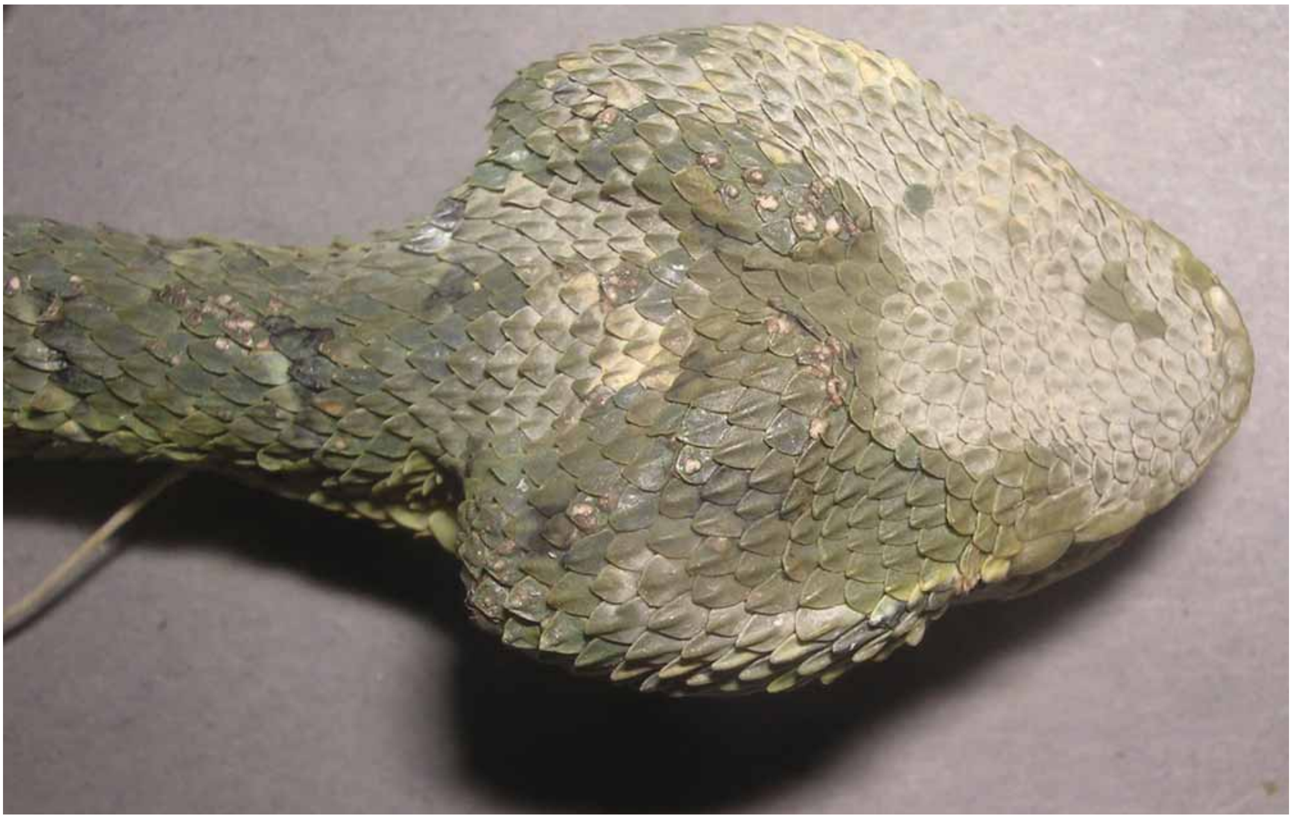

FIGURE 14. Syntype of *Tropidolaemus subannulatus* (BMNH 1946.1.19.32). Philippines. Dorsal view of the head. Photograph by Gernot Vogel.

FIGURE 15. Syntype of *Tropidolaemus subannulatus* (BMNH 1946.1.19.32). Philippines. Ventral view of the head. Photograph by Gernot Vogel.

FIGURE 16. Syntype of *Tropidolaemus subannulatus* (BMNH 1946.1.19.32). Philippines. Lateral view of the head, right side. Photograph by Gernot Vogel.

FIGURE 17. *Tropidolaemus subannulatus*. Living adult female from Sulawesi, Indonesia. Photograph by Henrik Hellemar.

FIGURE 18. *Tropidolaemus subannulatus*. Living male, Lambusango Forest reserve, Pulau Buton, Sulawesi, Indonesia. Photograph by Björn Lardner.

FIGURE 19. *Tropidolaemus subannulatus*. Living adult female Temburong District, Borneo, Brunei Darussalam, 100m. Photograph by Maximilian Dehling

FIGURE 20. *Tropidolaemus subannulatus*. Living adult female from Sarawak, Borneo. Photograph by Johan van Rooijen.

FIGURE 21. *Tropidolaemus subannulatus*. Living adult male, Bako NP, Sarawak, Ost Malaysia. Photograph by Pauli Hien.

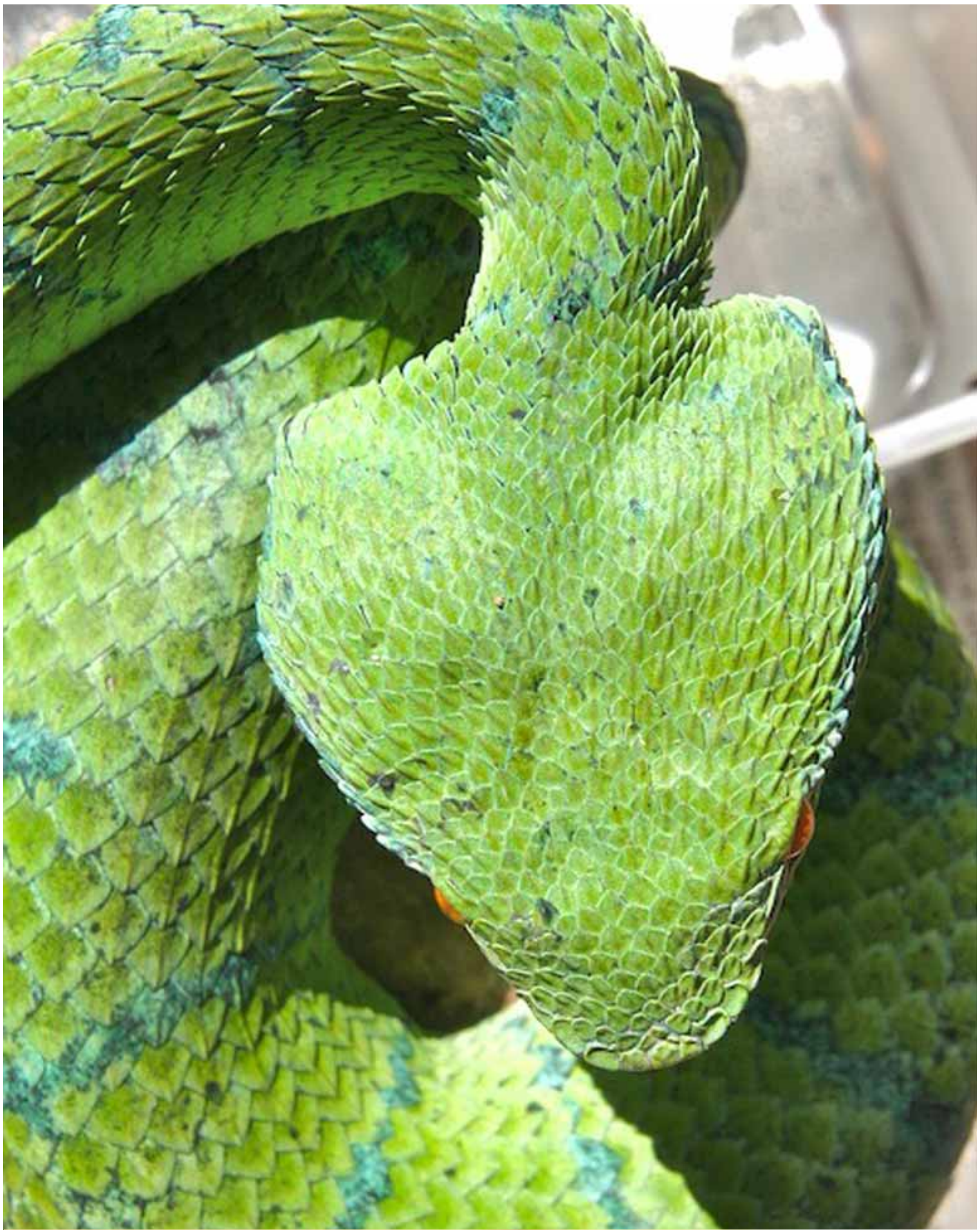

FIGURE 22. *Tropidolaemus subannulatus*. Living adult female from Negros Island, Philippines. Photograph by Mario Lutz.

FIGURE 23. *Tropidolaemus subannulatus*. Living adult female from Palawan Island, Philippines. Photograph by Mario Lutz.

FIGURE 24. *Tropidolaemus subannulatus*. Living adult male from Negros Island, Philippines. Photograph by Mario Lutz.

Material (64 specimens).—**Belitung Island**. ZMA 17709, "Billiton". —**Borneo**. Federation of Malaysia. FMNH 128265, FMNH 129467, Pengkalang Lobang, Fourth Division, State of Sarawak. - FMNH 128433, Tangap, Fourth Division, State of Sarawak; FMNH 131848, FMNH 131860, FMNH 131865, Niah, Fourth Division, State of Sarawak; FMNH 131852, Lower Niah, Fourth Division, State of Sarawak; FMNH 131857, Sungei Subis, Fourth Division, State of Sarawak; FMNH 131861, Niah, Sakaloh, Fourth Division, State of Sarawak; FMNH 131862, Niah, Pengkalan Lobang, Fourth Division, State of Sarawak; FMNH 138663-64, Sungei Mengiong, Nanga Tekalit Camp, Third Division, Kapit District, State of Sarawak; FMNH 148833, Labang Camp on Sungei Seran, Bintulu District, Fourth Division, State of Sarawak; FMNH 222869, Nanga Tekalit, Kapit District, Seventh Division, State of Sarawak. - MNHN 1880.0432, MNHN 1991.3167-68, Sandakan, State of Sabah; MNHN 1906.0014, No Sang, State of Sabah. - ZMH R 07438, "Mandalan River, Borneo", now Sungei Medalam, Limbang (Fifth) Division (04°12'N, 114°57'E), State of Sarawak. - Indonesia. MNHN 1891.0082, "Sebroeang", now Nangah Sebroeang, near Semitau, Province of Kalimantan

Barat; MNHN 2006.0419, Pontianak, Province of Kalimantan Barat. - No locality. MNHN 1880.0435, MNHN 1957.0817, "Borneo"; MNHN 1998.0488, MNHN 2002.0447-49, MNHN 2006.0420, "Borneo" (from the pet trade). —**Sulawesi**: BMNH 1980.1718, Ranu River, Morowali Nature Reserve; BMNH 1980.0936, Torro, Kulawi, Kabupaten Donggala, Central Sulawesi; BMNH 49.3.2.38, "Celebes"; BMNH 96.12.9.79, "Bone Valley, N. Celebes", now in Province of North Sulawesi. - MNHN 1999.9032, MNHN 2002.0408, "Sulawesi" (from the pet trade); MNHN 2002.0446, an island off South Sulawesi (from the pet trade). - ZMA 17711, "Posso", now Poso, Province of Central Sulawesi. —**Philippines.** Luzon Is. 95.1.11.10-12, "Albay, S. E. Luzon", now Albay Province, Luzon Is.; MNHN 1880.0232, "Province Albay (Luzon Philippines), now Albay Province, Luzon Is.; MNHN 1876.0032, "Dans la Laguna (Luzon)". - Mindanao Is. BMNH 77.10.9.71-72, "Butuan, N. Mindanao", now Butuan City, Province of Agusan del Norte; CAS 8679, "San Ramon, Zamboanga Prov.", now in Province of Zamboanga del Sur; FMNH 15046, "Agusan River, Mindanao Is"; FMNH 22580, Bunawan, Agusan del Sur Province; FMNH 53564-67, Tagum, Madaum, Davao Province, near sea level. - Negros Is. CAS-SUR 18792-93, Mabaja River area just West of Mayaposi Hill (Alt: 1800'), Negros Oriental Province. - Palawan Is. BMNH 79.11.16.12, CAS 15816, Puerta Princesa; BMNH 94.6.30.64-65, "Palawan"; CAS 28531, about 1 1/2 km. W.S.W. of Iwahig, Site 488 (300 ft), Palawan Prov. - Sulu Archipelago. MNHN 1880.0383, "Archipel de Sulu entre Bornéo et Mindanao". - No locality. BMNH 1946.1.19.32-33, MNHN 1884.0046, MNHN 1884.0181-0182 "Philippines". —**Unknown origin**. MNHN 1878.0365-66, both labelled as from "Mansinam, Nouvelle Guinée".

Tropidolaemus philippensis **(Gray, 1842)**
(Figs. 25–32)

Diagnosis. —A species of the genus *Tropidolaemus*, characterized by (1) the internasals separated by 1 or 2 scales; (2) only 6–7 cephalic scales between the middle of the supraoculars at both sexes; (3) 18–19 MSR in both sexes, smooth or weakly keeled; (4) 7–8 SL on each side, or a total number of 15–16 supralabials in both sexes; (5) 0, rarely 1 scale, between 3rd SL and subocular in both sexes; (6) 4–5 scales on the snout in both sexes; (7) a total number of 16–17 infralabials in both sexes; (8) a greenish-turquoise body background coloration in males, seemingly more green in females; (9) dorsal blotches on the body, black with unfilled dorsals so some kind of net is visible; (10) a black or rarely white postocular stripe in both sexes; (11) belly uniform in both sexes; (12) VEN: 131–135 in males and 129 in the sole available preserved female specimen, SC: 45–46 in males and 44 in a female; (13) tail moderate in males and females, with a ratio TaL/TL between 0.143 and 0.155, without sexual dimorphism; (14) occipital scales weekly keeled in males and strongly keeled, like partly raised in females.

Description and variation. —The maximal known TL is 455 mm (SVL 390 mm, TaL 65 mm) for a male (BMNH 1946.1.17.67; holotype). Our sole available female is not adult.

Body relatively slender in both sexes, laterally compressed. Head strongly triangular, wide at its base, clearly distinct from the neck (about 1.5 times as broad as the neck), amounting for 6.0–7.5 % of SVL (x = 6.5 %) in males, 6.3 % of SVL in a female, wide at its base, thick and rounded when seen from the side. Snout abruptly truncated, rounded when seen from the side, with a distinct canthus rostralis, rather massive, rounded when seen from above, amounting (in adults) for 26–29 % (x = 28 %) of HL in males and 27 % in a female, or 1.5–1.8 (x = 1.7) times as long as diameter of eye in males and 1.6 times as long as diameter of eye in females, rounded when seen from above. Nostrils small, piercing in the middle of the nasal. Eye average, amounting the distance eye–lip for 1.0–1.4 (x = 1.2) times in males and 0.9 time in a female. Tail tapering progressively and prehensile. Ratio TaL/TL: 0.143–0.151, without any sexual dimorphism. We did not note any ontogenetic variation of this ratio in our small sample.

DSR: 19-21 – 18-19 – 14-15, not or weekly keeled.
VEN: 129–135 (plus 1–2 preventrals); SC: 44–46, all paired. Anal shield entire.

FIGURE 25. Holotype of *Tropidolaemus philippensis* (BMNH 1946.1.17.7). Adult male from Philippines. General view. Photograph by Gernot Vogel.

FIGURE 26. Holotype of *Tropidolaemus philippensis* (BMNH 1946.1.17.7). Adult male from Philippines. General ventral view. Photograph by Gernot Vogel.

Rostral visible from above, about 1.1–1.2 times broader than high, triangular; nasals subrectangular, entire; 1 internasal on each side, rather squat, narrow, about 1.5 times as long as wide; internasals separated by 1 (1/5 specimens) or 2 (4/5) small scales; 2–3 canthal scales, not or barely larger than adjacent snout scales, bordering the *canthus rostralis*; 1 elongate triangular loreal scale between upper preocular and the nasal; 2 elongate upper preoculars above the loreal pit; lower preocular forming the lower margin of loreal pit; 2 postoculars on each side; 1 small, relatively wide, flat supraocular on each side, 1.8–2.0 (x = 1.9) times as long as wide, 0.8–1.0 (x = 0.9) times as wide as the internasals, irregularly bordered on their inner margins by the upper head scales; 4–5 (x = 4.4, s = 0.5) distinctly enlarged scales on upper snout surface on a line between the scales separating the internasals and a line connecting the anterior margins of eyes, rhomboid, strongly keeled and imbricate; 6–8 (x = 7.0; s = 0.6) cephalic scales between the middle of the supraoculars, enlarged, strongly keeled, flat and imbricate; occipital scales larger than cephalic scales, weakly keeled in males but strongly keeled, somewhat raised in some females; temporal scales small, irregular in size, in 3 rows, more or less strongly keeled in both sexes; 1 small, thin, elongated, subocular on each side; 7–8 SL (x = 7.9; s = 0.4) on each side (7 SL in only 1/10 occurrences), total number 15–16 (x = 15.8; s = 0.4); 1st SL short, entirely separated from nasal; 2nd SL short, subrectangular, not bordering the anterior margin of the loreal pit, topped by a prefoveal scale which borders the pit and is either in contact with the nasal in all examined specimens; 3rd SL longest but rather short, elongate, 1.5–2.0 (x = 1.8; s = 0.2) times as long as high, in contact (9 / 10 occurrences) with the subocular or separated by 1 small scale (1 / 10 occurrences) 4th SL 0.7–0.8 time as high as long, 1.0–1.2 (x = 1.1; s = 0.1) times as high as 3rd SL, either in contact (5 / 10 occurrences) with the subocular or separated by 1 (5 / 10 occurrences) small scale; 8 – 9 IL (x = 8.3; s = 0.3) on each side, total number 16–17 (x = 16.2; s = 0.5), strongly keeled; scales of the 1st pair longitudinally in contact at the exception of 1 specimen, first two pairs only in contact with anterior chin shields; 5 rows of strongly keeled gular scales on each side in all specimens.

This species does not show clear sexual dimorphism in coloration and pattern. There is no ontogenetic variation in males.

In life and in preservative, in males, the body and tail are bluish-green or turquoise, whereas they are more green or yellowish-green in females, with 27 to 36 irregular black vertical crossbars. These are 1 scale wide at the base and 2 or 3 scales wide on the vertebral row. The scales in the stripes are centered with the ground colour of the body. Sometimes there are rhombic markings instead of the stripes. The scales in these markings are centered green or yellowish green. The scales between these markings or bands may have dark margins. These are getting darker on the vertebral line. The dorsal and lateral head surface is in the colour of the body with all scales having dark margins. This is also true, although to a lesser extent, for most of the upper labials and the venter of the head, which is yellow in ground colour. Some of the scales of the venter surface of the head have a turquoise speckling. The belly is a bit lighter than the ground colour with several ventrals having dark margins. These may be present only on one lateral half of the scales or may be totally absent.

On the tail there are about 8 to 10 ill defined dark bands, also centered in the ground colour. All the scales on the tail have more or less dark margins, except on the tip which may be uniform light or uniform black. The subcaudals are turquoise to yellow and may or may not have dark margins.

Sexual dimorphism.—This species does not show any clear sexual dimorphism, in contrast to the two other taxa discussed above. There is not even clear difference in the ratio TaL/TL.

Males do not show ontogenetic shift in coloration. The two available females, including a living specimen, suggest a rather green or yellowish-green coloration in females vs. turquoise in males. For details, see Table 5.

Range.—Philippines. Known only from southern and western parts of the island of Mindanao.

Materials (5 specimens).—**Philippines**. Mindanao Island. BMNH 1946.1.17.67, “The Philippines” (holotype). - CAS SU-7265, Davao, Province of Davao del Sur. - FMNH 68902, “Zamboanga Province”; FMNH 124297, “Cotabato”. - MNHN 4064, “Samboangan, île Mindanao (archipel des Philippines)”, now

Zamboanga Peninsula.

To this material, we add a living specimen, a female, depicted in Vogel (2006: 131).

FIGURE 27. Holotype of *Tropidolaemus hombroni* (MNHN 4064). Adult male from Philippines. General view. Photograph by Gernot Vogel.

FIGURE 28. Holotype of *Tropidolaemus hombroni* (MNHN 4064). Adult male from Philippines. General ventral view. Photograph by Gernot Vogel.

FIGURE 29. Holotype of *Tropidolaemus hombroni* (MNHN 4064). Adult male from Philippines. Lateral view of the head, right side. Photograph by Gernot Vogel.

FIGURE 30. Holotype of *Tropidolaemus hombroni* (MNHN 4064). Adult male from Philippines. Dorsal view of the head. Photograph by Gernot Vogel.

DISCUSSION

Comparison between recognized species

Main differences between the *Tropidolaemus subannulatus* complex as here conceived and other members of the *Tropidolaemus wagleri* complex (at the exception of *T. huttoni* and *T. laticinctus*) are summarized in Tables 6-7. *Tropidolaemus subannulatus* differs from *T. wagleri* by (1) internasals never in contact, separated by two (rarely one) scales; (2) strong ontogenetic shift in coloration and pattern in females *T. wagleri*, with adult females black (never green) with yellow crossbands, vs. a basic colour of green retained in adult *T. subannulatus* of both sexes (despite some bluish forms); (3) 3rd SL nearly always separated from the suboculars in *T. subannulatus,* vs. separated in about one third of the cases in *T. wagleri*. Lastly, *T. subannulatus* has more infralabials in both sexes.

TABLE 6. Comparison of main morphological characters in the *Tropidolaemus wagleri* group.

TAXON	TaL/TL		VEN		SC		MSR		Keeling of MSR		SL		InN-sep
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	
Tropidolaemus wagleri	0.157–0.196 n=8	0.139–0.178 n=28	143–152 n=8	134–147 n=30	50–55 n=8	45–54 n=28	21–23 n=8	23–27 n=30	1 n=8	2 n=30	16–18 n=8	17–20 n=30	0 n=38
Tropidolaemus subannulatus	0.146–0.182 n=14	0.139–0.183 n=45	128–148 n=14	127–147 n=46	45–53 n=14	40–54 n=45	21–23 n=14	21–29 n=46	0–2 n=14	0–2 n=46	17–20 n=14	17–21 n=46	2 (1) n=60
Tropidolaemus philippensis	0.143–0.155 n=4	0.147 n=1	131–135 n=4	129 n=1	44–46 n=4	44 n=1	18–19 n=4	19 n=1	0–1 n=4	0 n=1	15–16 n=4	16 n=1	2 (1) n=5

Abbreviations.—See in Material and Methods, except: Keeling of MSR: 0: smooth, 1: weakly keeled, 2: strongly keeled.

TABLE 7. Comparison of main morphological characters in the *Tropidolaemus wagleri* group (continued).

TAXON	Cep		IL		C3SL/SubOc		Sn-SC		K-Occ	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Tropidolaemus wagleri	12–13 n=8	13–15 n=30	16–18 n=8	17–20 n=30	0 n=8	1 (0, 2) n=30	5–7 n=8	6-9 n=30	2 n=8	2 n=30
Tropidolaemus subannulatus	9–12 n=14	9–16 n=46	18-21 (24) n=14	18–26 n=46	1 (0) n=14	1 (0,2) n=46	4–7 n=14	5–8 n=46	2 n=14	2 (1) n=46
Tropidolaemus philippensis	6–7 n=4	8 n=1	16–17 n=4	16 n=1	0 (1) n=4	0 n=1	4–5 n=4	5 n=1	1–2 n=4	2 n=2

Abbreviations. —See in Material and Methods, except: KOcc (keels of occipital scales): 0: smooth, 1: weakly keeled, 2: strongly keeled.

Tropidolaemus philippensis differs from both *Tropidolaemus wagleri* and *Tropidolaemus subannulatus* by (1) a lower number of dorsal scale rows at midbody; (2) a blotched dorsum, instead of vertical crossbars in other taxa; and (3) a lower number of snout and cephalic scales, of supralabials and infralabials. Other characters appear in Tables 6–7.

Tropidolaemus huttoni is still known from only two very young specimens. They are very close to juveniles of *Tropidolaemus wagleri*. They differ by (1) a higher Tal/TL ratio, 0.279 vs. 0.179 – 0.196 in juvenile of *T. wagleri* of same size and sex (David & Vogel, 1998); (2) a bright red tip of snout alive (David & Hutton, in prep.). This coloration disappeared in alcohol but was conspicuous when the juveniles were collected; and (3) an upturned snout in *T. huttoni*.

Lastly, *Tropidolaemus laticinctus* differs from all other taxa mostly by its coloration. The short and somewhat abridged description of Kuch et al. (2007) did not provide much detail on scalation of this species.

Zoogeography

As explained above, we consider these three taxa to be distinct species, or, in the case of *Tropidolaemus subannulatus*, of a complex of species.

T. wagleri is entirely allopatric with both *T. subannulatus* and *T. philippensis*. The Biological Species Concept cannot be tested. Nevertheless, both *T. wagleri* and *T. subannulatus* are commonly imported by the pet trade, and no crossbreeding is known to us. At the present time, only *T. laticinctus* occurs in sympatry with *T. subannulatus* on Sulawesi, whereas *T. philippensis* and *T. subannulatus* occur in sympatry on Mindanao.

Out of its main range, *T. wagleri* has been recorded from South Vietnam. Some Indo-Malayan snake taxa have been discovered in a small part of southwestern Vietnam (Orlov et al., 2003). The occurrence of such taxa in South Vietnam and South Laos was discussed in Teynié et al. (2004). The main range of *T. wagleri* extends from southern Thailand across West Malaysia to Singapore and Sumatra (plus some adjacent islands). By all evidence, *T. wagleri* is not present on Java. There cannot be any doubt on the fact that the form present on Sumatra is the same than that from Thailand and West Malaysia, despite the fact that specimens from Sumatra are a little bit less colorful in having less yellow shades on the dorsum. We would like to point out that Bangka Island is inhabited by *T. wagleri*, whereas the nearby Belitung Island, half way between Sumatra and Borneo is undoubtedly inhabited by (at least) *T. subannulatus* (see the respective examined materials).

At this place we want to emphasize the still preliminary status of the herpetofauna of the Sunda region. Nearly every new review is changing the zoogeographical units (Vogel et al., 2004, de Lang & Vogel 2005, David et al. 2006, Vogel & David 2006, Vogel & van Rooijen, 2007).

It is well known that the fauna of Sulawesi shows a strong affinity with the fauna of some Philippine islands, especially Palawan, and on the other side is well connected to Borneo (de Lang & Vogel 2005). We will not discuss this in greater detail, as the taxonomic status of *T. subannulatus* will be reviewed soon. Nevertheless, specimens living in these three regions are more closely related to each other than to the other species (*Tropidolaemus wagleri* and *T. huttoni*). We will not discuss here the presence of two species on Sulawesi. Kuch et al. (2007) did not discuss the sympatry, syntopy or zoogeography of their new species *T. laticinctus*.

Lastly, the isolated occurrence of *T. philippensis* on Mindanao is quite problematic. While it is beyond doubt that this form is different from *T. subannulatus*, it leads to several questions about its zoogeography. Brown & Alcala (1970) noted high similarities between the fauna of extreme South Mindanao and the Eastern and Central Visayas, and supported the hypothesis of an “eastern route” which led to the colonisation of Mindanao from other Philippine islands. However, only *Tropidolaemus subannulatus* has been found in eastern Mindanao. Leviton (1964) failed to notice differences between the Philippine taxa and between Philippine taxa and *T. wagleri* respectively. Seemingly, Leviton (1964) did not examine many animals from outside the Philippines, especially no specimen from Borneo. Furthermore, Leviton did not examine the name-bearing types of all forms described from the Philippines, and obviously not *T. philippensis*.

Because of the likely presence of more than one form on some Philippine islands and of ontogenetic variation, the morphological analysis of Philippine populations is quite challenging. A thorough discussion on these populations, as well as on others of the *T. subannulatus* complex will be presented elsewhere. Nevertheless, all are definitely distinct from the species defined here as *Tropidolaemus wagleri* and *T. philippensis*. Thus, the genus *Tropidolaemus* currently contains five species: *T. wagleri*, *T. philippensis*, *T. subannulatus*, *T. laticinctus*, and *T. huttoni*.

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