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ON THE OCCURRENCE OF *TRIMERESURUS MEDOENSIS* DJAO IN: DJAO & JIANG, 1977 (SERPENTES, VIPERIDAE, CROTALINAE) IN INDIA, WITH A REDESCRIPTION OF THIS SPECIES AND NOTES ON ITS BIOLOGY

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(with eight text-figures)

ABSTRACT.– **Twenty-six specimens of a green pitviper of the genus *Trimeresurus* observed in eastern Changlang District, State of Arunachal Pradesh, north-eastern India, proved to belong to the species *Trimeresurus medoensis* Djao in: Djao & Jiang, 1977, hitherto definitely known only from south-western China and Myanmar. The morphology of these specimens is described in detail. The Indian specimens are described and compared with the types of the species, which are also redescribed in detail, and with two specimens from northern Myanmar. An expanded description of the species, based on a total of 30 specimens, notes on its biology, and comparisons with some other green pitvipers occurring in the Eastern Himalayas are provided.**

KEY WORDS.– ***Trimeresurus*, *Trimeresurus medoensis*, Viperidae, Crotalinae, India, Arunachal Pradesh, Myanmar, China.**

INTRODUCTION

The region of the Eastern Himalayas, a large and complex area of wet, forest covered hills, high mountain ranges and deep valleys spanning over south-western China (Xizang Autonomous Region and Yunnan Province), north-eastern India, Bhutan and northern Myanmar, is one of the richest in Asia for the pitvipers of the genus *Trimeresurus* sensu lato (David and Ineich, 1999). It is the home of at least six or seven species of predominantly green pitvipers of the genus *Trimeresurus*, namely *T. albolabris*, with the subspecies *albolabris* (Gray, 1842) and *septentrionalis* Kramer, 1977 (this latter probably a distinct species, see Malhotra and Thorpe, 2000), *T. erythrurus* (Cantor, 1839), *T. medoensis* Djao in: Djao and Jiang, 1977, *T. popeiorum* Smith, 1937, *T. stejnegeri* Schmidt, 1925, and *T. yunnanensis* Schmidt, 1925.

In the course of herpetological investigations in Changlang District, State of Arunachal Pradesh, north-eastern India, the second author examined 26 specimens of a green pitviper of the genus *Trimeresurus*, with only 17 dorsal scale rows at midbody. On the basis of recent literature on the genus *Trimeresurus* of this area (for example David and Tong, 1997), these specimens were identified as *Trimeresurus medoensis*. One of them was illustrated in colour in Anonymous (1999), a mention which was the first confirmed record of this species in India.

Trimeresurus medoensis Djao in: Djao and Jiang, 1977 is a poorly known species which was described from only two specimens collected in south-eastern Xizang Autonomous Region. Its validity has been accepted by subsequent authors (Anonymous, 1977; Hu and Zhao, 1979; Hoge and Romano Hoge, 1981; Tian et al., 1986; Yang and Inger, 1986; Zhao et al., 1986, 1998, 2000a, 2000b; Hu et al., 1987a, 1987b; Welch, 1988, 1994; Zhao, 1990, 1993, 1998; Zhao and Adler, 1993; Golay et al., 1993; David and Tong, 1997;

Ma and Xu, 1998; David and Ineich, 1999; McDiarmid et al., 1999; Zhu and Tan, 1999; Lu and Li, 2000; Rao, 2000), although it was not included in Regenass and Kramer's review (1981). A third specimen from the vicinity of Myitkyina, northern Myanmar was recently formally referred to this species by Zhao et al. (1998). Previously, Djao in: Djao and Jiang (1977) had only tentatively referred to this new species three female specimens from northern Myanmar cited by Smith (1943: 518), on the basis of their dorsal scale row formula. Hoge and Romano Hoge (1981) included also India in the range of this species, in citing Taji Lin, better known as Darjeeling, State of West Bengal, but the basis of this statement was not specified. Lastly, Welch (1988) and Das (1997), also without comments, included this species in the Indian snake fauna.

We provide in this paper a detailed description of these Indian specimens, with notes on their biology. The description of *Trimeresurus medoensis*, originally published in Chinese, was translated by David and Tong (1997). Although accurate, it was rather brief. A more thorough description of the type specimens was published in Zhao et al. (1998), but this was also in Chinese. Consequently, we take the opportunity of this paper to publish in English a full description of the type specimens based on our own data, and not on the text appearing in Zhao et al. (1998), which may explain the slight differences in some scale counts, such as the ventral and supralabial scales. We also give the description of one of the three specimens cited by Smith (1943) and of the specimen from Myitkyina. The Indian and Burmese specimens are compared with the types and their identification is discussed.

As a conclusion, variation of major morphological characters in *Trimeresurus medoensis* and its distribution are summarised, and a short discussion on the relationships of this species is provided. This species is also compared with *T. popeiorum* Smith, 1937 and *T. yunnanensis* Schmidt, 1925, both present in north-eastern India and northern Myanmar. A summary of data on *T. medoensis* concludes this paper.

MATERIALS AND METHODS

All data pertinent to the 26 Indian specimens were obtained from living animals. Our investigations were conducted in a protected area, in which we were not allowed to kill and preserve any specimen. Consequently, there is no voucher specimen for this population, although most specimens were photographed.

The snakes were examined during two field trips, in March-June 1999 (14 specimens) and November 1999-January 2000 (12 specimens), respectively. Habitats suitable for pitvipers were identified with the help of Lisu guides and searched thoroughly. Once the snakes were located, they were collected and transferred into snake bags. Examination and scale counts were made early in the morning when the temperatures were low and the snakes were sluggish. Their heads were restrained by a noose on a nylon cord ca. 3 mm diameter that passed through a hole in a bamboo (referred to as 'musa' by the Lisus), ca. 20 mm diameter x 600 mm long. The noose was placed behind the widest part of the head. The cord was then pulled tight and a spring loaded toggle from a windcheater prevented the noose from loosening. A Lensel L111B head loupe (2.75 x magnification) was used to facilitate counts. Scales were counted with the help of a 'uni-ball eye fine' black waterproof pen. Each scale was marked for dorsal body scale row counts; and every 10th ventral and subcaudal was marked for ventral and subcaudal counts. All counts were made at least twice. The snout-vent length and tail measurements were made by marking off corresponding lengths on a wooden railing and are consequently approximate; at best they indicate the rough size of the snake. This was done to avoid stressing the snakes more than absolutely necessary. Most specimens were photographed; record photographs were taken with a Nikon F5 body mated to a 105 mm 2.8 AFD Micro Nikkor lens. Illumination was with a SB 21B ring flash. The snakes were then released within 48 hours of capture close to their respective site of capture. Photographs are deposited both in the collections of the MNHN (Paris) and the Centre for Herpetology, Madras Crocodile Bank Trust, Vadanemmeli, India.

For the Indian snakes, we recorded data on the sex, colouration, head and dorsal patterns, and the following meristic characters: numbers of dorsal scale rows (behind head, midbody and before the vent, respectively), ventrals, subcaudals, supralabials, and cephalic scales between supraoculars. Other characters were not accessible on living specimens, but all characters regarded as diagnostic of *T. medoensis* could be recorded. On preserved specimens, such as the types of *Trimeresurus medoensis* and other specimens referred to this species, measurements were taken with a slide caliper to the nearest 0.1 mm. Throughout this paper, the number of ventral scales is counted after Dowling's (1951) method. The number of subcaudals excludes the terminal scute. The numbers of dorsal scale rows are given at two head lengths behind head (values counted at one head length are given in square brackets), at midbody (i.e. at the level of the ventral plate corresponding to a half number of the total ventrals; approximate midbody for the Indian examples), and at one head length before vent (ca. two head lengths for all the Indian examples), respectively. Values for symmetric head characters are given in left/right order.

Abbreviation of measures (all in mm) and other meristic characters are:

SVL: snout-vent length.- TaL: tail length.- TL: total length.- TaL/TL: ratio tail length/total length.- HL: head length.

Ven: number of ventrals.- SubC: number of subcaudals.- InNas: number of scale(s) separating the internasals.- SupL: number of supralabials (l/r).- Cep: number of cephalic scales on a line separating the supraoculars.- InfL: number of infralabials (l/r).

Museum abbreviations:

AMNH: American Museum of Natural History, New York.

BMNH: British Museum (Natural History), now the Natural History Museum, London.

CIB: Chengdu Institute of Biology, Academia Sinica, Chengdu, Sichuan, People's Republic of China.

MNHN: Museum National d'Histoire Naturelle, Paris.

RESULTS

Description of Indian specimens (Figs. 1-4).- All snakes were found within 3 km of Gandhigram village (also known as Shidi), at 27° 26' 27" N, 96° 54' 55" E, in Changlang District, Arunachal Pradesh, elevation 1,040 m a.s.l., although the surrounding mountains are much higher (Anonymous, 1990). This village is located in the north-eastern-most fingertip of India, on the upper reaches of the Noa Dihing River close to Chaukan Pass just next to the border with Myanmar. All specimens from both trips were found in an area just outside the upper limit of Namdapha National Park. A description of the physiogeography, climate and flora of Arunachal Pradesh appears in Hajra et al. (1996).

As there is no voucher for this series, we give in Table 1 the detailed raw morphological characters recorded from these specimens. Specific comments are provided below the table when necessary. General characters conclude our description of this series. As these snakes have no collection number, they are identified by their respective date of collection; when more than one specimen was collected on a single day, a number is associated with the date.

General morphology.- These specimens present a typical morphology of the green, arboreal pitvipers of the *Trimeresurus* group (see Malhotra and Thorpe, 2000), with a rather elongated body; a wide, flat, triangular head, well distinct from the neck; and a strongly prehensile tail. Uniformly dark grass green or dark bamboo-leaf green dorsal background colour, some scales sometimes edged with turquoise blue.

General characters.- These 26 specimens share the following meristic characters: Dorsal scale rows in 17 rows at midbody, more or less keeled with obtuse keels on flanks and upper rows, sometimes nearly entirely smooth, 1st row always smooth; anal single; subcaudals paired, unless otherwise stated below; canthus rostralis sharply defined; tail rather long for a pitviper.

Nasal undivided; internasals large, kidney shaped, separated by a single smaller triangular downward pointing scale, unless otherwise mentioned below; usually 1 small triangular scale separating the internasal from the 2nd

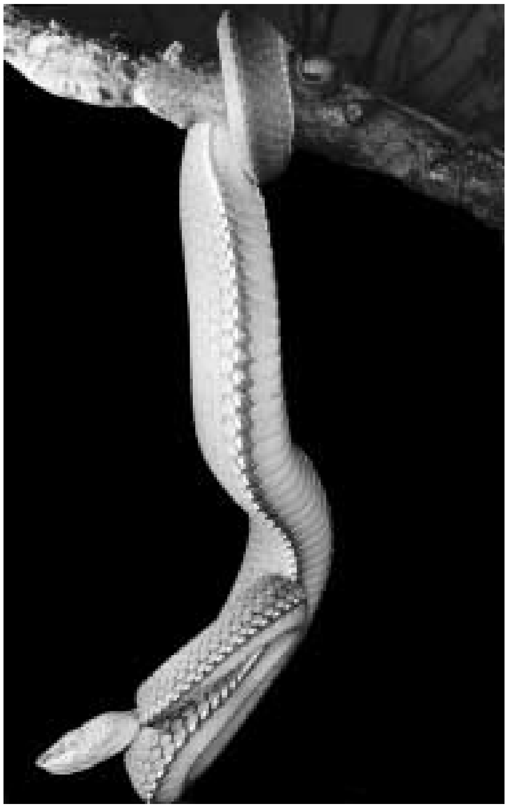

FIGURE 1: General view of an Indian specimen of *Trimeresurus medoensis*.

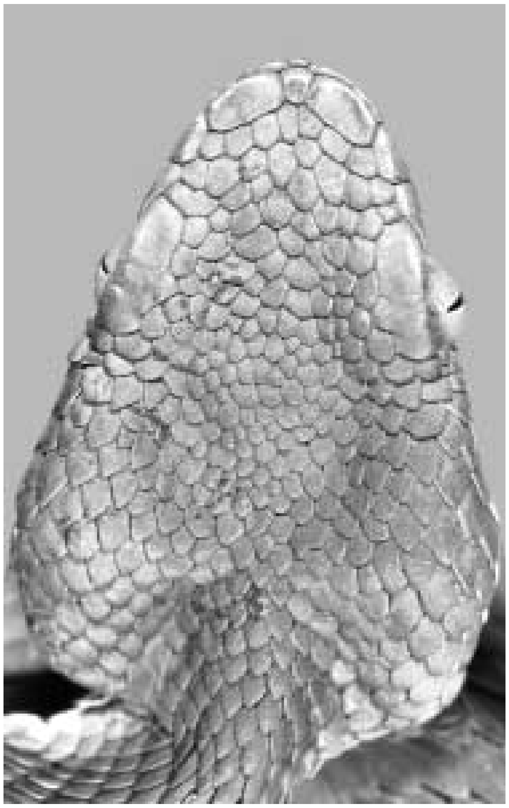

FIGURE 2: Dorsal view of head an Indian specimen of *Trimeresurus medoensis*.

supralabial; scales on the snout not numerous, large, larger than cephalic scales; 1 loreal between the internasal and the upper preocular, just below the canthus rostralis; 3 preoculars; 2 or 3 postoculars; 1 supraocular on each side, large, wide, with its inner margin sometimes indented; 1 elongate subocular; first supralabial completely separated from the nasal; supralabials 3 to 5 in contact with the subocular or sometimes separated by a single small scale; temporals: smooth.

Body uniformly dark grass green or dark bamboo-leaf green, interstitial skin between scales dark blue, some scales sometimes edged with turquoise blue, with, in all specimens, a bicoloured coral red and white ventrolateral stripe from behind the head to tail base on the first and second dorsal scale rows, red on its lower half, namely on lower half of 1st dorsal scale row, white on upper half, on upper half of 1st and lower third of second dorsal scale rows respectively; top of head same colour as dorsum, without postocular streaks in all specimens, with paler, yellowish green (“paddy field” green) supralabials and infralabials, the latter scales sometimes with pale turquoise margin, and with a pale brown, sometimes blue-black temporal interstitial skin; venter mostly “paddy field” green; tail more or less entirely rusty reddish-brown above, with the midline, namely the sutures between the subcaudals being more or less turquoise blue or speckled with the same colour; eye green or yellowish green with a black pupil; tongue ranging from black to pale brown.

Although the bicoloured ventrolateral stripes are consistently present both in males and females, as in Chinese specimens of *Trimeresurus stejnegeri*, the postocular streak is totally lacking in all specimens.

Individual characters.- Description of hemipenis (Fig. 5). The organs are short and thick, deeply divided and rounded at extremity.

FIGURE 3: Left side of head of an Indian specimen of *Trimeresurus medoensis*.

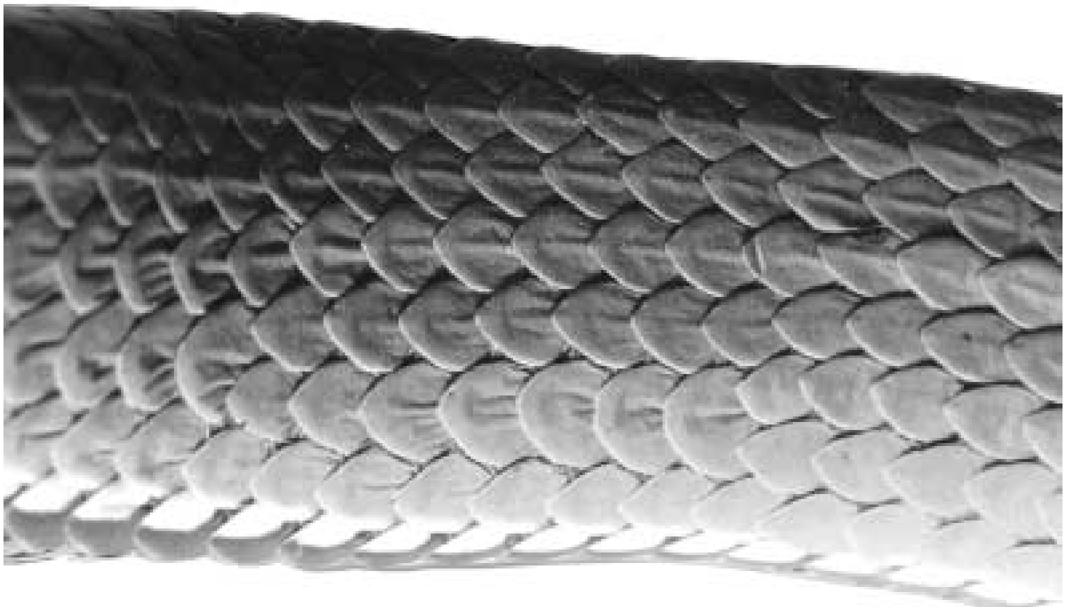

FIGURE 4: Dorsal scales of an Indian specimen of *Trimeresurus medoensis*. Note the bicoloured ventrolateral stripe.

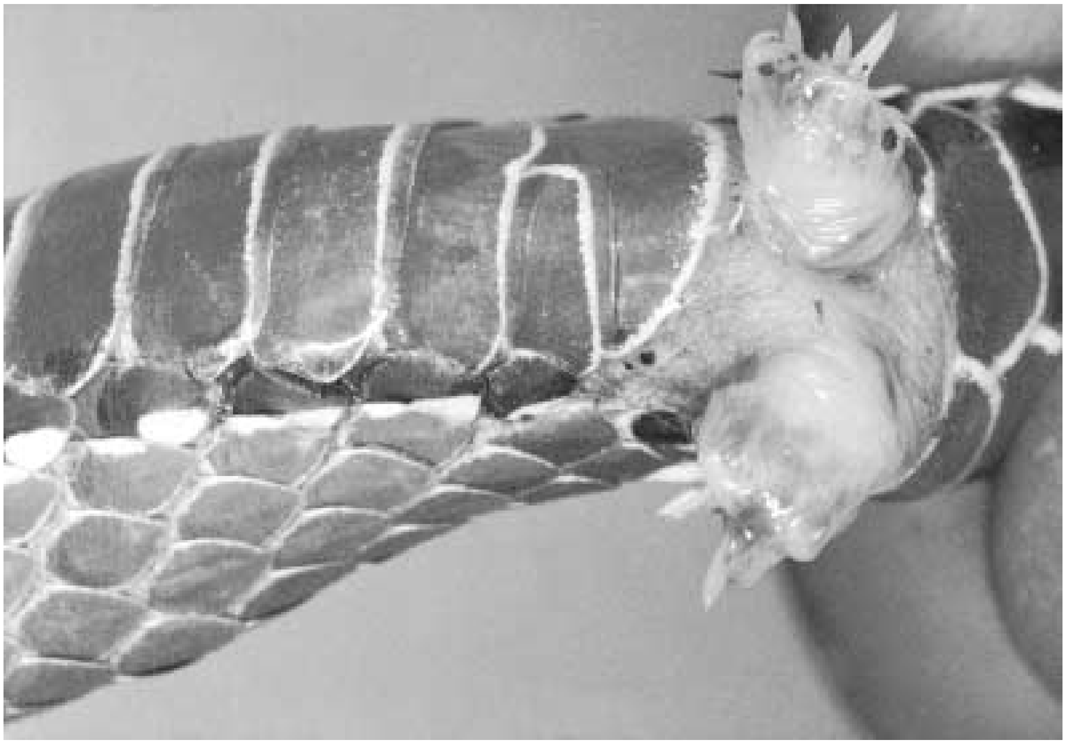

FIGURE 5: Hemipenis of an Indian specimen of *Trimeresurus medoensis* (specimen 14.xii.99[1]).

FIGURE 6: General view of the holotype of *Trimeresurus medoensis*.

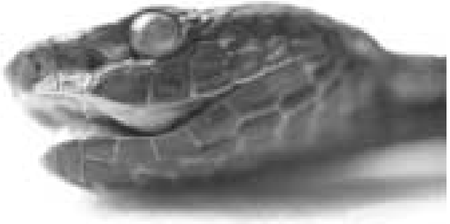

FIGURE 7: Close-up of left side of head of the holotype of *Trimeresurus medoensis*.

The proximal two thirds of the organ are spinous, furnished with about 12 spines of irregular size, of which four or five are much enlarged and two or three are shorter but much more developped than the other spines. Its distal third is calyculate. The shallow sulcus spermaticus divides at the base of the organ, near the first two large spines, and extends to the distal end of each lobe. In Fig. 5, we provide the first photograph of the hemipenes of this species.

Biology.- The surveyed area has steep slopes that are largely covered with wet montane forests and bamboo thickets. The sub-alpine zone merges with the tropical rain forest around the Noa-Dehing valley; there is such a floral diversity that no single plant species can be said to be dominant. The climate is cool and wet, with heavy rains from March-November, however winter rains are not uncommon. Annual rainfall is 3,500-4,000 mm and average winter tempera-

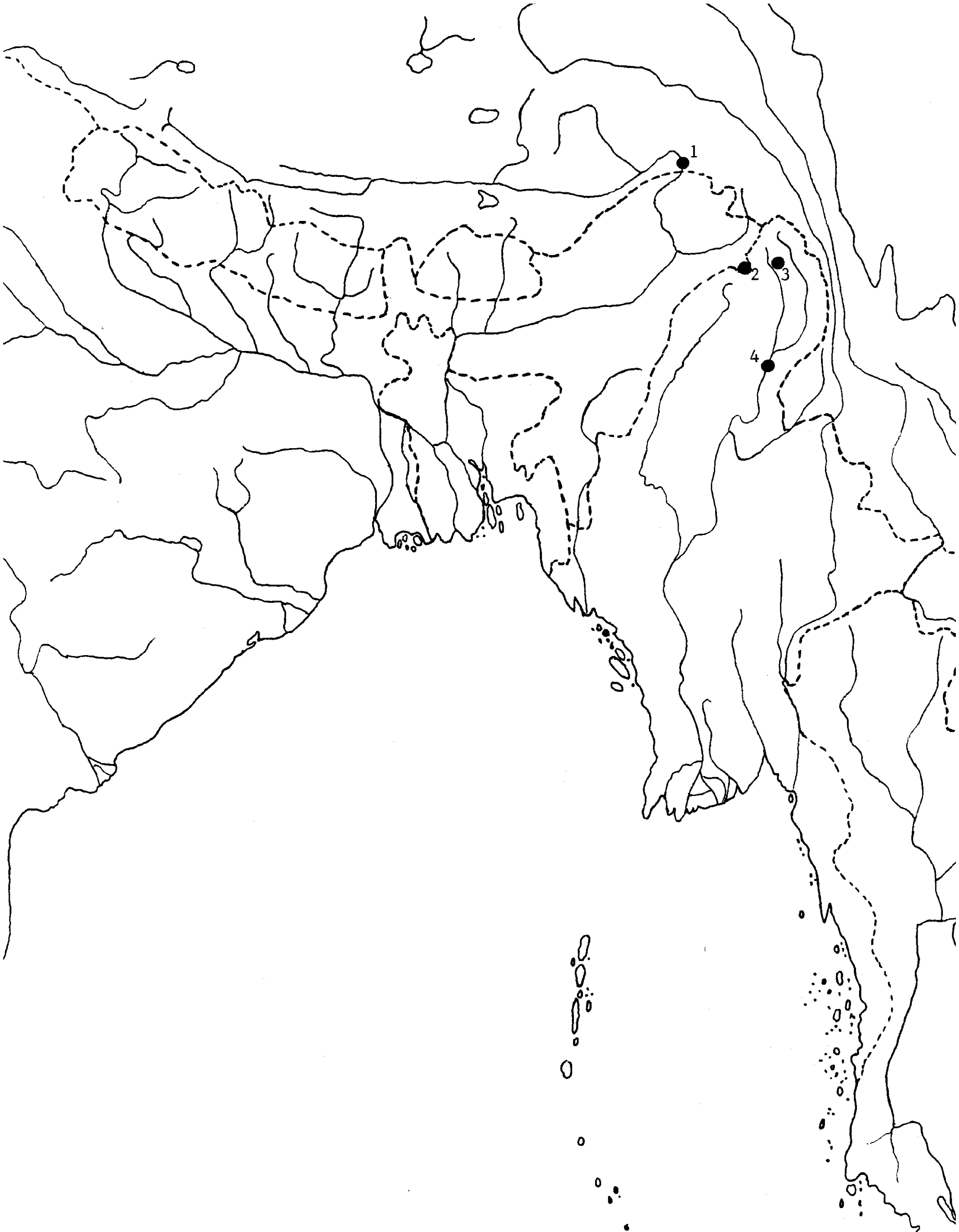

FIGURE 8: Map of north-eastern India and adjacent regions, showing the distribution of *Trimeresurus medoensis*. References: 1. Motuo (type locality), People's Republic of China; 2. Gandhigram, India; 3. Nam Ti Valley, Myanmar; and 4. Myitkina, Myanmar.

TABLE 1 : Main morphological and meristic characters of *Trimeresurus medoensis* from India. Abbreviations. See under Materials and Methods, except: Keels: keels of dorsal scales at midbody: 0 smooth; + keeled (in brackets, keeling of the first dorsal scale row). Notes: 19.iii.99: Umbilical scar at Ven 19-21 from anal; supraoculars large; 20.iii.99: The keels are like loose folds of skin; dark blue interscalar skin visible; distal few subcaudals had turquoise blue flecks near their mid sutures; tongue pale brown; 30.iii.99(1): Upper 8 dorsal scale rows weakly keeled; only the tail tip is reddish brown; 30.iii.99(2): Upper 8 dorsal scale rows weakly keeled; 22.v.99: Eye green; some subcaudal sutures near tail tip speckled with turquoise; 26.v.99(1): 21 scale rows counted from immediately behind neck, some irregular reductions happening to 19 then 17 rows two head lengths behind neck; 13 rows two head lengths before vent; dorsal scales edged with turquoise; subcaudals paired, except subcaudals 2 to 11 and 58-59 single; eye greenish yellow; tail tip rust red above, turquoise below (till 24th subcaudal from tip), then yellowish green; terminal scute totally rust reddish brown. This individual has blue-black temporal interscalar skin instead of the usual pale brown colour; 26.v.99(2): 21 scale rows counted from immediately behind neck, 17 rows two head lengths behind neck, 17 rows at midbody, and 13 rows two head lengths before vent; head at widest 22 mm, head length 28 mm, body diameter about 25 mm. The elongate subocular touches SupLab 3-5; eye green; 28.v.99: Ventrals 2, 134 and 141 (counted from the anal end) stretched only ½ way across the 'belly'; tail entirely dorsally rust reddish brown; infralabials yellowish green with upper pale turquoise margin; temporal skin pale brown; 2.vi.99(1): 19 scale rows behind head, reduced to 17 rows at 2 head lengths behind the head, 17 at midbody up to two head lengths before vent, then reduced to 13 rows two head lengths before vent; 3.vi.99(1): 19 scale rows behind head, all more or less smooth; internasals separated by 2 small triangular scales; a single row of scales between elongate subocular and supralabials; eye green; 3.vi.99(2): 19 scales behind head, reduced to 17 rows at 2 head lengths behind the head, 17 at midbody, reduced to 13 rows two head lengths before vent; 4.vi.99: The secretion of the anal glands was colourless, watery and smells of crushed leaves. This specimen slithered off smartly upon release; 14.xii.99(1): 19 rows at one head length behind neck, reducing to 17 at 2 head lengths, 13 rows at 2 head lengths before vent; dorsum and upper head beautifully coloured dark bamboo or grass green with cobalt/prussian blue skin in between; the bicoloured ventrolateral stripe runs along most of the outermost scale row on either side, but, in this specimen, the stripe continues 5 scales past the vent, then, after a gap of 2 scales, it carries on for 2 more scales on the tail; tail dorsally reddish-brown, ventrally mostly yellowish green with some turquoise patches; ventrals yellowish green, bounded anteriorly and posteriorly by grey, or perhaps a lighter shade of the cobalt/prussian blue that is present between the dorsal scales; eye yellowish green; pupil black, area surrounding it slightly orange; 14.xii.99(2): Tongue black with light tips; 14.xii.99(4): 18 scale rows at one head length behind head, reducing to 17 at two head lengths, 17 at midbody, and 13 rows at two head lengths before vent; 2 postocular scales on each side; 28.xii.99(1): 21 scale rows at one head length behind head, reducing to 17 at two head lengths, 17 at midbody, and 13 rows at two head lengths before vent; 28.xii.99(2): First subcaudal paired, SubC 2-4 single, all others paired; 28.xii.99(3): Pressing the tailbase yielded a thin stream of fluid (like from a syringe), which smell of crushed leaves.

Specimen	Sex	SVL	TaL	TaL/TL	Ven	SubC	Dorsal rows	Keels	InNas	SupL	Cep	InfL	Pos
19.iii.99	F	305	> 35	—	144	54	17- 17- 13	0	1	9/9	8	—	—
20.iii.99	M	525	105	0.17	138	54	17- 17- 13	+ (0)	1	9/9	7- 8	10/10	—
30.iii.99 (1)	F	530	103	0.16	143	52	17- 17- 13	0 /+ (0)	1	9/9	—	10/11	—
30.iii.99 (2)	?	470	102	0.18	141	58	17- 17- 13	0/+ (0)	1	9/9	—	10/10	—
30.iii.99 (3)	M	—	—	—	148	65	17- 17- 13	0	2	9/9	8	—	—
22.v.99	M	460	117	0.20	142	55	17- 17- 13	+ (0)	1	9/9	—	—	—
26.v.99 (1)	?	—	—	—	146	61	17- 17- 13	+ (0)	1	9/9	8	10/11	—
26.v.99 (2)	?	500	109	0.18	146	56	17- 17- 13	+ (0)	2	8/9	8- 10	11/11	—
28.v.99	F	485	95	0.16	149	54	17- 17- 13	+ (0)	1	8/8	7- 8	10/10	—
2.vi.99(1)	M	475	115	0.20	144	61	17- 17- 13	+ (0)	1	8/8	8	10/10	—
2.vi.99(2)	M	400	105	0.21	143	61	17- 17- 13	+ (0)	2	8/8	8	10/10	—
3.vi.99(1)	M	490	97	0.16	143	54	17- 17- 13	+ (0)	2	8/9	8	10/9	—
3.vi.99(2)	M	467	122	0.21	142	63	17- 17- 13	+ (0)	2	8/8	9	10/10	—
4.vi.99	M	490	123	0.20	141	61	17- 17- 13	0	1	8/9	9	11/10	—
14.xii.99(1)	M	455	105	0.19	144	61	17- 17- 13	+ (0)	1	9/9	7	10/10	3/2
14.xii.99(2)	F	480	98	0.17	143	57	17- 17- 13	+ (0)	1	9/8	7- 9	9/10	3/3
14.xii.99(3)	M	455	55 +	—	145	26+	17- 17- 13	+ (0)	1	8/9	6- 8	10/9	—
14.xii.99(4)	M	433	100	0.19	147	59	17- 17- 13	+ (0)	1	9/9	8- 9	10/10	2/2
14.xii.99(5)	F	385	82	0.18	143	53	17- 17- 13	+ (0)	3	8/8	8	10/11	2/2
14.xii.99(6)	F	365	79	0.18	142	55	17- 17- 13	+ (0)	1	9/8	9	10/10	2/3
28.xii.99(1)	F	555	122	0.18	146	56	17- 17- 13	+ (0)	1 (+1)	9/9	7	10/10	—

28.xii.99(2)	M	350	83	0.19	144	58	17- 17- 13	+ (0)	1	9/9	8	10/10	3/2
28.xii.99(3)	F	490	98	0.17	142	56	17- 17- 13	+ (0)	1	8/9	8	9/9	2/2
28.xii.99(4)	M	490	123	0.20	144	59	17- 17- 13	+ (0)	1	8/8	8	10/10	2/3
28.xii.99(5)	M	455	112	0.20	145	59	17- 17- 13	+ (0)	1	8/7	6	10/9	2/3

TABLE 2: Main morphological characters of *Trimeresurus medoensis*. Key: (1): green in life according to the description; green also in preservative; (2): the red pigment may have disappeared in AMNH 58532 after more than 60 years in preservative. The poor condition of the latter specimen may also be responsible for this fact. In BMNH 1936.7.4.43, the red pigment turned brownish grey, but is still visible.

Specimen	Dorsal colour (alive)	Ventrolateral stripe	Postocular streak	Red tail	TaL/TL	SnL/HL	dO/DOL
CIB 73II5208	grass green	Bicoloured	none	yes	0.19	0.292	1.25
CIB 73II5209	grass green	Bicoloured	faint	yes	0.18	0.280	1.18
BMNH 1936.7.4. 43	green (1)	Bicoloured	none	yes	0.18	0.26	1.87 (juv.)
AMNH 58532	green	White ? (2)	none	yes	0.18	0.28	0.81
Indian specimens (n = 26)	grass or dark green	Bicoloured	none	yes	0.17- 0.20 (0.16- 0.22)	—	—

TABLE 3 : Main meristic characters of *Trimeresurus medoensis.* Key: (1): the two other specimens of this series, not examined here, but described by Smith (1943), present the following values respectively: 17 : 17 : 13 rows; 143- 149 ventrals; 57-60 subcaudals; (2): from 6 photographed specimens.

Specimen	Ven	SubC	Dorsal rows	Keels	InNas	Snout scales	SupL	SupL/sobOc	Pos	Cep	InfL
CIB 73II5208	149	59	17 : 17 : 13	0/+	1	3	8	0	2	9	8- 9
CIB 73II5209	146	55	17 : 17 : 13	0/+	0	4	8	0	2	9	8- 9
BMNH 1936.7.43	142 (1)	57 (1)	17 : 17 : 13	0	1	4	8	0	2- 3	8	9- 10
AMNH 58532	141	52	17 : 17 : 15	0/+	1	4	8- 9	0	2	9	10- 11
Indian specimens (n = 26)	138- 149	52- 65	17 : 17 : 13	0/+	1- 2 (3)	4- 5 (2)	(7) 8- 9	0- 1	2- 3	6- 9	(9) 10- 11

TABLE 4 : Comparison between some green pitvipers (genus *Trimeresurus*) of the Eastern Himalayas and China. Key: (1): for specimens from China only, excluding Hainan Island; based on Zhao et al. (1998) and our data; (2): based on Zhao et al. (1998) and our data; (3): values for specimens of this area, from Regenass & Kramer (1981).

Species	Co (m)	Ven	SubC	SupL	Ventrolateral stripe (M/F)	Hemipenis
T. medoensis	17	138- 149	52- 65	(7) 8- 9	Bicoloured/bicoloured	short, thick, spinose
T. stejnegeri (1)	21	154- 172	43- 75	(8) 9- 11 (12)	Bicoloured/bicoloured	short, thick, spinose
T. yunnanensis (2)	19 (21)	150- 172	52- 71	9- 10 (11)	Bicoloured/white or absent	short, thick, spinose
T. popeiorum (3)	21	155- 169	52- 76	9- 11	Bicoloured/white	long, thin, smooth

tures- 15-21°C, in March-October they vary between 22-30°C, maximum being in June-August where temperatures go up to 40-42°C (fide an unpublished paper produced by the State Forest Department Officers at Namdapha National Park).

Most specimens were discovered among bamboos. According to two Lisus who were interviewed separately, these particular “funiche” (green snakes) are often found “sleeping in bamboo” in groups of two or three. The Lisus say that they “sit” in standing bamboos which have worm (?) holes, where they eat frogs and mice. All the specimens that we found in March, and some in early/mid April were found in standing bamboos, in which we found also small frogs and one mouse. Later in the season, from mid- to late May, depending on the climate, specimens are found on bushes and trees. A Lisu reported us that “if the snakes continue to get food inside the bamboo, they won’t come out or will do so much later”. According to the Lisus, this species is active at night, when they can be found on the ground hunting for frogs.

This species is rather common in this area, where the second author collected six specimens within two hours in a single day. In another instance, three animals were observed inside two adjacent internodes of the same bamboo.

The specimen 22.v.99 was found outside a bamboo internode, while the 26.v.99 was discovered resting on a tree. It appears that hibernation in this mountainous, relatively cold area ends between March and May. These snakes are active at least till October, the Lisus even claiming to see them out till November. During our trip conducted from November 1999 to January 2000, all collected snakes were found hibernating (dates on which the snakes were found have been incorporated into the assigned field numbers). They were found inside internodes of a species of bamboo called by the Lisus "wachu alyuh" (wachu meaning bamboo). This is a relatively thin-walled species, often with holes made by rats which sometimes live inside. Frogs and centipedes were also found in these holed internodes. Three of the snakes (28.xii.99[3] to [5]) were found in adjacent internodes of the same "rat-holed" bamboo (two together and one in the next internode).

A reliable source has seen these snakes eating frogs. Another specimen was found dead with a mouse in its stomach.

Juveniles were aggressive and delicate to handle, whereas adults were of a more even disposition, unless irritated, but were found to be noticeably more alert and trickier to handle in the late evenings. The bites of *Trimeresurus medoensis* does not appear to be fatal. Several Lisus have been bitten by this species, including children, and no fatal case was reported. Bites produce pain and swelling, which lasts from 3- 4 days up to 2 weeks. When pressure was applied to the tail base, to sex the snakes, several adults ejected a thin stream of fluid, probably the anal gland secretion, which was colourless, watery and smells like crushed leaves.

DISCUSSION

The systematics of the genus *Trimeresurus* remain controversial, especially among species with an overall green colouration, and all specimens of this group likely to present a taxonomic or distributional interest should be carefully compared either with type specimens of relevant species, or with soundly identified vouchers. Within the frame of an ongoing project on the *Trimeresurus* group, the senior author examined the type specimens of *Trimeresurus medoensis*, which are here redescribed. We also provide a comparison between the types and both our Indian specimens and two specimens from Myanmar which were referred to this taxon. These data are presented below.

Redescription of the types of *Trimeresurus medoensis* (Figs. 6-7).

Holotype.- CIB 73II5208, male, from "Ani bridge, Motuo, Xizang, alt. 1200m", Motuo County, Xizang Autonomous Region, People's Republic of China, collected by Zhao Ermi and Gao Yuan, 3 August, 1973.

Paratype.- CIB 73II5209, male, from the same locality, 1400 m, collected by Zhao Ermi and Wu Xue-en, 3 August, 1973.

In the following description, the first and second values given for each character refer to those in CIB 73II5208 and CIB 73II5209, respectively. Values for symmetric head characters are given in left- right order. When unspecified, the state of a given character is shared by both specimens.

Holotype:

SVL: 546 mm; TaL: 125 mm; TL: 671 mm; HL: 26.25 mm; ratio TaL/TL: 0.186.

Ven: 149 (no preventrals); SubC: 59, paired, plus one terminal scale; anal entire.

Co: [18 at 1HL] : 17 : 17 : 13 scales, rhomboid, moderately keeled, with the exception of those in outermost row which are smooth.

Dorsal scale rows reduction, from17 to 13 rows (17 rows at Ven 30; reductions before Ven 30 were not considered)

3+4 (Ven 100)3+4 (Ven 107)(right)
171513
3+4 (Ven 101)3+4 (Ven 113)(left)

Paratype:

SVL: 496 mm; TaL: 111 mm; TL: 607 mm; HL: 25.87 mm; ratio TaL/TL: 0.183.

Ven: 146 (+ 1 preventral); SubC: 55, paired, plus one terminal scale; anal entire.

Co: [18 at 1HL] : 17 : 17 : 13 scales, rhomboid, moderately keeled like holotype, smooth on first row.

Dorsal scale rows reduction, from 17 to 13 rows (17 rows at Ven 30; reductions before Ven 30 were not considered):

3+4 (Ven 95)3+4 (Ven 101)(right)
171513
3+4 (Ven 95)3+4 (Ven 103)(left)

Body rather elongated for members of the genus *Trimeresurus*, cylindrical but slightly laterally compressed; head triangular, distinctly flattened, rather short, 1.4/1.5 times as long as wide, wide at its base, clearly distinct from a thin neck; snout long, accounting for 29.2/28.0% of total head length, 1.8/1.8 times as long as diameter of eye, flattened, rounded when seen from above, obliquely truncated when seen from lateral side, with a distinct and sharp canthus rostralis; eye very large for a pitviper, eye diameter/distance lower margin of eye- upper lip border ratio 1.25/1.18 (mean values of both sides); nostril-loreal pit distance/nostril-eye distance ratio 0.56/0.58 (mean values of both sides); tail long, cylindrical, tapering, distinctly prehensile.

The hemipenes of the holotype were recently described and illustrated by Guo and Zhang (2001). It is about 15.6 mm long, short and thick, deeply divided and rounded at the extremity of each lobe. The proximal two thirds of the organ bear about 15 spines, with four or five ones distinctly enlarged and two or three shorter but much more developped than the other spines covering the organ; its distal third is calyculate. The shallow sulcus spermaticus divides at the base of the organ and extends to the distal end of each lobe.

Rostral visible from above, 1.4/1.5 times broader than high, triangular; nasal subrectangular, 1.7/1.7 times as long as high, undivided, with nostril in its middle; one pair of enlarged, bean-shaped internasals, 1.6/1.8 times as wide as deep, being about 1.3/1.5 times as long as and about 1.1/1.0 times as wide as adjacent upper snout scales, separated by a small, triangular scale in the holotype, in contact in the paratype; 3- 3/3- 3 canthal scales bordering the canthus rostralis between internasal and corresponding supraocular, of similar size or even smaller than adjacent snout scales; a triangular loreal between upper preocular and nasal; two upper preoculars above loreal pit, both elongated and in contact with loreal; lower preocular forming lower margin of loreal pit; 2-2/2-2 postoculars; one large supraocular on each side, long and wide, about 2.3/2.2 times as long as wide, much wider than the adjacent upper head scales and about 0.9/0.7 time as wide as internasals, strongly indented by upper head scales; scales on upper snout surface enlarged, smooth, juxtaposed, irregular in shape, at the number of 3/4 on a line between the internasals and a line connecting the anterior margins of eyes, slightly larger than scales of the frontal-parietal region; cephalic scales irregular, juxtaposed, smooth on upper head, slightly keeled backwards on occipital region; 9/9 cephalic scales on a line between supraoculars; temporals large, unequal, in 2 or 3 rows, smooth, the lower row much larger than others; one thin, elongated, crescent-like subocular; 8- 8/8- 8 supralabials (SupL); first SupL small and short, totally separated from the corresponding nasal; 2nd SupL high, forming the anterior border of loreal pit, separated from nasal by 1/1 small triangular scale; 3rd SupL largest, pentagonal, approximately 1.3- 1.4/1.4- 1.4 times as long as high, placed in front of the subocular with which it is in contact in both specimens; 4th SupL nearly as high but smaller than 3rd, in contact with subocular in both specimens; 5th and other posterior supralabials distinctly smaller than 4th one, 5th separated from subocular by one scale of similar size, others in contact with first row of temporals; 8-9/8-9 infralabials, first pair in contact with each other, first, second and third pairs in contact with chin shields; 6/5 rows of smooth gular scales; chin shields irregularly arranged.

In preservative, dorsal and upper tail surfaces are very dark brown, nearly black, with a bicoured ventrolateral stripe, orange-red below, white above, running from the neck up to the beginning of the tail on first and second rows of dorsal scales; tail like body, with upper part of posterior half rusty red; upper head surface and temporal regions of same colour than dorsal surface; a faint, whitish yellow postocular streak in holotype, absent in the paratype; venter, chin and throat blackish-brown.

For colouration in life of the types specimens, we refer to Djao and Jiang (1977) and Zhao et al. (1998). It is identical to the Indian specimens described in this paper.

Comparison of available material.- It seems that no further specimens were collected within the People's Republic of China since the discovery of the types, but four specimens, all from Myanmar, have previously been implicitly or explicitly referred to *Trimeresurus medoensis*.

Smith (1943: 518) tentatively, and rather reluctantly, identified three specimens of pitvipers from Myanmar as *Trimeresurus stejnegeri*. In fact, Smith noted the unusual low number of dorsal scale rows, 17 at midbody and 13 before vent, whereas *T. stejnegeri* and *T. yunnanensis* (formerly *T. s. yunnanensis*, see Zhao, 1995) have 21 and 19 (or seldom 21) rows at midbody, respectively, and 15 or 13 rows before vent. These specimens were collected by Mr. R. Kaulback in "Ratnamhti", at 27° 35' N- 97° 47' E (Smith, 1940) and "Nam Ti Valley" (Smith, 1943), Upper Burma, in the area then known as "The Triangle", a region located between the Nmai or Laung Pit River and Mali Kha River. Nam Ti Valley or Ratnamhti is located north of the village of Alangdunhku, at about middistance between Langtao and Nogmung, in northern Kachin State, Myanmar (Finlay, 1995). Djao and Jiang (1977) tentatively referred these specimens to their newly described species *Trimeresurus medoensis* (see the translation in David and Tong, 1977). Of these three specimens, we examined only BMNH 1936.7.4.43. The two other specimens, cited by Smith (1940, 1943), are by all evidence BMNH 1940.6.5.73-74, according to C. J. McCarthy (pers. comm., March 2000). We also examined the specimen of *T. medoensis* cited by Zhao et al. (1998), AMNH 58532, from "Burma: (Myitkyina): Gora", collected on 24 January, 1935 by H. C. Raven. Besides the Chinese types, this specimen was thus the third ever mentioned specimen of *T. medoensis* and confirm the occurrence of this species in northern Myanmar.

These two Burmese specimens are succintly described below, in the order BMNH 1936.7.4.43 then AMNH 58532. (Values for symmetric head characters are given in left/right order. When nothing is mentioned, state of a given character is shared by both specimens).

BMNH 1936.7.4.43 (female):

SVL: 214 mm; TaL: 46 mm; TL: 260 mm; HL: 13.50 mm; ratio TaL/TL: 0.177; Ven: 142 (+ 1 preventral); SubC: 57, all paired; Co: [19 at 1 HL] : 17 : 17 : 13 scales, all smooth.

AMNH 58532 (female):

SVL: 535 mm; TaL: 115 mm; TL: 650 mm; HL: 27.85 mm; ratio TaL/TL: 0.177; Ven: 141 (+ 2 preventrals); SubC: 52, all paired; Co: [21 at 1 HL] : 17 : 17 : 15 scales, nearly all smooth.

Body and head shapes as in the types, head 1.7 times as long as wide in BMNH 1936.7.4.43; snout accounting for 25.9/28.3 % of total head length, 1.6/2.0 times as long as diameter of eye; eye diameter/distance lower margin of eye- upper lip border ratio 1.9/1.2 (mean values of both sides); nostril-loreal pit distance/nostril-eye distance ratio 0.59/0.55 (mean values of both sides); tail long, cylindrical and distinctly prehensile.

Head scalation as in the type specimens, with one pair of bean shaped, enlarged internasals, separated by 1/1 small, triangular scale; 1 triangular loreal; 2- 3/2- 2 postoculars; one large supraocular on each side, long and wide, about 1.6 (measure approximate)/2.3 times as long as wide, much wider than the adjacent upper head scales and about 0.9/0.9 time as wide as the internasals, strongly indented by upper head scales; scales on upper snout surface enlarged, slightly larger than cephalic scales; cephalic scales irregular, juxtaposed, smooth on upper head, weakly keeled backwards on occipital region, at the number of 8/9 on a line between supraoculars; temporals large and smooth; 8-8/8- 9 supralabials (SupL); 1st SupL short and totally separated from the corresponding nasal; 2nd SupL high, in contact with nasal in BMNH 1936.7.4.43, separated by 1 small scale in AMNH 58532; 3rd SupL largest, pentagonal; 4th SupL nearly as high but smaller than 3rd, both in contact with subocular on each side in both specimens; 9- 10/11- 10 infralabials, in contact with chin shields as in the types; 6/6 rows of smooth gular scales.

Dorsal surfaces are dark bluish green, with a ventrolateral stripe, bicoloured in BMNH 1936.7.4.43 (although the red hue has turned to a brownish grey), white, although possibly bicoloured in life in AMNH 58532, running from the neck up to the beginning of the tail on first and second rows of dorsal scales; tail like body, with upper part of posterior half rusty red; upper head surface and temporal regions of same colour than dorsal surface; no postocular streak; venter, chin and throat slightly paler green.

The comparison of the main morphological data appear in Tables 2 and 3 (see Table 1 for abbreviations; other abbreviations are: SnL/HL: snout length/head length ratio.- do/DOL: diameter of eye/distance eye- lower margin of lip.- SupL/SubOc: number of scales between the 3rd and 4th supraoculars and the subocular).

The great morphological similarities of all these specimens allow us to regard them unambiguously as conspecific, thus confirming the presence of *T. medoensis* in north-eastern India and northern Myanmar.

CONCLUSIONS

The examination of 30 specimens, namely a 10-fold increase compared with the number of specimens previously reported in the literature, allow us to present a new definition of this species, and a summary of our knowledge on this species.

Trimeresurus medoensis Djao in: Djao and Jiang, 1977

Trimeresurus medoensis Djao *in* Djao and Djiang, 1977: 66, Pl. 2, fig. 9-1 to 9-5.- Type locality. "Ani bridge, Motuo, Xizang, alt. 1200m", Motuo County, Xizang Autonomous Region (Tibet), People's Republic of China.- Holotype. CIB 73II5208 (male); paratype CIB 73II5209 (male).

Note.- We give above the type locality as it appears in the Chinese text. In the English summary, the type locality reads as: "Near A-nie bridge, Medo Xian, Xizang, alt. 1200m." Motuo, a large city of south-eastern Xizang Autonomous Region, chief of the county of the same name, is often spelt as Medôg or Medo.

Diagnosis and variation.- A species of the *Trimeresurus* group, referrable to the informal subgroup of *Trimeresurus stejnegeri* on the basis of the morphology of short and spinose hemipenes (see below), characterized by an overall bright green dorsum, a first supralabial distinct from nasal, a number of 17 weakly keeled dorsal scale rows at about two head-lengths behind neck and at midbody, 8 or 9 (rarely 7) supralabials, upper-snout scales enlarged, wide supraoculars, and a bicoloured white/red ventrolateral stripe present in both males and females.

The largest known specimen for this species is a female from India, with a snout vent length and total length of 555 mm and 677 mm respectively. The largest male is the holotype from China, with a total length of 671 mm (SVL 546 mm).

Dorsal scale rows: [17-19, rarely 18 or 21, at 1 HL] : 17 [at 2 HL] : 17 : 13 (rarely 15), weakly keeled on upper rows or nearly wholly smooth; Ventrals 138- 149, subcaudals 52- 65.

Hemipenes.- The organs of the holotype were recently described in detail by Guo and Zhang (2001). For a general description of the hemipenes of this species, we refer to the descriptions given above for both the holotype and the Indian specimens, which are very similar.

Guo and Zhang (2001) put emphasis on a difference in the morphology of the hemipenes of *T. stejnegeri* and *T. medoensis*, and placed the two species in two different groups. If the hemipenes of *T. medoensis* are indeed more elongated and divided than those of *T. stejnegeri*, we do not regard this difference as warranting such a distinction. On the basis of the hemipenial morphology, Guo and Zhang (2001) also referred to their *medoensis*-type the species *Protobothrops kaulbacki* and *P. xiangchengensis*, which are otherwise morphologically very distinct. We here still regard the hemipenes of *T. medoensis* and *T. stejnegeri* as closely related, and these species as belonging to the same subgroup within the genus *Trimeresurus*.

Similar species.- This species is the only one in the *Trimeresurus stejnegeri* subgroup to have

17 rows at midbody. However, it may be superficially confused with any other green species of *Trimeresurus*. It differs immediately from *T. albolabris* and *T. erythrurus* by its flat head, elongated body, a first supralabial distinct from the nasal, a much lower number of dorsal scale rows (at least 21 for *T. albolabris* and *T. erythrurus*), and the presence of the bicoloured ventrolateral stripe.

However, it could be confused with green species which have the first supralabial totally separated from nasal, namely *T. gramineus*, *T. popeiorum*, *T. stejnegeri*, *T. tibetanus* and *T. yunnanensis*. From all these species, *T. medoensis* differs by the lower number of dorsal scale rows, 17 vs. 19 (rarely 21) in *T. yunnanensis* and 21 in other taxa. Furthermore, it is separated from *T. gramineus* by the presence of the bicoloured ventrolateral stripe. From *T. tibetanus*, it is distinguished by the absence of the reddish brown vertebral and cephalic markings of this species, a much flatter head and a much higher number of subcaudals. From *T. popeiorum*, it is also separated by the totally different shape of the hemipenes, long, thin and not spinose in *T. popeiorum*.

In its range, *T. medoensis* could be confused only with *T. popeiorum*, if hemipenes are not available, and *T. yunnanensis*. Main characters allowing to distinguish these species, as well as *T. stejnegeri*, occurring as far west as Yunnan Province in China, are given in Table 4.

T. medoensis shows also some similarities, such as the enlarged upper snout scales, with some specimens from Thailand currently referred to as *T. stejnegeri*. The systematics of the *stejnegeri*-group is extremely confused and is still provisional, but the validity of *T. medoensis* cannot be questioned.

Sexual dimorphism.- The base of the tail in the adult male is distinctly swollen. The numbers of ventrals show little conclusive variation correlated to the sex. There are only few differences in the relative size of the tail and the average number of subcaudals, with the following values:

Ventrals:males: 138- 149 (x = 144.0)females: 141-149 (x = 143.5)

Subcaudals:males: 54- 65 (x = 59.1) females: 52-60 (x = 54.6)

Ratio TaL/TL males: 0.17- 0.21 (x = 0.193) females: 0.16- 0.19 (x = 0.172)

Lastly, the sexual dimorphism is not marked by the presence of the bicoloured ventrolateral stripe, which occurs in both males and females, as in Chinese specimens of *T. stejnegeri*, but to the contrary of the southern Indochinese populations currently referred to *T. stejnegeri*, in which the ventrolateral stripe in females is either white or absent (David et al, unpublished).

Distribution (Map 1).- This species inhabits montainous areas under wet tropical and subtropical climates. Up to now, it is known from a few scattered localities of the three following countries:

India: Definitely known only from the vicinity of Gandhigram, Upper valley of the Noa Dihing River, State of Arunachal Pradesh, as reported here.

Myanmar: It is only known only from two localities in the north of this country, namely Nam Ti Valley, in the north of Kachin State, and an unidentified place in the vicinity of Myitkyina, southern Kachin State.

People's Republic of China: It is currently known only from Xizang Autonomous Region(Tibet), in the vicinity of Motuo (or Medôg), which is the type locality.

Natural history.- This species inhabits wet, forest-covered hills and mountains between 1000 and 1400 m a.s.l. Data for Indian specimens were provided above, and represent as yet most of our knowledge of this species. Most specimens were associated with a local species of bamboo, having been collected either hidden inside nodes of bamboos or perched on these bamboos. The types were collected on a mountain path crossing a forest on a wet slope. *Trimeresurus medoensis* is mainly an arboreal species, but also forages on the ground, as the type specimens were collected in day time while they were crossing a path bordered with vegetation in a rainy day. Other data on its biology are very limited. The known preys include frogs and mammals. Lastly, the reproduction of this species is still entirely unknown.

Further surveys of the herpetofauna of remote, montane areas of Eastern Himalaya will undoubtedly reveal a wider range for *T. medoensis*. Its occurrence may be expected in the Yunnan Province of China, and in other mountain ranges of India and northern Myanmar. Also, the examination of preserved specimens registered as *Trimeresurus stejnegeri* might show up more specimens.

The herpetological biodiversity of this area is high. The list of reptiles observed in the region of Gandhigram will be published elsewhere, but, as far as pitvipers are concerned, two species are already known besides *T. medoensis*, namely *Ovophis monticola* and *Protobothrops jerdonii*. The addition of *T. medoensis* to the Indian snake fauna increases to 37 the number of venomous landsnakes (Elapidae, Viperidae and Crotalinae) and to 18 pitvipers, respectively, in this country, of which 15 belong to the *Trimeresurus* group (David and Ineich, 1999).

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CYTOGENETIC REVIEW AND EVOLUTION OF KARYOTYPES IN THE SPECIES OF THE GENUS *PHRYNOCEPHALUS* KAUP, 1825 (SAURIA, AGAMIDAE) FROM THE EAST PALAEARCTIC

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(with one text-figure)

ABSTRACT.– **Comparative cytogenetic analysis of 25 species and subspecies of *Phrynocephalus* has shown more karyological heterogeneity than considered earlier. The group having 48 chromosomes (*P. ocellatus* and *P. interscapularis*) and the group with 46 chromosomes (*P. guttatus* and *P. helioscopus*) are distinguished, the group "*rossikowi*" is characterised by the presence of 48 and 46 chromosome sets. The basic number (NF) varies from NF = 46 (the group "*guttatus*") to NF = 72 (the group "*interscapularis*"). It is suggested, that an ancestral karyotype included 48 telocentric chromosomes, and evolutionary diversification of the group took place in two directions - without changing diploid number and with its reduction. Increase of the NF might be explained mainly by paracentric inversions, deletions and duplications, while reduction of macrochromosomes number in diploid set (the group "*helioscopus*"), by the centric fusion of two telocentric chromosomes in the course of evolution.**

KEY WORDS.– ***Phrynocephalus*, Agamidae, cytogenetics, karyotypes, evolution, East Palearctic.**

INTRODUCTION

Systematic revision of the genus *Phrynocephalus*, undertaken by Sokolovsky (1974, 1975, 1977) on the base of karyotype as the principal taxonomic character, clarified several questions concerning taxonomy and evolution of the group. In particular, five groups of closely related species were recognized: the "*rossikowi*" group, the "*reticulatus*" group, the "*helioscopus*" group, the "*interscapularis*" group, and the "*guttatus*" group. This division appeared to be meaningful and is referred to in the present work; at the same time, taxonomic status of some species remained problematic. A number of new species and subspecies were described by subsequent authors (Shcherbak and Golubev, 1979; Sattorov, 1981, 1984, et. al.).

Karyological investigations of the genus *Phrynocephalus* were carried out at our laboratory since 15 years and included all species and subspecies known from the East Palaearctic (territory of the former USSR), with the only exception of *P. maculatus*. The latter species should be considered critically endangered, since only a few specimens were registered on the studied territory in the last 10 years (S. Shammakov, personal communication). The present paper is a review summarising and analysing all the data on cytogenetics and chromosome evolution of the genus *Phrynocephalus* within the studied territory.

MATERIALS AND METHODS

Materials for this study were collected during the expeditions to Central Asia, Kazakhstan and southern Russia organized by the National Museum of Natural History, Kiev (with participation of the author) in 1986-1991. Altogether, 119 specimens belonging to 18 species, subspecies and forms were investigated (Table 1, Fig. 1).

Chromosome preparations were obtained from cellular suspensions of blood and testis by the smear and the so called dripping (pipetting) methods, as described by MacGregor and Warley (1986) and modified by Manilo (1989). The cells at the stage of spermatogonial division (mitotic metaphase), spermatocyte 1 (diakinesis bivalents) and spermatocyte 2 (meiotic metaphase II) were observed in samples of testis tissues. All slides were examined under the microscope Biolam L-212 with magnification 90x10. Metaphase plates with clear distribution and configuration of chromosomes were photographed.

The form of chromosomes was defined basing on the position of centromere according to the classification of Lewan et al. (1964), modified after Manilo (1989). As microchromosomes were defined the chromosomes smaller than 1 mkm, of visually unrecognizable form (King, 1973).

RESULTS AND DISCUSSION

Descriptions of karyotypes.- The "*rossikowi*" group. Only one species with two subspecies, viz. *P. rossikowi rossikowi* and *P. r. shammakovi*, is included here. Karyotype of the former subspecies is characterized by the interpopulational polymorphism in diploid number (2n = 46 in population from Lebab and 2n = 48 in that from Baktybulakh, both in Turkmenistan). In the other subspecies, we observed polymorphism even between the specimens of one and the same population (Serniy Zavod, Turkmenistan) (Manilo and Golubev, 1993a; Golubev et al., 1994; Table 1).

The "*guttatus*" group. Two species, viz. *P. guttatus* and *P. versicolor*, are recognized now. Such forms as *alpherakii* Bedr., *moltschanovi* Nik., *kushackewitschii* Bedr. and *salenskyi* Bedr. have been included by previous reviewers in *P. guttatus* or regarded as closely related species, while the forms *bogdanowi* Bedr., *paraskiwi* Semenov et al., and *hispida* Bedr. have been assigned to *P. versicolor (*Bedriaga, 1909; Nikolsky, 1915; Terentjev and Chernov, 1949; Peters, 1984; Semenov et al., 1987).

Karyological investigation of all *P. guttatus* forms showed identity of their chromosome numbers and basic morphologies (Table 1). However, the forms *guttatus*, *moltschanovi* and *kushackewitschii* were characterised by the occasional presence of satellites on the first pair of macrochromosomes. Furthermore, some remarkable differences in the chromosome morphology were observed at the diakinesis stage (metaphase I of the meiosis in the testis). Three groups could be distinguished by different numbers of ring and cross bivalents (Manilo and Golubev, 1993b):

all bivalents ring or stick-shaped: the forms *moltschanovi*, *kushackewitschii*, *alpherakii*, and, partially, *guttatus* s.str.;

one or two cross-shaped bivalents, the remainder as in the previous group: the form *salenskyi* and some specimens of *guttatus* s.str.;

two to four cross-shaped bivalents, the other as in the first group: the form *hispida*.

Thus, the varieties discussed here can be ordered according to the shape of their diakinesis bivalents. Noteworthy, *P. g. salenskii* from Zaissan Depression is closer in this aspect to *P. v. hispida* than the other varieties of *P. guttatus* and actually occupies an intermediate position between the two species.

The "*ocellatus*" group (= "*reticulatus*" of Sokolovsky, 1974). Modern reviewers (Darevsky et al., 1976; Golubev, 1991) include here *P. raddei raddei, P. raddei boettgeri, P. ocellatus ocellatus* and *P. o. bannikovi*. Sokolovsky (1974) described karyotypes of *P. raddei* from near Uch-Adji, Turkmenistan, and *P. reticulatus* from Termez, Uzbekistan (Table 1). However, the latter material was probably misidentified, since only *P. raddei boettgeri* occurs around Termez, and *P. ocellatus* (= *P. reticulatus*) was never reliably recorded in this area. The first description of *P. ocellatus* karyotype is therefore that of Manilo (2000), and the karyological characteristics reported by Sokolowsky can be attributed to *P. r. boettgeri*. Karyotypes of *P. o. ocellatus, P. o. bannikowi* and *P. r. raddei* are similar to each other (2n = 24M (A + T) + 24m (a + t) = 48, NF = 48). In contrast, *P. r. boettgeri* has two pairs of metacentric chromosomes (9th and 12th), while retaining the same diploid number: 2n = 24M (4sV + 20A) + 24m (24a + t) = 48; NF = 52. This difference may

TABLE 1: Karyotypes in the genus *Phrynocephalus* from the Eastern Palearctic. Abbreviations: N - number of studied specimens, n - gaploid chromosome number, 2n - diploid chromosome number, NF - basic number (number of arms), M - macro-, m - microchromosomes, A - acrocentric, T - telocentric, sT - subtelocentric, sV - submetacentric, V - meta-centric chromosomes, v. - village, st. - railway station

Taxon	Locality	N	n	2n	Chromosomal formula	NF	References
Phrynocephalus rossikowi	Turkmenistan, 70 km NW of Chardzhow			48	All chromosomes telocentric 24M+24m	48	Sokolovski, 1974
P. rossikowi rossikowi	Turkmenistan, v. Lebab; Turkmenistan, v. Baktybulakh	2 4	23 24	46 48	22M(22A+T)+24m(24a) 22M(22A+T)+26m(26a)	46 48	Manilo and Golubev. 1993a; Golubev et al., 1994.
P. rossikowi schammakowi	Turkmenistan, Unguz, Serniy Zavod	5	23 24	46 48	24M(24A+T)+22m(22a) 24M(24A+T)+24m(24a)	46 48	Manilo and Golubev, 1993a
P. raddei raddei	Turkmenistan, st. Uch-Adji of the Middle-Asian Railway			48	All chromosomes telocentric, 24M+24m	48	Sokolovski, 1974.
	Turkmenistan, North of Small Balkhan	3	24	48	24M(24A+T)+24m(24a+t)	48	Manilo, 2000
P. boettgeri	South Tadjikistan, near Ayvadzh	7	24	48	24M(4sV+20A)+24m(24a+t)	52	Manilo, 2000
P. reticulatus	Uzbekistan, 14 km N of Termez			48	All chromosomes telocentric, 24M+24m	48	Sokolovski, 1974
P. ocellatus ocellatus	Uzbekistan, near Bukhara; Uzbekistan, near v. Uchkuduk	1 1	24	48	24M(A+T)+24m(a+t)	48	Manilo, 2000
P. ocellatus bannikowi	West Turkmenistan, Near Kyzylkaj	2	24	48	24M(A+T)+24m(a+t)	48	Manilo, 2000
P. helioscopus	Turkmenistan, st. Bami			46	22M(2sV+20T)+24m(24t)	48	Sokolovski, 1974
P. helioscopus persicus	Armenia			44	20M(2V+18T)+24m(24t)	46	Arronet (Kulikova), 1965
P. helioscopus helioscopus	Turkmenistan, valley of Uzboj; Turkmenistan, near Maly Balkhan, plateau Meshkhed-i-Messerian Kazakhstan, plateau Usturt	3 7 3	23	46	22(2sV+20A)+24m(24a)	48	Manilo, 2000
P. helioscopus Saidalievi	Tadjikistan, near v. Kim	6	23	46	20M(2sV+18A)+26m(26a)	48	Manilo, Golubev, Sattorov, 1991
P. strauchi	Tadjikistan, st. Djumshi; Tadjikistan. Near v. Kijaly; Tadjikistan, Near Kanibadam; Tadjikistan, near v. Yakkateran; Tadjikistan, Leninabad Region, right bank of Kajrakkum Reservoir	3 6 2 4 4	23	46	22M(2sV+20A)+24m(24a)	48	Manilo, 2000
P. maculatus	Turkmenistan			46	22M(2sV+20T)+24m(24t)	48	Sokolovski, 1975
P. interscapularis	Uzbekistan, 17 km north of Sherabad			48	24M(24T)+24m(24t)	48	Sokolovski, 1974;
	Turkmenistan, near Ashkhabad; Turkmenistan, District of Unguz.	5 1		48	24M(6sT+8sV+4V+6A)+ +24m(6v+18a)	72	Manilo, 2000
P. sogdianus				48	24M(24T)+24m(24t)		Sokolovski, 1974;
	South Tadjikistan, near Ajvadzh	4	24	48	24M(6sT+8sV+4V+6A)+ +24m(6v+18a)	72	Manilo, 2000
P. mystaceus	Turkmenistan, st. Karabata of the Middle				24M(24sT)+24m(24t)		Sokolovski, 1974

	Asian Railway; Turkmenistan, near Ashkhabad;	2					
	Turkmenistan, Serniy Zavod;						
	Turkmenistan, near Chaban-Kazgan;	1	24	48	24M(6sT+8sV+4V+6A)+ +24m(6v+18a)	72	Manilo, 2000
	Kazakhstan, near Andreevka	2 2					
P. guttatus	Daghestan, Kara-Nogaj District, state farm "Chervlennyje Buruny"			46	24 M(T)+22m(t)	46	Sokolovski, 1974
P. guttatus guttatus	Russia, Stavropol Region; North Dagestan	2 3	23	46	24M(24A)+22m(22a)	46	Manilo and Golubev, 1993b
P. guttatus moltschanovi	Karakalpakia, North Kyzylkum	2	23	46	24M(24A)+22m(22a)	46	Manilo and Golubev, 1993b
P. guttatus alpheraki	East Kazakhstan. Karakuldek	3	23	46	24M(24A)+22m(22a)	46	Manilo and Golubev, 1993b
P. guttatus kushackewitschii	East Kazakhstan. NW shore of Kapchagaj Reservoir;	5					Manilo and Golubev, 1993b
	Kazakhstan, Taldy-Kurgan Region, near v. Andreevka	9	23	46	24M(24A)+22m(22a)	46	
P. guttatus salenskyi	East Kazakhstan, Zaissan Depression near Kartal West	6					
	Kazakhstan, Kulundzha sands near Kaznakovskaja Pereprava; East	2	26	46	24M(24A)+22m(22a)	46	Manilo and Golubev, 1993b
	Kazakhstan, North Zaissan and Irtysh sands near Chingilda	3					
P. versicolor	Mongolia, Central Gobi			46	24M(T)+22m(22t)	46	Sokolovski, 1974

support the higher taxonomic status of the latter subspecies.

The "*helioscopus*" group. According to the latest reviews, it includes three species: *P. strauchi*, *P. maculatus* and *P. helioscopus*, the latter with three subspecies (*P. h. helioscopus, P. h. persicus* and *P. h. saidalievi*). All these taxa were studied cytogenetically by Arronet (1965), Sokolovsky (1974), Manilo et al. (1991) and Manilo (2000) (Table 1). Their karyotypes differ from those of the other *Phrynocephalus* species in their smaller chromosome number (2n = 46), presence of a big submetacentric chromosome and satellite chromosomes (B-chromosomes) attached to the second pair.

The "*interscapularis*" group. Three species included here (*P. interscapularis, P. mystaceus* and *P. sogdianus*) differ in the presence of many biarmed chromosomes and, consequently, high value of NF (Table 1).

Evolution of karyotypes in the genus *Phrynocephalus*.- According to the world catalogue of agamids (Wermuth, 1967), the genus *Phrynocephalus* includes 38 species; the later revision (Moody, 1980) deals with 39 species. Phylogenetically this taxon is most tightly connected with the genera *Stellio* and *Trapelus* (Sokolovsky, 1974, 1975, 1977; Joger, Arano, 1987). Furthermore, the data obtained by the genetical and biochemical methods, including DNA hybridization, have shown, that *Trapelus* is the oldest group, while dichotomy (divergence) of *Phrynocephalus* and *Stellio* took place later (Ananyeva and Sokolova, 1990). On the other hand, the hypothesis about the common origin of *Trapelus* and *Phrynocephalus* is supported by the data on the morphology, ecology and biogeogfraphy of agamids (Moody, 1980).

There are two modern hypotheses explaining the evolution of *Phrynocephalus* karyotypes.

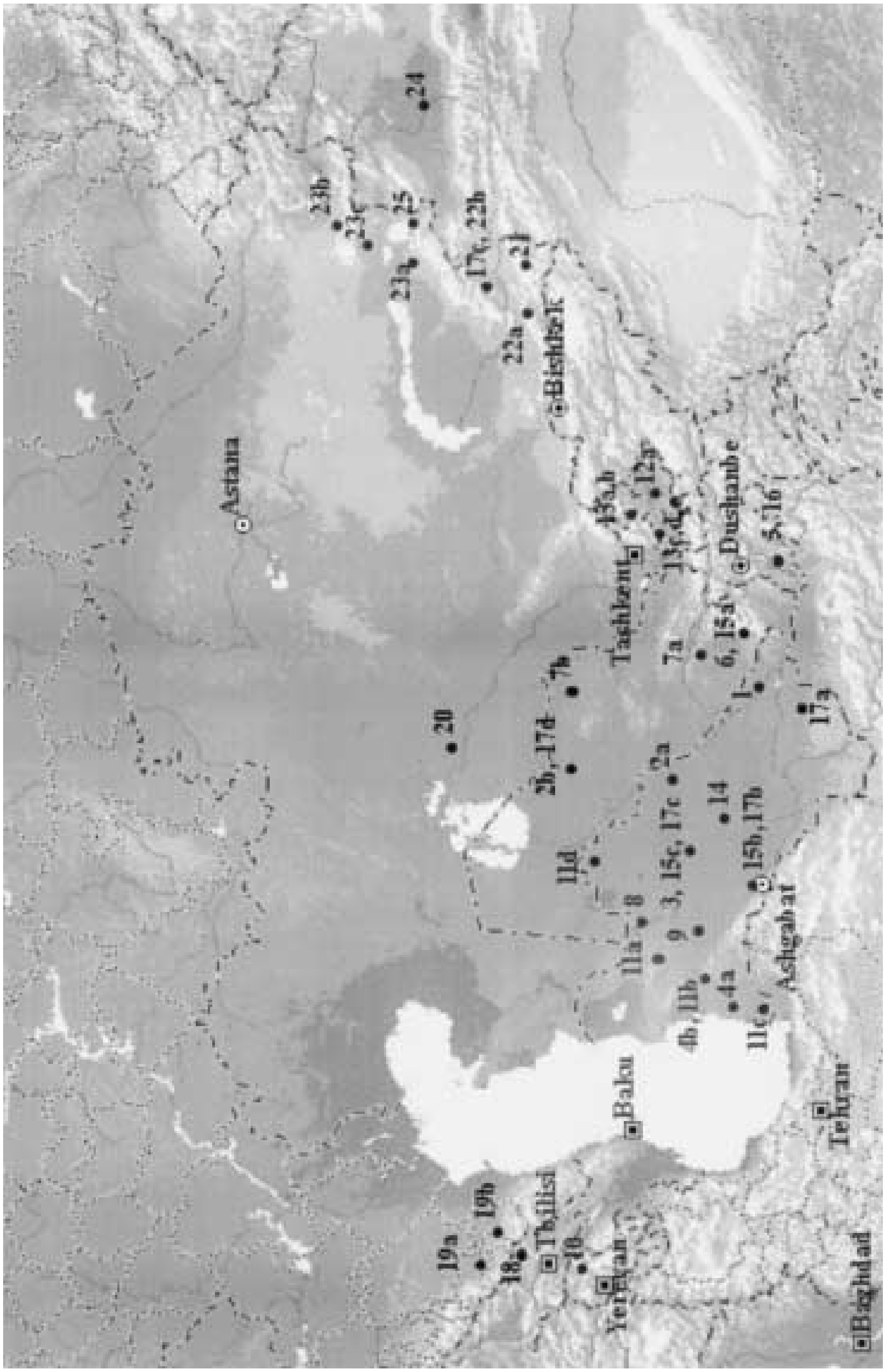

FIGURE 1: Probable path of karyotypic evolution in the genus *Phrynocephalus* within the East Palaearctic (territory of the former USSR).

Both define an ancestral karyotype as that characterizing morphologically primitive groups. According to Sokolovsky (1975), it included 48 telocentric chromosomes being most near to that of *P. raddei* and *P. ocellatus*. The second hypothesis suggests an ancestral karyotype of 36 biarmed chromosomes; such a karyotype corresponds to that of the primitive rock agamas (*Stellio*) and might give origin to the chromosome sets of *Agama* and *Phrynocephalus* by means of centric divisions (Gorman, 1973).

The data on karyotype evolution in reptiles accumulated in the literature (Vorontsov, 1966; Sokolovsky, 1975; Kupriyanova, 1986; Kluge, 1967; Gorman, 1973; King, 1973, 1979, 1985; Bickham, Baker, 1979; Lowe et. al., 1979, et al.) suggest that chromosome fusion was a prevailing trend in the evolution of Squamata, leading to the diminution of chromosome numbers (in comparison with initial state) accompanied by the internal rearrangements in some chromosomes without any change in their number. Division of chromosomes is also possible, but seems to be a very complicated and therefore an improbable process (Mattey, 1931; White, 1954, 1957, 1965, 1973, 1978; Olmo, 1986). Taking into account the mentioned arguments, we assume that initial karyotype of the studied group included 48 telocentric chromosomes. This set ($2n = 48$, $NF = 48$) is seen in the group "*ocellatus*". In the "*interscapularis*" group, the diploid number was retained, but the number of arms has increased ($NF = 72$). The "*rossikowi*" group demonstrates polymorphism in diploid number ($2n = 46\text{-}48$). Finally, two groups ("*guttatus*" and "*helioscopus*") show chromosome rearrangements changing the diploid number ($2n = 46$) and, sometimes, also the number of arms (Table 1, Fig. 2).

CONCLUSIONS

Analysis of 25 species and subspecies of *Phrynocephalus* has shown that this group is rather peculiar and heterogeneous from the cytogenetic point of view. The main features of the genus are clear distinction between macro- and microchromosomes, limited variation of the diploid and the basic numbers (except the "*helioscopus*" and "*interscapularis*" groups), prevalence of acro- and subtelocentric chromosomes in the karyotype and presence of satellites (B-chromosomes) on the first and second pairs in the majority of forms.

Polymorphic pairs indicating presence of the morphologically distinct sex chromosomes were not found.

Some variation of the diploid numbers was shown on the interspecific level (the groups characterised by 46 and 48 chromosomes), as well as within particular species or even subspecies (populations with 46 and 48 chromosomes in *P. rossikowi schammakowi*).

Comparison of *Phrynocephalus* with the other groups of lizards shows more cytogenetic similarity to gekkonids than to lacertids, in contrast to the point of view of Sokolovsky (1974). Ancestral karyotype of the genus included in all probability 48 telocentric chromosomes. Evolutionary transformations in most of the species might include chromosome re-arrangements changing or not changing the diploid number (deletions, duplications, inversions, as well as translocations and fusions).

The present analysis confirms significance of karyotype for the systematics of closely related species and subspecies, and may provide differentiating or integrating characters in those cases when the traditional morphological methods are insufficient. Phylogenetic interpretation of the similarities and differences observed between the genera should be based on more complete cytogenetic data and an analysis of morphological characters; this is a task for the future study.

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DESCRIPTION OF ADVERTISEMENT CALLS OF FIVE *BUFO* SPECIES (BUFONIDAE) FROM SOUTH AND SOUTH-EAST ASIA

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(with five text-figures)

ABSTRACT.– **The advertisement calls of five Asian species of the genus *Bufo* are described, three of them (*Bufo asper*, *Bufo parvus* and *Bufo stomaticus*) for the first time. For each species, numerous temporal parameters are given, as well as the mean values of the frequency bands. Each call is illustrated by an oscillogram and a spectrogram, and is compared with available data from the literature for the calls of the same as well as closely-related species.**

KEY WORDS.– **Bufonidae, advertisement call, oscillogram, spectrogram, south and south-east Asia.**

INTRODUCTION

Advertisement call in frogs is the primordial factor in breeding: it advertises the male's presence to reproductive females, and plays a role in species recognition, mate choice and establishment of males territories (e. g., Blair, 1956, 1958, 1962, 1964; Bogert, 1960; Littlejohn, 1977; Gerhardt, 1991). A knowledge of a large array of advertisement calls belonging to numerous species from different habitats would permit the understanding of the influence of the environment on call structure, and what proportion of the call comes from a common ancestor, and for adding new characters in phylogenies (Nelson, 1973; Cocroft and Ryan, 1995).

In the morphologically conservative species of the genus *Bufo* (225 species: Glaw et al., 1998), bioacoustical analysis is a powerful taxonomic tool (e. g., Blair, 1972; Tandy and Keith, 1972).

Studies on the advertisement calls of the Asiatic toads are not numerous and the calls of only a few species have been described: *Bufo scaber* (Bogert and Senanayake, 1966; Kanamadi et al., 1995), *B. melanostictus* (Heyer, 1971; Martin, 1972; Kanamadi et al., 1995; Roy et al., 1998), *B. latastii* (Dubois and Martens, 1977), and the species of the *B. viridis* group (Dubois and Martens, 1977; Schneider and Egiasaryan, 1995; Castellano et al., 1998), *B. juxtasper* (Matsui, 1982), *B. gargarizans miyakonis* (Maeda and Matsui, 1999), *B. japonicus* (Maeda and Matsui, 1999), *B. torrenticola* (Maeda and Matsui, 1999) and *B. pseudoraddei* (Stöck et al., 1999).

MATERIALS AND METHODS

The calls of five bufonid species were recorded in the field in Nepal, India, and Thailand (Table 1). All specimens are deposited in the collection of the Muséum National d'Histoire Naturelle, Paris (MNHN). The air and water temperatures are reported for each locality when available.

Recordings were made using either a Uher Report 4000 and a Sony TCDM-5 tape recorders, and Scotch magnetic 215 and TDK SA-X90 tapes. Oscillograms, spectrograms and spectrum were prepared with the software tool Canary 1.2 from the Cornell Laboratory of Ornithology (Charif et al., 1995). The sampling rate used to convert the signals to digital format was 22.254 Hz with 16-bit precision. A filter bandwidths of 349.70 Hz and frame length of 512 points were used for both spectrogram and spectrum analyses.

Measurements were taken from the oscillogram (time measurements) and the spectrum (frequency measurements). The time parameters are duration of the calls (dc) and intervals between the end of one call and the beginning of the following (dic), duration of notes (dn) and intervals between notes (din), number of notes per call (nn) and the note rate (number of notes per second, nns). When the notes were groups of pulses, we give the number of pulses per note (np), duration of pulses (dp) and intervals between pulses (dip), and the pulse rate (number of pulses per second, nps). We analysed the spectrum of few notes of the signal. The values given in the tables are the means of the values of the same frequency band of these notes. The frequency parameters are dominant frequencies and harmonic bands (f1b to f3b, corresponding to the three first emphazised frequency bands including the dominant frequency, when possible).

DESCRIPTION OF CALLS

The call of *Bufo asper* Gravenhorst, 1829 from Khao Chong, Thailand was recorded in captivity. It is composed of two long notes (0.298 ± 0.072 s; n = 11), the former (0.361 ± 32 s; n = 11) always longer than the latter (0.234 ± 0.028 s; n = 11), with a periodic amplitude modulation (Fig. 1, Table 2) of 6 ± 1 ms (n = 6). The amplitude of notes increases regularly until midway then decreases regularly, or reaches its maximum amplitude quickly and decreases slowly. The notes are emitted at a low note rate (2.94 notes per second on average). The fundamental component is the same as the dominant which lies at 866 ± 34 Hz (n = 22). This call is very distinct from the other *Bufo* calls studied here and differs by its short duration, its reduced number of notes and its low note rate. The conditions of the recording leave some doubt about the accuracy of some temporal parameters but we present them nonetheless, as no other data for the species are avaible. In spite of the singular shape of the signal among the bufonids, it is certainly an advertisement call: the calls are repeated at regular intervals and all identical. Furthermore, the release call has been observed in captivity.

The recording of *Bufo latastii* Boulenger, 1882 was done at Shergol in Wakka River bed, a steppe area of Ladakh, Jammu & Kashmir, India. By the end of June, the retreat of the river left small swampy areas from which males called sitting in water. The males began to sing at dusk, the calls lasted about one hour and stopped when the temperature fell (e. g., at 13.5°C on the day of the recording). The call parameters of two sequences emitted by the same individual have been measured in detail (Table 2). The call of *B. latastii* (Fig. 2) lasts on average 3.43 s and consists of a continous series of 24-30 unmodulated notes. The notes are produced regularly with the same intensity from the beginning until the end and with a note repetition rate of about 8 notes per second. The notes do not have a multi-pulse structure and their amplitude increases gently, reaches its maximum in the middle and decreases slowly. Each note sounds like a faint whistle. The dominant frequency is 1466 ± 8 Hz (n = 6) and corresponds to the fundamental frequency. These data agree with those measured by Dubois and Martens (1977) although our data point to a slightly higher frequency: these authors measured a fundamental frequency of 1200-1300 Hz and identified the first harmonic band between 1800-2000 Hz. The duration of notes is similar but the note rate is slower in the advertisement calls described in this study (Nns < 8 versus 8 and 13 notes per second in the results of Dubois and Martens, 1977). However, it is worth noting that Stöck (1998) put forward the hypothesis that the toad recorded by Dubois and Martens (1977) could be a tetraploid green toad (*Bufo viridis* complex).

The calls of individuals of several populations of *Bufo melanostictus* Schneider, 1799 were analysed. In Sanichare (low altitude plain of Terai in Nepal) the recording was done at the beginning of the monsoon, at the end of April. The males (Fig. 3) were singing isolated from each other on hummocks, out of the water, in the paddy-fields near a road. When disturbed they jumped into the water like European green frogs. The calls were emitted toward the water. *B. melanostictus* was observed singing with *B. stomaticus* as well as *Fejervarya limnocharis* and *Euphlyctis* *cyanophlyctis*. The male *B. melanostictus* recorded in India was captured during the first rains of the monsoon, on 1 July 1984, and was recorded after capture in a house where it was kept before fixation. The two calls recorded in Nepal are the beginning of two different calls emitted by the same individual. The advertisement call of *B. melanostictus* (Fig. 4, Table 3) is a long call, usually lasting between 10 and 20 sec (mean = 13.5 ± 8.0; n = 32) but can reach 45 sec. This call consists of a continuous series of notes (themselves composed of groups of pulses). The first notes are long with amplitude modulation. The length of the notes increases quickly forming pulse groups within the note and the amplitude modulation becomes more pronounced. The duration of pulses (even within the same note) is extremely variable but always lower than 10 ms (Fig. 4c). The acoustic features of the call of *B. melanostictus* is very similar to the call of *B. latastii*, except for the structure of the notes. The note rate is similar in both the species. However, to the human ear, it sounds quite different from that of *B. latastii*. The call of *B. melanostictus* sounds rather like a rattle.

Bufo parvus Boulenger, 1887 is a typical forest species. Both males (MNHN 1987.3671 and 1987.3685) were recorded in the field, while calling on the ground or perched on the vegetation near water (puddle, brook). The males (MNHN 1987.3670 and 1987.3684) continued to emit their advertisement call after capture and were recorded in the hand. The male (MNHN 1987.3670) had a brown reddish colouration with orange cephalic crests, parotoid glands and upper arms showing that it was in full breeding condition. The call of *B. parvus* (Fig. 5, Table 2) consists of short sequences of notes (5 to 11 notes per sequence) lasting on average 0.58 s. The amplitude of notes varies within a sequence. The amplitude of the notes increases at the beginning, until a peak in the middle of the note, then decreases until the end. The dominant frequency is equal to the second frequency band when the software calculates a mean for the whole note. However, in the middle of the note, the dominant frequency changes to the third band.

At Sanasar (in Jammu and Kashmir, India), the males of *Bufo stomaticus* Lütken, 1862 were calling while gathered in numerous ponds. At Burimorang Uku Dokan, Nepal, all males (Fig. 6) were singing in a paddyfield, in sympatry with *Sphaerotheca breviceps*, at the confluence of two rivers. The recording was made on 24 July 1973 after the moonson. The individuals recorded belong to two distinct populations in two widely distant regions of the Himalayan range. The call of *B. stomaticus* (Fig. 7, Table 3) is quite long (21.4 ± 3.4 s; n = 5 in the Indian male and 8.9 ± 4.4 s; n = 22 in the Nepalese individuals) and composed of a series of relatively long note at a train of 20.5 ± 4.1 pulses. Because of the long duration of notes, the call rate is slow (about 3 notes per second). There are intervals between pulses and the amplitude of pulses is greater near the middle of the note. In the male (MNHN 1995.2546) from Jammu and Kashmir, India, the beginning note of the call is longer than those following (see Fig. 7b). This feature is not present in the call samples of the males from Nepal which were obtained in the middle of a call. The intensity of the notes increases with time and the duration of notes decreases under 300 ms, and stays constant until the end of the call. The notes begin with a group of four pulses, followed by groups of two pulses. The interpulse intervals are extremely variable within the same note. The amplitude of the pulses is maximal initially, then decreases quickly. The dominant frequency is about 2442.6 ± 116.9 Hz (n = 12) and is the same as the fundamental. As in *B. melanostictus*, the call of *B. stomaticus* is composed of pulses but the structure of their notes differs greatly. Furthermore, in *B. stomaticus*, the number of pulses per note is much higher and relatively stable throughout the call, except for the beginning note. The notes break up into a 4-pulse group followed by a 2-pulse group.

DISCUSSION

The pattern of the advertisement calls of the species belonging to the genus *Bufo* is relatively uniform (Cocroft and Ryan, 1995). They tend to share a similar structure consisting of a long train of pulses or notes, the maximum energy released

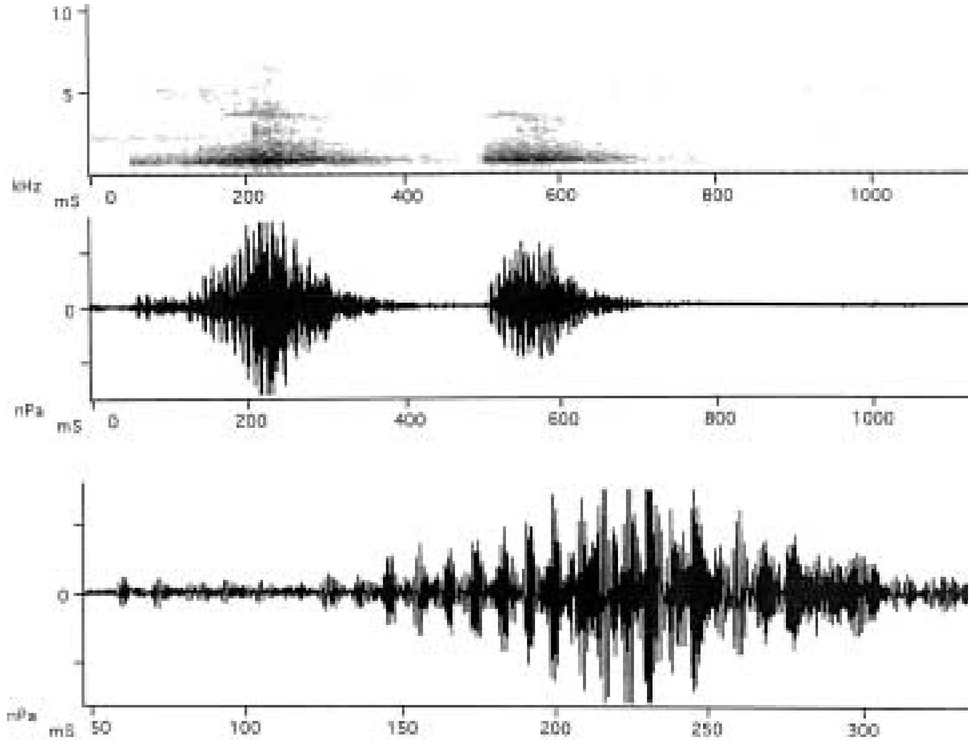

FIGURE 1: The two notes of the mating call of *Bufo asper* (a: spectrogram, b: oscillogram, c: detailed oscillogram of note 1).

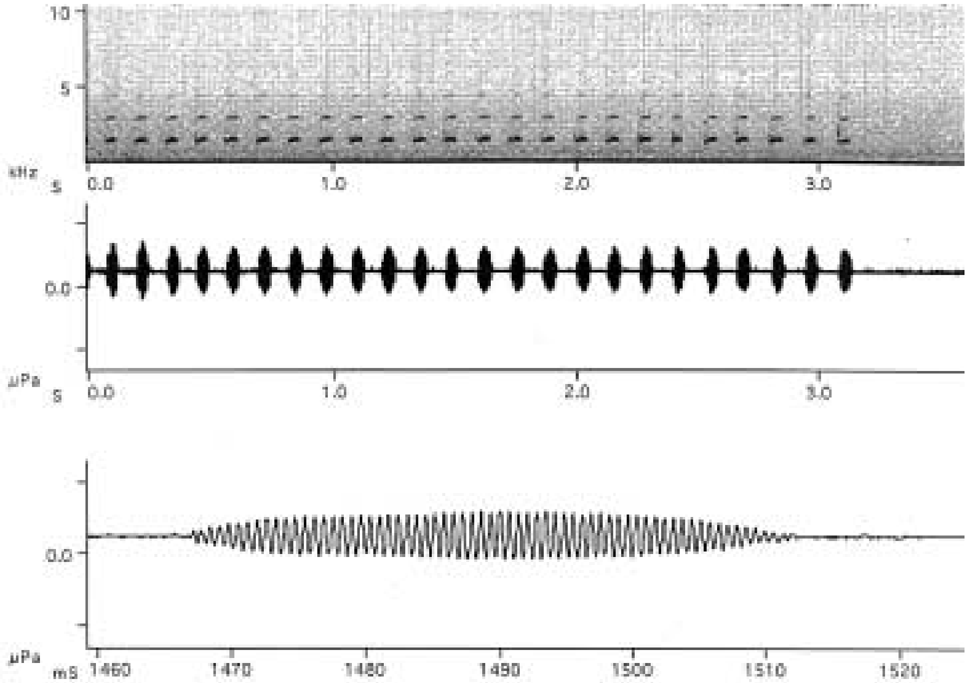

FIGURE 2: The mating call of *Bufo latastii* MNHN 1979.8463, svl = 66.0 mm, air temperature = 16.0°C (a: spectrogram, b: oscillogram, c: detailed oscillogram of note 12).

FIGURE 3: *Bufo melanostictus*, male MNHN 1976.1324, with vocal sac inflated, photographed the 22 IV 1973 at Sanichare (Nepal).

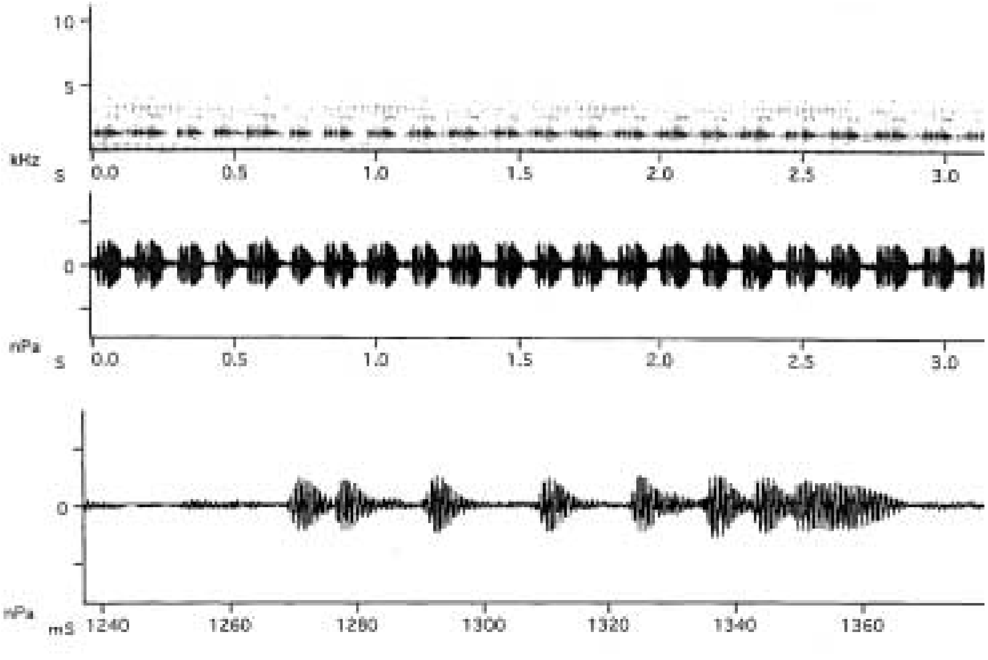

FIGURE 4: A part (23 notes) of the mating call of *Bufo melanostictus* of Thailand MNHN 1987.3635, svl = 78.5 mm, no temperature data (a: spectrogram, b: oscillogram, c: detailed oscillogram of note 10 showing the different groups of pulses).

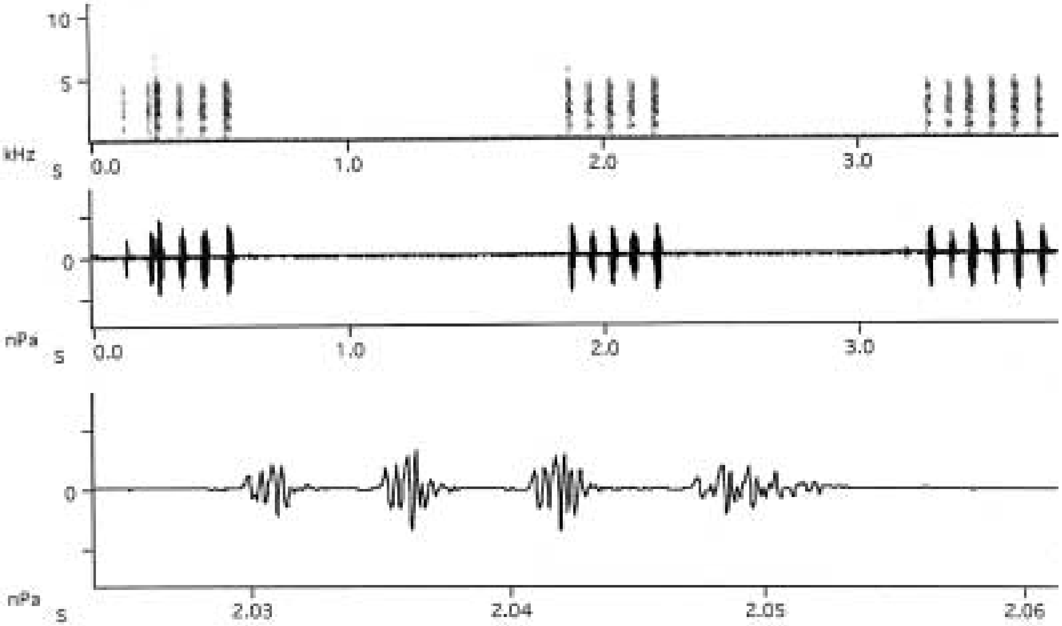

FIGURE 5: Three sequences (respectively 5 ; 5 and 6 notes per sequence) of the mating call of *Bufo parvus* MNHN 1987.3684, svl = 29.5 mm, no temperature data (a: spectrogram, b: oscillogram, c: detailed oscillogram of note 3 of the sequence 2).

FIGURE 6: *Bufo stomaticus*, male MNHN 1976.1762, with vocal sac inflated, photographed the 24.VII.1973 at Burimorang (Nepal).

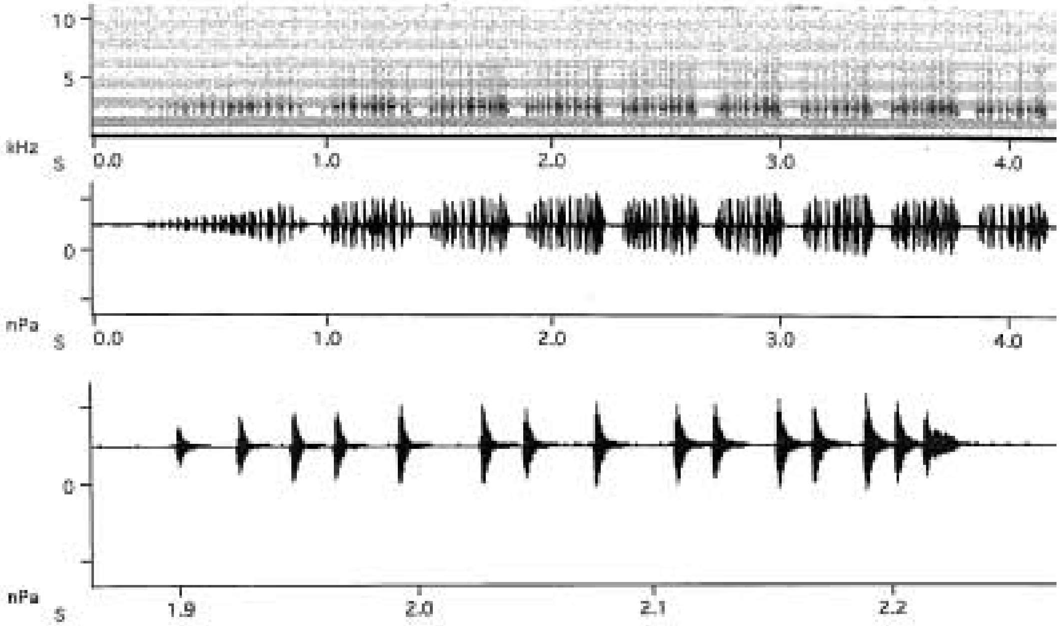

FIGURE 7: The beginning of the call (9 notes) of *Bufo stomaticus* from Sanasar (Jammu and Kashmir) MNHN 1995.2546, svl = 43.5 mm, air temperature = 21.0°C (a: spectrogram, b: oscillogram, c: detailed oscillogram of note 4 showing the different groups of pulses).

TABLE 1: List of the species studied with the localities where they were recorded. Registration numbers of the specimens refer to the Paris Museum collection (MNHN); Air T°: air temperature; Water T°: water temperature.

Species	MNHN registration number	Date of recording	Locality; Country; Altitude	Coordinates	Air T°	Water T°
Bufo asper	(1)	7-8.IX.1986	Khao Chong, Trang Prov.; Thailand; 130 m	7°35’N, 99°35’E	No data	No data
Bufo latastii	1979.8463	25.VI.1977	Shergol, Jammu & Kashmir; India; 3180 m	34°22’N, 76°22’E	16°C	15°C
Bufo melanostictus	1976.1324 1998.4913 1987.3635	22.IV.1973 1.VII.1984 21.IX.1986	Sanichare; Nepal; 250 m Bangalore, Karnataka; India; 960 m Chiangmai, Chiang Mai Prov.; Thailand; 350 m	26°41’N, 87°59’E 12°58’N, 77°35’E 18°48’N, 98°59’E	No data No data No data	No data No data No data
Bufo parvus	1987.3670 1987.3671 1987.3684 1987.3685	5.IX.1986 5. IX.1986 15. IX.1986 15. IX.1986	Khao Chong, Trang Prov.; Thailand; 130 m Khao Chong, Trang Prov.; Thailand; 130 m Khao Phra Tew, Phuket Prov.; Thailand; No data Khao Phra Tew, Phuket Prov.; Thailand; No data	7°35’N, 99°35’E 7°35’N, 99°35’E 8°04’N, 98°22’E 8°04’N, 98°22’E	No data No data No data No data	No data No data No data No data
Bufo stomaticus	1995.2546 1976.1761 1976.1762	12. VII.1977 24. VII.1973 24. VII.1973	Sanasar, Jammu & Kashmir; India; 2060 m Burimorang Uku Dokan; Nepal; 400 m Burimorang Uku Dokan; Nepal; 400 m	33°07’N, 73°24’E 26°54’N, 87°21E 26°54’N, 87°21E	21°C 27°C 27°C	23°C No data No data

TABLE 2: Characteristics of the advertisement call of *Bufo asper* and *Bufo parvus* from Thailand, and of *Bufo latastii* from Shergol, Ladakh, Jammu and Kashmir, India. MNHN: registrated number; svl: snouth-vent length (followed by standard deviation when the value was obtained by the mean of svl of several individuals). Parameters of calls (mean followed by standard deviation; range in brackets; number of measurements in parentheses): dc = duration of the call from first to last note; dic = duration of silent intervals between the end of one call and the beginning of the following; dn = duration of notes; din = duration of silent interval between two subsequent notes; nn = number of notes per call; nns = number of notes per second; f*i*b = frequence of the band *i*. Svl are expressed in mm, time measurements in seconds, frequencies in Hz

Species	MNHN	svl	dc	dic	dn	din	nn	nns	f1b	f2b	f3b
B. asper	1987.3706-3711; 1987.3720	82.4 ± 6.4	0.683 ± 0.050 [0.599-0.760] (11)	6.21 ± 2.23 [4.05-8.74] (5)	0.298 ± 0.072 [0.200-0.414] (22)	0.095 ± 0.029 [0.056-0.137] (11)	2 ± 0 [2-2] (11)	2.94 ± 0.22 [2.63-3.33] (11)	866 ± 34 (22)	3574 ± 195 (22)	6441 ± 139 (18)
B. parvus	1987.3670	32.0	0.707 ± 0.291 [0.502-0.913] (2)	1,156	0.016 ± 0.004 [0.007-0.021] (17)	0.075 ± 0.007 [0.066-0.092] (15)	8.5 ± 3.5 [6-11] (2)	12.0	1066 ± 38 (5)	2171 ± 66 (5)	3288 ± 65 (5)
B. parvus	1987.3671	33.3	0.516	/	0.016 ± 0.003 [0.012-0.019] (6)	0.083 ± 0.018 [0.067-0.112] (5)	6	11,6	1469 ± 0 (3)	2018 ± 52 (3)	2952 ± 57 (3)
B. parvus	1987.3684	29.5	0.437 ± 0.049 [0.385-0.481] (3)	1.169 ± 0.204 [1.024-1.313] (2)	0.018 ± 0.005 [0.006-0.023] (17)	0.066 ± 0.015 [0.021-0.088] (14)	5.7 ± 0.6 [5-6] (3)	13.0	960 ± 71 (5)	2073 ± 62 (5)	2896 ± 43 (5)
B. parvus	1987.3685	29.5	0.655 ± 0.006 [0.651-0.659] (2)	1.327	0.022 ± 0.001 [0.019-0.023] (14)	0.083 ± 0.013 [0.069-0.105] (12)	7 [7-7] (2)	10.7	1038 ± 0 (4)	2116 ± 45 (4)	3326 ± 67 (4)
B. Latastii	1979.8463	66.0	3.43 ± 0.52 [3.07-3.80] (2)	/	0.050 ± 0.008 [0.016-0.059] (54)	0.080 ± 0.011 [0.026-0.110] (52)	27 ± 4 [24-30] (2)	7.9	1466 ± 8 (6)	2893 ± 32 (6)	4336 ± 41 (6)

TABLE 3: Characteristics of the advertisement call of *Bufo melanostictus* from India, Nepal and Thailand, and of *Bufo stomaticus* from Nepal and Jammu and Kashmir. Legends: see Table 2. dp = duration of pulses; dip = duration of silent interval between two consecutive pulses; np = number of pulses per note; nps = number of pulses per seconds.

MNHN	svl	dn	din	nns	dp	dip	np	Nps	f1b	f2b	f3b
B. melanostictus, Tamil Nadu, India											
1998.4913	63.3	0.042 ± 0.006 [0.029-0.048] (27)	0.119 ± 0.014 [0.096-0.149] (26)	6.3	/	/	/	/	1469 ± 0 (4)	2537 ± 57 (4)	4178 ± 88 (4)
B. melanostictus, Nepal											
1976.1324	58.8	0.062 ± 0.016 [0.036-0.112] (63)	0.067 ± 0.009 [0.040-0.115] (61)	7.8 ± 0.4 [7.5-8.1] (2)	/	/	/	/	1635 ± 70 (9)	3200 ± 94 (9)	3964 ± 212 (9)
B. melanostictus, Chiang Mai, Thailand											
1987.3635	78.5	0.097 ± 0.012 [0.068-0.118] (23)	0.055 ± 0.003 [0.050-0.061] (22)	6.7	/	/	/	/	1293 ± 0 (3)	2553 ± 57 (3)	3096 ± 0 (2)
B. stomaticus, Jammu & Kashmir, India											
1995.2546	43.5	0.358 ± 0.123 [0.286-0.675] (9)	0.090 ± 0.002 [0.087-0.094] (8)	2.3	0.012 ± 0.001 [0.011-0.014] (15)	0.014 ± 0.009 [0.003-0.023] (10)	16.8 ± 5.0 [14-30] (9)	47.4	2562 ± 37 (4)	4350 ± 56 (2)	5648 ± 81 (4)
B. stomaticus, Nepal											
1976.1761	59.9	0.237 ± 0.030 [0.196-0.273] (12)	0.073 ± 0.004 [0.063-0.078] (11)	3.3	0.006 ± 0.001 [0.005-0.007] (10)	0.009 ± 0.005 [0.003-0.016] (15)	20.8 ± 1.9 [18-23] (12)	88.5	2297 ± 24 (4)	3825 ± 67 (4)	7014 ± 36 (4)
1976.1762	47.8	0.288 ± 0.012 [0.267-0.301] (8)	0.079 ± 0.006 [0.070-0.085] (7)	2.8	0.007 ± 0.001 [0.005-0.008] (15)	0.006 ± 0.004 [0.001-0.012] (12)	24.0 ± 1.1 [23-26] (8)	83.2	2469 ± 0 (4)	4565 ± 0 (4)	7455 ± 20 (4)

as the fundamental frequency band. These similarities are due to a relatively uniform configuration of vocal structures that is very different from other anurans (Martin, 1972). Our measurements confirm that the maximum energy is emitted at the lowest frequencies (except in *Bufo parvus*). The notes or the pulses of the set of the species studied here possess a relatively high number of frequency bands. The spectrum of *B. parvus* call shows up to six harmonic bands.

The advertisement calls of the different species studied here can be distinguished from each other in the field, except, perhaps, for those of *B. latastii* and *B. melanostictus* which sound similar to the human ear but differ in their note structures, as there is no division of the notes into pulse groups in *B. latastii*. However, the calls differ from each other by several time parameters and differences in structure.

The call of *Bufo asper* is peculiar among the more widespread pattern in this genus (i. e. a long train of notes or of pulses). However, the call of a closely related species, *B. juxtasper*, has already been described (Matsui, 1982). This species has two call types : the commonest consists of a short call from two to four identical notes, the other consists of a long trill, typical in the genus *Bufo*. The commonest call bears no resemblance to the call of *B. asper*: the number of notes is variable in *B. juxtasper* whereas it is fixed in *B. asper*; the duration of notes is identical in the former species whereas it is of variable duration in the latter species. Thus, differences in the shape of the signal are not the expression of phylogenetic relationship but rather an adaptation to the physical constraints of the environment in which the animals breed. Striking differences between temporal and frequency parameters are frequent in sympatric species.

The notes emitted by *Bufo melanostictus* have a particular structure: they are formed by a variable number of pulses (variable from one population to another and presumably variable according to the temperature as in *B. viridis*: e. g., Schneider and Egiasaryan, 1995) organized in pulse groups within the note (Fig. 4c). The call of *B. melanostictus* described by Bourret (1942) is like a series of three high-pitched notes. This description is not in agreement with our observations. Indeed, the present call is composed of a long series of high-pitched notes. Heyer (1971) described the advertisement call of *B. melanostictus* from Thailand as long trills, lasting from 4 to 30 seconds and having a pulse rate of 13.2 pulses per second at 25° C. It would seem that what Heyer (1971) called pulses were in fact notes. Indeed, the number of pulses per second of the advertisement calls described in this paper is approximately 45, whereas the number of notes per second is between six and eight. In agreement with our results, Heyer (1971) noticed that the maximum of energy is released in a narrow frequency band (1000-1700 Hz). However, he did not pick up harmonics, whereas we observed several in the spectra. The calls emitted by Indian individuals of this species (Kanamadi et al., 1995) last an average of 19 seconds, with a note duration of 0.0868 s and a duration of the silence between notes of 0.0642 s. The dominant frequency is at 1450 Hz and up to five harmonic bands are visible. These values agree well with the ones of the Nepalese individual, although the animals were recorded in a locality (Dharwad) close to Tamil Nadu (the locality of one of our samples). Lastly, Roy et al. (1998) analysed the advertisement call of a population of *B. melanostictus* from northeastern India for which the call parameters fit well with those from Nepal, although the duration of notes reaches the maximum values of those of the Nepalese individual. Roy et al. (1998) defined each note as a call and found a mean of 105 pulses per notes.

Among these five *Bufo* species, some are sympatric. It is generally considered that in most species, the advertisement call is the most important parameter bringing the mates of a same species together. It is therefore interesting to see how the advertisement calls of the sympatric species differ from each other. *B. melanostictus*, *B. asper* and *B. parvus* occur at the same locality in Thailand, but only the last two occur syntopically near streams. The advertisement calls of these two species differ enormously, principally in their structure, and prevent the risk of hybridization. Furthermore, the dominant frequency bands do not overlap. *B. melanostictus* and *B. stomaticus* are syntopic in Nepal and the Western Himalaya (*B. latastii* also lives in the Western Himalaya, but at higher altitudes). Their calls differ significantly from each other. The most striking difference between the two is the structure of notes. However numerous other time and frequency parameters differ as well such as duration of call, duration of notes, note rate and dominant frequency among the most obvious. These differences are not due to a different ecology of the two species, since they share the same habitat but rather to a different strategy in order to avoid acoustic interference.

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FIRST RECORD OF *XENOCHROPHIS PUNCTULATUS* (GÜNTHER, 1858) (SERPENTES: COLUBRIDAE: NATRICINAE) FROM THAILAND

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(with four text-figures)

ABSTRACT.– **The rare natricine snake *Xenochrophis punctulatus* (Günther, 1858), previously known only from Myanmar and perhaps eastern India, is added to the herpetofauna of Thailand on the basis of an adult specimen collected in Muang District, Mae Hong Son Province. The specimen is described in detail and compared with voucher material. The species is for the first time depicted by photographs. A brief discussion on biogeographical implications is given.**

KEY WORDS.– **Colubridae, *Xenochrophis punctulatus*, Mae Hong Son Province, Thailand.**

INTRODUCTION

The diversity of aquatic or riparian natricine snakes is especially high in south-east Asia. Since Malnate (1960), these taxa, formerly placed in the genus *Natrix* Laurenti, 1768, have been reallocated to several genera. The genus *Xenochrophis* Günther, 1864 (type species: *Psammophis cerasogaster* Cantor, 1839, by monotypy) was resurrected to accommodate aquatic species. Following Malnate (1960), Malnate and Minton (1965), Malnate and Underwood (1988), Das (1996) and De Silva (1998), this genus currently includes 10 or 11 species, namely *X. asperrimus* (Boulenger, 1891), *X. bellulus* (Stoliczka, 1871), *X. cerasogaster* (Cantor, 1839), *X. flavipunctatus* (Hallowell, 1861), *X. maculatus* (Edeling, 1864), *X. piscator* (Schneider, 1799), *X. punctulatus* (Günther, 1858), *X. sanctijohannis* (Boulenger, 1890), *X. trianguligerus* (Boie, 1827) and *X. vittatus* (Linnaeus, 1758). To this list, Das (1996) added *X. melanzostus* (Gravenhorst, 1807), previously regarded as a subspecies of *X. piscator*. The systematics of the informal *X. piscator* group is highly controversial. We regard *X. flavipunctatus* as a valid species, distinct from *X. piscator*. The status of the taxon *melanzostus*, from Indonesia and the Andaman and Nicobar Archipelago, needs to be re-evaluated. Although its relationships are by all available evidence with *X. flavipunctatus*, its status, namely a subspecies of the latter (as proposed in a new combination by Manthey and Grossmann, 1997: 397, causing a nomenclatural problem, since *melanzostus* has priority over the widely used specific nomen *flavipunctatus*) or a distinct species (Das, 1996; pers. comm.), remains unresolved.

Among these species, one of the lesser known forms from the Asian mainland is *X. punctulatus*, described as *Tropidonotus punctulatus* by Günther (1858: 247, type locality unknown). This species is known from Myanmar and perhaps north-eastern India (see below in Discussion). However, in the early 1980s, one of us (W.N.) collected a natricine snake in Mae Hong

Son Province in north-western Thailand, that we unambiguously identified as *Xenochrophis punctulatus*, a species not yet recorded from the country. This specimen is described in detail and compared with the original description and other material. Its occurrence in Thailand is discussed.

ABBREVIATIONS

Measurements.- SVL: snout-vent length; TaL: tail length; TaL/TL: ratio tail length/total length;

Museums.- BMNH: British Museum (Natural History), now the Natural History Museum, London ; IRSNB: Institut Royal des Sciences naturelles de Belgique, Brussels.

DESCRIPTION OF THE SPECIMEN (FIGS. 1 – 4)

IRSNB 15493, adult female (sex verified by tail dissection) from Muang District, Mae Hong Son Province, Thailand.

Habitus: Body stout, cylindrical but slightly depressed; SVL 642 mm; TaL > 53 mm (cut and healed). Head rounded, distinct from the neck, strongly depressed; snout rather short; head length 30.2 mm. Eye rather small; its horizontal diameter about 15.4% head length, greater than distance eye-border of lip; pupil rounded.

Body scalation: 2 preventrals (namely the ventral scales wider than long but not contacting the first row of dorsals) + 148 ventrals (counted after Dowling, 1951), all smooth; anal divided; > 16 paired subcaudals. Dorsal scales in 17-17-13 rows, very slightly keeled in the posterior part of the body; no apical pits; complete body dorsal scale row reduction formula from 19 to 14 (ventral numbers at which reductions or additions occur are indicated left/right): 19 2+3?2 (6/6) 17 4+5?4 (85/84) 15 1+2?1 (140/140) 13 2?2+3 (146/) 14.

Head scalation: Rostral about 1.5 times wider than high, its upper tip visible from above; nasal divided, rectangular; nostril vertically elongate, linked to the first supralabial by a suture, and to the internasal by a weak crease; internasals much narrowed anteriorly, distinctly smaller and slightly shorter than the prefrontals; frontal 1.7 times longer than wide (7.4 mm long, 4.4 mm wide), straight anteriorly, shorter than parietals, longer than suture between parietals, longer than its distance to snout tip; 1/1 subrectangular loreal; 9/9 supralabials, 2nd and 3rd in contact with the loreal, and 4th and 5th entering orbit on each side, 6th separated from the orbit by the lower postocular, 7th largest; no subocular; 1/1 preocular; 3/3 postoculars; 1/1 supraocular; 2/2 anterior temporals; 10/10 infralabials, 5/5 first contacting the anterior chin shields; two pairs of chin shields, the anterior slightly shorter than the posterior, the scales of the posterior pair not in contact with each other; mental about 1.9 times wider than deep, narrower than rostral; first pair of infralabials widely in contact behind mental.

Colouration in alcohol: Upper surface of body and tail dark brown, with small whitish yellow dots on back, mainly on scale rows 4-5 on forebody, on rows 5 to 7 behind; dorsal scales of the 1st and 2nd rows whitish yellow, those of the 1st row edged with dark brown on their anterior and lower margins, those of the 2nd row edged with the same colour on their upper and posterior margins, giving the appearance of a succession of large whitish yellow spots on rows 1-2 forming a continuous lateral line from immediately behind the neck to the vent and on tail; lateral sides of the neck whitish yellow, contrasting with the dark brown colour of the body. Upper head surface dark brown like the body, paler on lateral sides of the snout; supralabials 1-6 whitish yellow, supralabials 8 and 9 of the same colour but marked with dark brown on their upper margin; underside of head cream; ventrals and subcaudals cream, anteriorly and laterally edged with dark brown margins.

DISCUSSION

Our specimen agrees with the original description of the species provided by Günther (1858: 247-248), as well as with the morphological accounts provided by Boulenger (1893: 228-229) and Smith (1943: 292), and is readily referrable to *Xenochrophis punctulatus* both on the basis of scalation and its characteristic colour pattern. The colouration of its head and forebody (see Figs) perfectly agrees with the sole existing illustration of this species, which appeared in Boulenger (1893: pl. XIV). As far as we know,

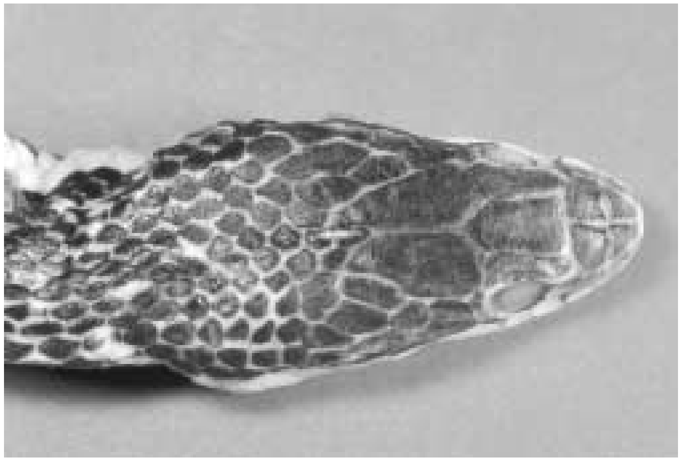

FIGURE 1: *Xenochrophis punctulatus* (Günther, 1858). IRSNB 15493. Dorsal view of the head.

FIGURE 2: *Xenochrophis punctulatus* (Günther, 1858). IRSNB 15493. Ventral view of the head.

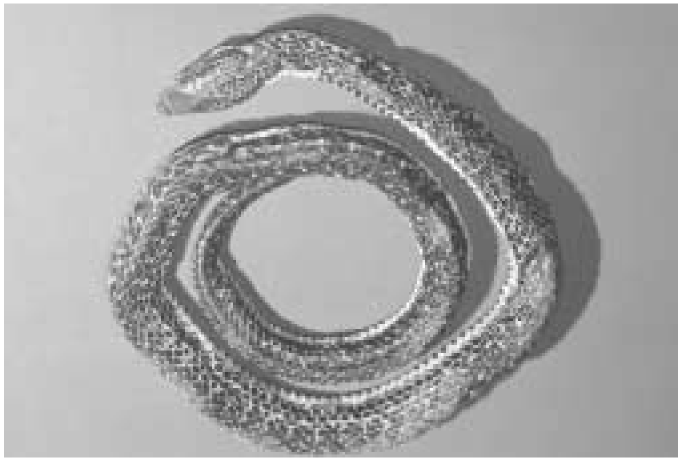

FIGURE 3: *Xenochrophis punctulatus* (Günther, 1858). IRSNB 15493. General dorsal view of the body.

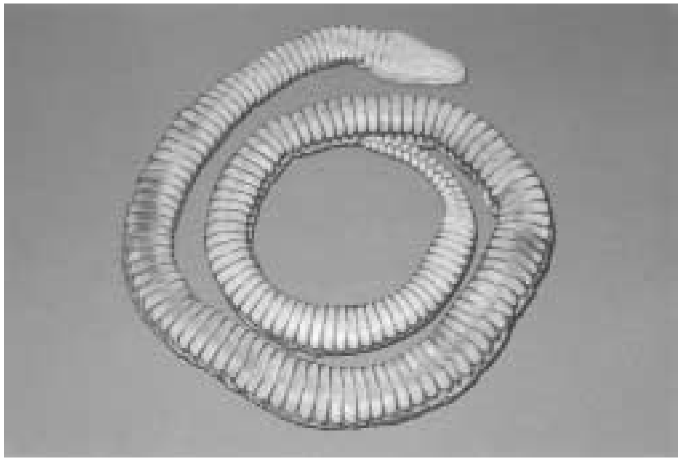

FIGURE 4: *Xenochrophis punctulatus* (Günther, 1858). IRSNB 15493. General ventral view of the body.

this species has never been illustrated by a photograph before the present paper. No description of a living specimen has ever been published.

We compared our specimen with another (BMNH 68.4.3.19, male, from 'Pegu, Burma'), with which it is obviously conspecific. The morphology, colouration and pattern of this latter specimen are nearly identical with the present Thai one, and are not repeated here. Its main morphological characters are: SVL 398 mm; TaL 143 mm; TaL/TL 0.26; 2 preventrals + 150 ventrals; anal divided; 67 paired subcaudals plus one terminal scale; dorsal scales in 17-17-13 rows; 10/10 supralabials; 1/1 preocular; 3/3 postoculars; 2/2 anterior temporals.

According to Smith (1943), Mahendra (1984) and the present data, variations for main scale characters in this species are: 134-154 ventrals (Smith's data include preventrals), subcaudals 62-84, 17 dorsal scale rows at midbody, 9-10 supralabials, 2 anterior temporals.

It should be noted that, with a SVL of 642 mm, the Thai specimen is by far the longest recorded. Its tail is unfortunately cut shortly after the vent. Smith (1943) cited a female with a TL of 630 mm, including a tail of 160 mm long. Such a ratio would give our specimen a TL of about 860 mm.

Günther did not know the geographical origin of the holotype. Since the original description, *X. punctulatus* has been recorded from several localities of southern and south-western Myanmar, namely 'Rangoon' (now Yangon), 'Pegu' (now Bago), 'Watiya' (now Wataya, a locality just northwest of Yangon in the Yangon Division), 'Amherst' (now Kyaikkami, in Mon State), and 'Mergui, Tenasserim" (now Beik or Myeik, in the Taninthayi State) (Wall, 1923; Smith, 1943; Malnate, 1960: 54; Hundley, 1964; Dowling & Jenner, 1988: 9; Welch, 1988: 107). All these localities are in the lowlands of lower Myanmar, relatively close to the Myanmar-Thailand border. Mae Hong Son Province, the north-westernmost province of Thailand, largely borders Myanmar at the level of the Burmese Kayah and Kayin States. Muang District, namely the district around the head city of the province, although located in its northern part, is at only about 265 airline km from Bago.

Recently, the species has been added to the fauna of India, on the basis of a male specimen collected in Lamphal, State of Manipur, in north-eastern India (Singh, 1995: 137). This record would represent a rather surprising major extension towards north-east of at least 850 km across the whole of Myanmar, in an ecologically rather different area. Unfortunately, the author did not provide any description of his sole specimen, except that it had a SVL of 450 mm, a TaL of 210 mm (TaL/TL 0.32), and 19-19-17 scale rows. Although the pattern of this species makes it quite easy to recognize, and although we could not examine the involved Indian specimen, we however prefer to regard its identification as dubious on the basis of both the number of dorsal rows and the geography. This species was nevertheless included in recent lists of Indian snakes (Das, 1996, 1997).

Virtually nothing is known on the biology of *Xenochrophis punctulatus*. Smith (1943) stated that it is largely aquatic. There was a report of one specimen observed swimming in salt water (Keswal, 1886). However, this is obviously a confusion, or a lapsus calami of the author, for *Tropidonotus quincunciatus* Schlegel, 1837, now *X. piscator*. Chatterji (1940) reported a specimen from Myanmar infected by parasite worms. Unfortunately, no ecological data were recorded for the Thai specimen.

The present record brings to four the number of representatives of the genus *Xenochrophis* in Thailand. The wide ranging *X. flavipunctatus* is ubiquitous and one of the most often encountered Thai snakes, whereas *X. piscator* is currently known only from some localities in the north and north-east of the country. *X. piscator* (see Chérot et al., 1998) and *X. flavipunctatus* (C.C. & O.P., pers. obs., September 1997) also occur in Mae Hong Son Province. To the contrary, *X. trianguligerus* is currently known within Thailand only from the south according to Cox (1991: 249), in spite of the fact that it has also been reported from Laos, Cambodia and Vietnam (Welch, 1988; Manthey and Grossmann, 1997). In view of its wide distribution in south-eastern

Myanmar, *X. punctulatus* should also occur in the western Thai provinces of Tak and Kanchanaburi, in following the western mountain range of the country, and, on the basis of its occurrence in the Tenasserim as far south as Beik (Mergui), might also be expected in Phetchaburi and Prachuap Khiri Khan provinces.

The herpetology of the hilly or mountainous areas of Western Thailand is largely unprospected. However, recent investigations in the regions of Kanchanaburi and Chiang Mai suggest that the long mountain range bordering western Thailand is of major biogeographical importance in allowing northern taxa occurring in the elevated areas of southern China, northern Vietnam and Myanmar to extend their range at considerable distance towards the south. This part of western Thailand will undoubtedly reveal taxa new for the country, notably among the colubrid fauna. A recent and interesting example, which sheds light on the zoogeographical affinities of the area, can be found in the discovery of the typical Indo-Himalayan taxon, *Amphiesma bitaeniatum* (Wall, 1925) in Doi Inthanon National Park, Chiang Mai Province (David and Pauwels, 2000: 89).

In conclusion, we would like to emphasize again the fact that, in spite of numerous contributions by notable herpetologists such as M. A. Smith and E. H. Taylor, the herpetofauna of Thailand, with the exception of rather limited areas, remains very poorly known. Additional herpetological surveys must obtain adequate local samples and deposit these vouchers in research/museum collections that are accessible to researchers.

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HERPETOFAUNAL MORTALITY ON ROADS IN THE ANAMALAI HILLS, SOUTHERN WESTERN GHATS

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(with two text-figures)

ABSTRACT.– **We sampled road-killed amphibians and reptiles from the highway segments passing through rainforest fragments and tea gardens in the Anamalai hills in order to evaluate the effects of vehicular traffic on the herpetofauna. There was greater mortality among amphibians than reptiles due to vehicular movement. A total of 73 reptiles belonging to 24 species, 13 genera and seven families and 311 amphibians belonging to eight genera and five families killed on the highway were recorded. These figures included several endemic species of amphibians and reptiles. Rainfall resulted in increased activity of amphibians and uropeltids, thereby making them vulnerable to road traffic. Amphibian roadkills were associated with coffee and forest habitats while reptiles were found only in forested habitats. Road segments passing through tea plantations had the lowest number of amphibian and reptile roadkills compared with other vegetation categories. Possible explanations for differences in species richness and relative counts in the forest in relation to roadkill are discussed. The long-term effects of mortality due to roads is of conservation importance considering the low abundance of herpetofauna in the rainforests.**

KEY WORDS.– **Roadkills, herpetofauna, rainforest, Western Ghats, India.**

INTRODUCTION

The increase in road networks throughout the world has brought about for a concern for the effects of vehicular traffic on flora and fauna. This concern is evidenced by the increasing amount of literature dealing with the ecological effects of roads and traffic (Spellerberg, 1998. Forman and Alexandra, 1998). Roads are known to cause forest fragmentation (Reed et al., 1996. Forman and Alexandra, 1998. Goosem, 1997), affect the density of amphibians (Fahrig et al., 1995), cause barriers to dispersal of arthropods (Mader et al., 1990), reduce average heterozygosity and genetic polymorphism among frogs (Reh and Seitz, 1990) and affect the physical environment (Spellerberg, 1998). Development in any area generally leads to extensive road networks and subsequent traffic. The effects of such landscape changes can be dramatic on fragile habitats, such as the rainforests of the Western Ghats. The Western Ghats of south India have experienced large-scale changes over the last century because of expansion of plantations and townships (Nair, 1991). The impact of roads on the flora and fauna of this region is poorly documented. At a landscape level, such features may be permeable to vagile forms or filter them out by acting as a barrier to dispersal (Gibbs, 1998). Thus the presence of roads can be of conservation importance since the Western Ghats supports large number of endemic forms among the reptiles and amphibians (Inger and Dutta, 1986). Apart from a single study which reported mortality in snakes due to highway traffic in the dry deciduous forest of Mudumalai Wildlife Sanctuary, Tamil Nadu (Gokula, 1997), there is no information on the effect of road traffic on the fauna of the Western Ghats. This present study provides evidence of the impacts of vehicular traffic on the rainforest herpetofauna of the Western Ghats. We explore

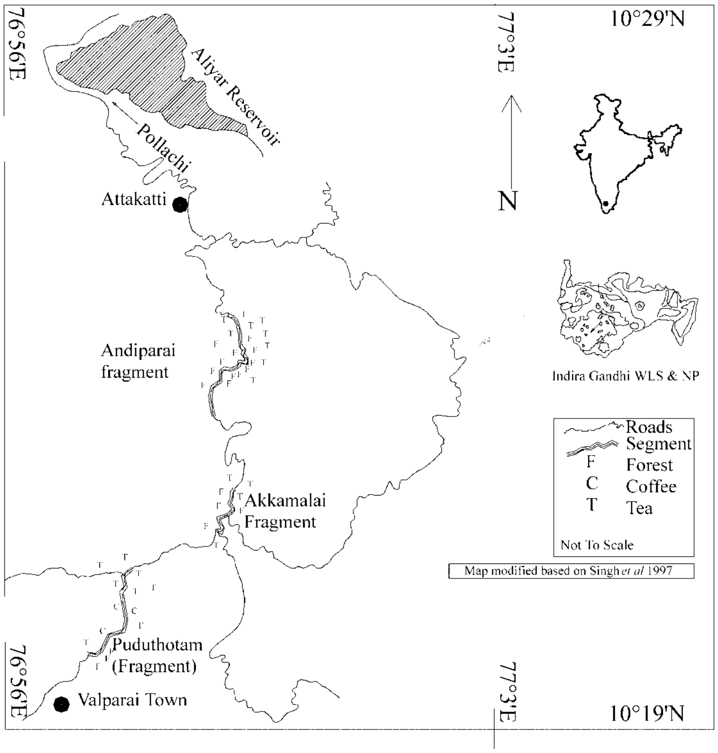

FIGURE 1: Map showing road segments sampled in the Indira Gandhi Wildlife Sanctuary.

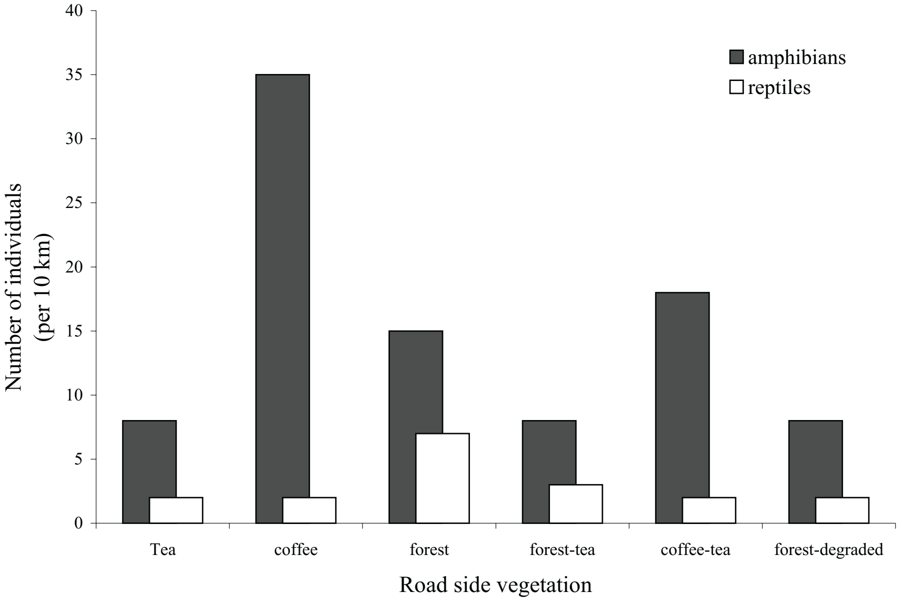

FIGURE 2: Number of amphibian and reptile road kills per 10 km of different roadside vegetation categories in IGWLS during May-June 1998.

the probable causes for such mortality and examine some secondary effects of roads and traffic on the herpetofauna.

STUDY AREA

The study was conducted in and around the town of Valparai situated in the Anamalai hills of the southern Western Ghats. The township is surrounded by forests which are part of the Indira Gandhi Wildlife Sanctuary and National Park (10° 00-30' N to 76° 48'-77° 30' E; Fig. 1). The road segment sampled forms part of the highway connecting the Pollachi and Valparai in the Tamil Nadu with Chalakudi in Kerala across the Western Ghats mountains. The roadside vegetation is regularly cleared and maintained by the Public Works Department. Valparai township forms part of the tourism network of the state. The town is one of the fast expanding commercial areas for cash crops like tea, coffee and cardomom. These factors have led to an increase in the volume of traffic by tourist and commercial vehicles over the years.

METHODS

Roadkills were sampled in four different road segments. The length of the road section sampled, the area of fragment, altitude, and the numbers of days walked are given in Table 1. The natural vegetation of the area has been classified as wet-evergreen forests (Pascal, 1998). Two segments (Andiparai and Akkamalai) traversed through the fragments of rainforest and one segment (Pudhuthottam) went along the edge of the fragment (Fig. 1). The fourth segment was entirely in a tea plantation. One of us (SPV) walked these road segments during early hours in the morning looking for road kills. On sighting a roadkill, the roadside habitat, state of the roadkill, and the location of the roadkill on the road segment were recorded. All road-killed individuals were examined and collected. Voucher specimens are in the museum of the Wildlife Institute of India. Based on the state, highly damaged specimens were not collected, although all of them were removed from the road to avoid multiple counts of the same kill. Wherever possible, individuals crossing roads were caught, identified and released at the same location. Sampling was repeated every day but the order of sampling the road segments was randomized. Individuals collected were preserved in 10% formalin and tagged for later identification. Most road-killed amphibians were damaged, thus sometimes impeding identification to the species level. In such cases, specimens were identified to the family level; a few specimens were identified to genus or species. In the case of road-killed reptiles, specimens were identified to the genus or species. Data on other fauna, such as rodents, birds and insects also were collected. We restrict our discussion in the results to reptiles and amphibians. Data from the four road segments were pooled for the purpose of analysis. We did not attempt to compare road segments, because of their variability in slope, altitude, distance sampled, and vegetation categories along the road. Roadside vegetation was divided into six categories, viz. forest, coffee, tea, forest-tea, coffee-tea and forest-degraded based on the combination that existed on either side of the road. In order to make comparisons of roadkills across these vegetation categories, the frequency of roadkills was expressed as the number of individuals per 10 km. We recorded the occurrence of rainfall during the study period.

We used the non-parametric test for comparison of independent samples (Mann-Whitney U-test) to test the difference between the number of roadkills on rainy and dry days. We used the frequency of kills in different vegetation categories (expressed as the number of individuals per 10 km of vegetation segment) to test for the effect of vegetation. Information on species richness

TABLE 1: Summary of the sampling sites in IGWLS during May-June 1998. Total distance walked – 170.70 km (9.05.1998-19-06.1998).

Fragment	Area (ha)	Altitude (m)	Length of road segment walked (km)	Number of days walked
Pudhuthotam	50	1070-1100	3.00	20
Andiparai	185	1205-1320	2.50	19
Akkamalai	2500	1220-1365	2.90	18
Tea Plantation	–	1370-1405	1.10	10

and relative abundance of the herpetofauna in the three forest fragments was provided by Karthikeyan Vasudevan and N.M. Ishwar through their respective ongoing studies in the region.

RESULTS

A total of 73 individuals of roadkilled reptile (0.43 individuals/km), belonging to 24 species, 13 genera and 7 families and 311 roadkilled amphibians (2 individuals/km) represented by 8 genera and 5 families, were recorded (Appendix Ia).

In the case of amphibians, the family Bufonidae represented almost half (46.6%, N = 144) the total number of individuals recorded, followed by Ranidae (23.3%, N = 73), Rhacophoridae (11.3%, N = 35), Icthyophidae and Uraeotyphlidae (3.7%, N = 27). *Bufo melanostictus* was the only recorded Bufonid. Endemic genera, such as *Indirana* (Family: Ranidae), and several endemic species of the genus *Philautus* were among individuals killed on the road.

For reptiles, more than 80% (N = 49) of the road kills are snakes. Families included Colubridae (30.1%, N = 22), Uropeltidae (19.2%, N=14), Viperidae (12.3%, N = 9) and Elapidae (4.1%, N = 6). The Viperidae was represented by a single species, the large scaled green pitviper *Trimeresurus macrolepis.* The family Elapidae was represented solely by the coral snake, *Calliophis melanurus.* Lizards were represented by the family Agamidae, which had two endemic species *Calotes ellioti* (N = 5) and *Calotes nemoricola* (N = 2). There were fewer roadkills in the family Gekkonidae (N = 1) and Scincidae (N = 3) than among any other reptile taxa. There was a high representation (45%) of forest litter dwelling reptiles such as *Calliophis, Lycodon* and *Amphiesma* among the road kills. The arboreal (e.g., *Boiga* and *Calotes*) and fossorial genera (e.g., *Uropeltidae*) formed 30% and 20% of the roadkills, respectively.

The number of individuals collected as roadkills during rainy and non-rainy days was different for amphibians (Mann Whitney U test. $Z = -1.869$, $n_1 = 6$, $n_2 = 14$, $P = 0.06$). Field observations at night hours during rains, supports the hypothesis of a positive influence on the activity of amphibians on roads. In the case of reptiles, there was no such influence (Mann Whitney U-test. $Z = -0.38$, $n_1 = 6$, $n_2 = 14$, $P = 0.35$).

There was greater mortality of amphibians in coffee plantations compared with other vegetation (Fig. 2, Chi-square test. $^{2} = 51.11$, df = 5, $P < 0.001$). On the other hand, there was higher number of roadkilled reptiles associated with forests (Fig. 2). However, the number of roadkills was independent of vegetation (Chi-square test. $^{2} = 6.65$, df = 5, $P > 0.05$). There were high proportions of caecilians 51.9 % (N = 14), agamids 90 % (N = 9), skinks 66.7% (N = 2), colubrids 81.8 % (N = 18), elapids 66.7 % (N = 4) and vipers 55.6 % (N = 5) associated with forest. In coffee, rhacophorids 65.7 % (N = 23), bufonids 44.1 % (N = 64) and uropeltids 42.9 % (N = 6) were the dominant roadkills. Roadkills were relatively low in road sections associated with other vegetation categories. The lowest mortality of amphibians and reptiles was found associated with tea plantation (Fig. 2).

The number of reptile species counted as roadkill formed 50% of the total number of reptile species observed in each fragment (based on independent sampling by NMI). Species such as *Uropeltis macrorhyncha*, *Uropeltis phipsoni*, *Boiga dightoni*, found among the roadkills were not documented during intensive sampling (NMI) in the rainforest fragments.

Apart from the animals killed, we also observed a number of individuals crossing roads during formal sampling. A list of these species is provided in Appendix Ib. These data provides additional information on the species that cross roads to move between habitats, or for activities such as basking which make them vulnerable to traffic.

Among other vertebrates, rodents formed the dominant group, including the endemic spiny dormouse (*Platacanthomys lasiurus*) and a few unidentified rodents. Among birds, a spotted dove (*Streptopelia chinensis)* was the only roadkill. Invertebrates included several individuals of millipedes, lepidoptera (mostly butterflies), and hemipterans (mostly bugs).

DISCUSSION

Rainforest amphibians and reptiles occur in low numbers (for amphibians, Vasudevan et al., 2001; for reptiles, Ishwar et al., 2001) and the mortality due to roadkill could deplete local population. Vehicular traffic causes negative effects on amphibian density (Fahrig et al., 1995) and the traffic-related mortality is highly detrimental, especially for species with small and declining populations (Spellerberg, 1998). Considering the unique herpetofaunal diversity of the rainforests of the Western Ghats (Groombridge, 1990), the long-term effects of such mortality should be cause for conservation planning.

On the forest floor, bufonids were fewer in numbers and ranked third after ranids and rhacophorids in abundance (K. Vasudevan, unpublished data). However, the only species that represented in the roadkills among the bufonids was *Bufo melanostictus*. This species was present in degraded rainforest fragments and in coffee estates (Vasudevan, pers. obs.). A majority of *B. melanostictus* kills were in coffee vegetation, although it occurred in all vegetation types. *Bufo melanostictus* is cosmopolitan in distribution (Dutta, 1997) and is known to occur in a variety of habitats, especially in disturbed areas (Inger et al., 1984). The greater proportion of this species among roadkills probably reflects the disturbed nature of the area sampled.

Because more than 50% of the amphibian kills were ranids, rhacophorids and caecilians, a number of endemic species could constitute the roadkilled amphibians. The family Rhacophoridae was dominated by several species in the genus *Philautus,* and most roadkills were associated with coffee vegetation. The greater representation of *Philautus* in coffee probably reflects on their resistance to habitat alteration. This might be specific to some species, a question, which needs further data. Caecilians not found in the forests were commonly found as roadkills in other vegetation such as coffee. This suggests that subterranean caecilians are probably more vagile and tolerant to habitat alterations than popularly believed.

The high incidence of reptile roadkills in forested areas probably implies greater abundance of reptiles, and the permeability of roads to forest reptiles, compared to road segments associated other vegetation types. Low incidence of roadkills associated with vegetation types such as tea might be due to the unsuitability of these highly modified habitats for rainforest reptiles and amphibians. The substantial representation of snakes and other amphibians such as caecillians, among the roadkills is striking when compared to their rarity in the forest. This results likely demonstrate the inefficiency of conventional sampling methods such as quadrats or transects, in estimating their abundance in the forest.

Snakes might be using roads as substrates for thermoregulation, a likely reason for their vulnerability to vehicular traffic. Scincids and Geckkonids although found in numbers greater than snakes in the forest (Ishwar et al., 2001), were poorly represented as roadkills. However, we have observed *Mabuya* species (Scincidae) crossing the road, they might be escaping the traffic by their swift movement unlike gekkonids. Unlike other reptiles, more uropeltid roadkills were associated with coffee, probably indicating their persistence and abundance in human modified habitats.

Amphibian roadkills occurred more on rainy nights, and caecilians invariably were found on such occasions. Rains probably trigger some kind of movement in these animals, which makes them vulnerable to traffic. Caecilians probably use the roads as conduits or, since the soil under the road is compacted they may emerge to the surface to continue their previously impeded journey. The reptiles did not show any increase in mortality because of to rains. The activity of reptiles, except for uropeltids, was probably not influenced by rains. Uropeltids, like the caecilians, were killed more often on roads when there were rains.

The disparity in the number of species and the proportion of counts of species in the roadkills when compared to the estimates made within the fragments can probably be attributed to the following reasons: (1) The number of individuals of different taxa that use the roads were in similar proportion to their abundance in the forest floor, but they had different probabilities of being roadkilled. This could be because of their differential ability in crossing roads. (2) The difference in species richness and relative counts between roads and inside forests could be because of the differential permeability (ability to cross) of species to the roads. In such a case the roads acted as a barrier for some taxa. (3) Difference could result because some species use streams or the canopy and hence did not appear as roadkills. (4) Animals that were killed on the roads generally resided on the roads or at the edge of the road, and they occurred in direct proportion to numbers that were killed. This explanation is not supported by our observations and through extensive sampling in these areas. The absence of stream dwelling amphibians such as *Micrixalus* and *Nyctibatrachus* among the roadkills supports our third explanation, and they are probably least influenced by traffic on roads. Species such as *Trimeresurus macrolepis*, is an example for our first explanation. This species was prominent in the roadkills was also found to be abundant in the forest among snakes. However, the fact that *T. macrolepis* moves slowly on the ground predisposes it to mortality due to traffic on roads. Arboreal taxa such as gekkonids probably provide evidence for the second explanation. This taxon despite their high abundance in the forests, was represented by only one individual among the roadkills. The example provided for the second explanation is speculative, and needs further investigation. The fact that our sampling regime was short and covered only a single season poses limitations on our ideas regarding the barrier effect to the herpetofauna. Amphibians and reptiles show stronger avoidance to roads with increasing traffic volume (Goosem, 1997). Hence, species are likely to be isolated over a period of time by roads. An with increase in traffic volume coupled with this innate barrier effect probably has pronounced ecological effects other than the mortality (Forman and Alexandra, 1998).

There is a dearth of information regarding highway-related mortality on amphibians and reptiles from the Western Ghats. It is crucial to quantify the magnitude of the effect due to vehicular traffic on different faunal groups. As an ad hoc measure the park authorities of the Indira Gandhi Wildlife Sanctuary should explore the possibility of closing heavy vehicle traffic at night hours beyond Attakatti check post in order to reduce the road-related mortality on the herpetofauna.

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APPENDIX I

List of fauna represented in the road kill sample in IGWLS during May-June 1998.

	REPTILES	Individuals (N)
	Family Agamidae	
1.	*Calotes ellioti*	5
2.	*Calotes nemoricola*	2
3.	*Calotes* sp.	3
	Family Scincidae	
4.	*Mabuya carinata*	1
5.	*Mabuya* sp.	
	Family Gekkonidae	
6.	*Cnemaspis* sp.	1
	Family uropeltidae	
7.	*Uropeltis macrorhyncha*	2
8.	*Uropeltis ceylanicus*	3
9.	*Melanophidium bilineatum*	1
10.	*Uropeltis phipsonii*	3
11.	*Uropeltis* sp.	1
	Unidentified	4
	Family Colubridae	
12.	*Amphiesma beddomei*	2
13.	*Lycodon* spp 1	4
14.	*Lycodon* spp 2	1
15.	*Xenochrophis piscator*	1
16.	*Boiga ceylonensis*	2
17.	*Boiga dightoni*	1
18.	*Boiga* sp.	1
19.	*Atretium schistosum*	1
20.	*Oligodon brevicaudus*	1
21.	Unidentified sp. 1.	1
22.	Unidentified sp. 2.	1
	Unidentified (others)	6
	Family Elapidae	
23.	*Calliophis melanurus*	6
	Family Viperidae	
24.	*Trimeresurus macrolepis*	9
	Unidentified reptiles	8
	Total	73

AMPHIBIANS		
	Family Bufonidae	145
1.	*Bufo melanostictus*	145
	Family Ranidae	73
	Family Rhacophoridae	35
	Family Ureotyphlidae	19
7.	*Uraeotyphlus* sp.	19
	Family Icthyophidae	8
8.	*Icthyophis* sp.	8
	Unidentified (Ranids & Rhacophorids)	31
	Total	311
	Other faunal groups*	
MAMMALS		
	Platacanthomys lasiurus Spiny dormouse	1
BIRDS		
	Streptopelia chinensis Spotted dove	1
ARTHROPODS		
	Millipede	-
	Lepidopterans	-
	Hemipterans	-

APPENDIX II

List of herpetofaunal species observed crossing roads in IGWLS during May-June 1998.

REPTILES
Atretium schistosum
Calotes ellioti
Trimeresurus malabaricus
Calotes grandisquamis
Oligodon taeniolata
Mabuya carinata

AMPHIBIANS
Rana temporalis
Bufo melanostictus
Uraeotyphlus sp.
Philautus temporalis
Fejervarya cf. limnocharis
Philautus spp.

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COMMENTS ON THE SCINCID LIZARD GENUS *OPHIOMORUS*, WITH A CLADISTIC ANALYSIS OF THE SPECIES

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(with five text-figures)

ABSTRACT.– **The limb-reduced, cryptozoic scincid lizard genus *Ophiomorus* (10 species) is diagnosed vis-à-vis the primitive genus *Eumeces*. The species *O. latastii* is unusual in showing truncation in both the snout and neck. *O. persicus* is unusual in having the distal ends of the sacral pleurapophyses widely separated despite retaining a rear limb with two digits. Sexual dimorphism is evident in that females are generally larger and have more transverse scale rows than males. Strong interspecific correlations are: the number of digits on the front and rear limbs; the number of digits and the number of longitudinal scale rows at midbody (an index of attenuation?), and the number of presacral vertebrae and the number of transverse scale rows on the body. Cladistic analysis of 26 characters resulted in a single most parsimonious tree that only partly supported previous views of species relationships. The cladistic analysis suggests that changes in limb morphology may have involved reversals and saltations and that the external ear opening was lost twice. However, a tree one step longer suggests that limb reduction could have occurred without reversals, although it also suggests that the external ear opening may have been reacquired.**

KEY WORDS.– **Cladistics, limb reduction, *Ophiomorus*, Scincidae.**

INTRODUCTION

The scincid lizard genus *Ophiomorus* consists of 10 species (Anderson and Leviton, 1966; Nilson and Andrén, 1978; Anderson, 1999) and ranges from southeastern Europe to extreme northwestern India (Anderson and Leviton, 1966: Fig. 1). The species are largely cryptozoic and, depending on the species, live on substrates varying from loams for *O. punctatissimus* (Rödel et al., 1989, inferred from the small holes in the earth under stones where the animals were sheltering), to "almost bare gravel ground" for *O. nuchalis* (Nilson and Andrén, 1978) to loosely consolidated sand for *O. blanfordi* (Shockley, 1949), *O. brevipes* (Anderson, 1963) and *O. raithmai* (Minton, 1966; Rathor, 1970a-c; all as *O. tridactylus*).

The lineage is of interest for two reasons. First, it appears to be relatively ancestral within skinks, arising fairly basally in the family phylogenetic tree (Anderson and Leviton, 1966; AG, pers. obs.). And second, it represents one of the better cases of limb reduction in skinks in that it is clearly monophyletic and displays a relatively wide range of limb morphologies. The apparently most primitive limb morphology occurs in the four species which have four digits on the manus and three on the pes (*O. blandfordi, O. brevipes, O. chernovi* and *O. nuchalis*) and the most derived morphology occurs in the two species which lack limbs (*O. latastii* and *O. punctatissimus*).

The purpose of this note is to present a detailed diagnosis of the genus; comment on some of the peculiar aspects of the morphology of *Ophiomorus latastii*; examine two aspects of sexual dimorphism in three species for which there are the most data; make some observations about limb reduction in the genus, and provide a cladistic analysis of the species' relationships.

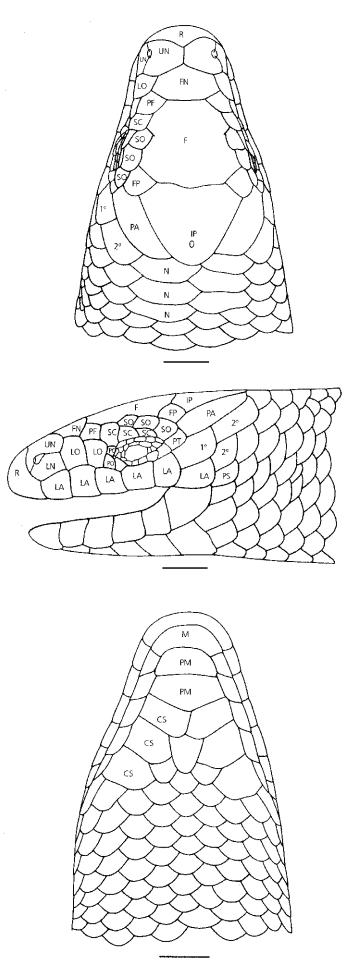

FIGURE 1: Head of *Ophiomorus punctatissimus* (AMNH 17819). Abbreviations: cs - chin scale; fn - frontonasal; ip - interparietal; la - upper labial; ln - lower nasal; lo - loreal; m - mental; n - nuchal; pa - parietal; pm - postmental; po - preocular; ps - postsupralabial; pt - pretemporal; r - rostral; sc - supraciliary; so - supraocular; un – upper nasal; 1° - primary temporal; 2° - secondary temporal. Scale bar = 1 mm. Drawing: H. Finlay.

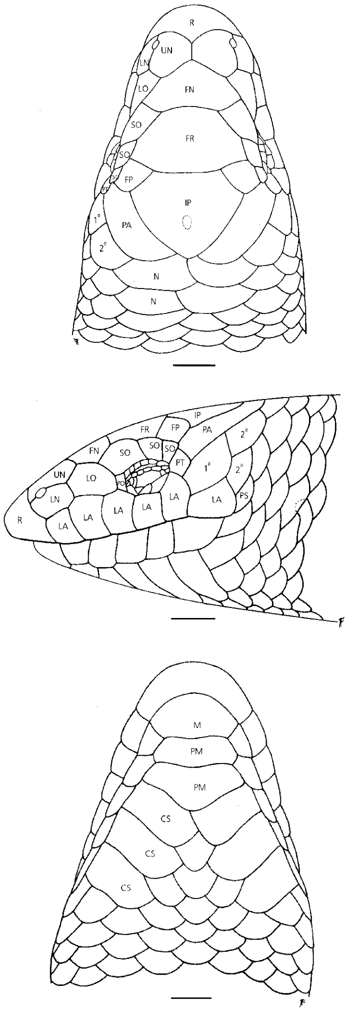

FIGURE 2: Head of *Ophiomorus latastii* (AMS R 156217). Abbreviations: see Fig. 1. Scale bar = 1 mm. Drawing: H. Finlay.

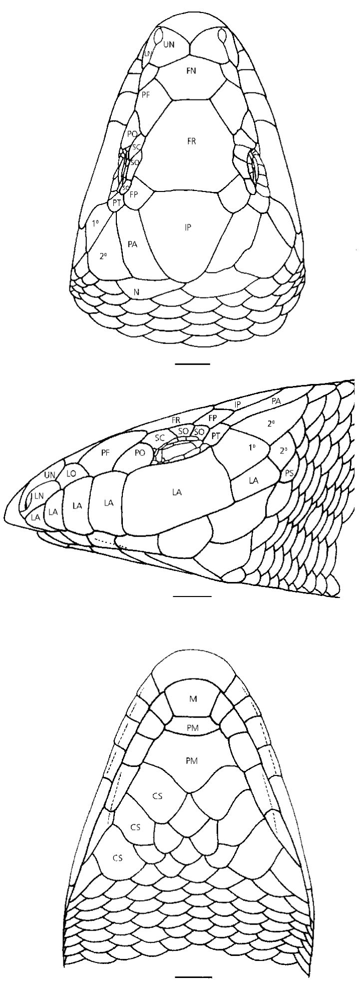

FIGURE 3: Head of *Ophiomorus raithmai* (CAS 99838). Abbreviations: see Fig. 1. Scale bar = 1 mm. Drawing: H. Finlay.

MATERIALS AND METHODS

Specimens and materials examined included whole alcoholics, extracted dried skulls and radiographs (Appendix I). Data were also taken from the literature (Boulenger, 1887; Anderson and Leviton, 1966 and Nilson and Andrén, 1978).

The number of presacral vertebrae, sternal ribs, mesosternal ribs and complete inscriptional chevrons were counted from radiographs.

Statistical analysis was carried out using Systat 9.0 software. Statistical significance was taken at the 0.05 level.

Museum acronyms follow Leviton et al., 1985.

The cladistic analysis was based on 26 characters (Fig. 4; Appendix II), with all characters considered unordered. The outgroup was the genus *Eumeces*, especially the subgenus *Pariocela* (Griffith et al., 2000), the most generally primitive group of skinks based on the list of characters used by all recent workers on relationships within squamates in general (Greer and Broadley, 2000). In the character matrix (Appendix III), a "B" (for "both" states) denotes variability in a character and a "?" denotes lack of information. The small size of the dataset permitted all analyses to be done with the branch and bound method, using the PAUP* portable version 4.0b8 for Windows (Swofford, 2001). Branch robustness and support were evaluated using the Bootstrap (Felsenstein, 1985) and Bremer support (Bremer, 1994; also called "decay index"). Study of character distributions on the tree and generation of a command file to generate Bremer support values in PAUP was done using MacClade version 4 (Maddision and Maddison, 2000).

RESULTS AND DISCUSSION

Diagnosis of the Genus *Ophiomorus*.- The genus *Ophiomorus* may be diagnosed vis-à- vis the generally primitive scincid genus *Eumeces* on the basis of the following derived character states: nostril between an upper and lower nasal scale, both of uncertain homology (Figs 1-3); prefrontal scales separated; frontal scale hour-glass shaped due to constriction of frontal by first supraocular (except in *O. latastii*- below)(Greer and Shea, 2000); supraoculars three (as opposed to four); supraciliary row incomplete lateral to most posterior supraocular, i.e., most posterior supraocular enters supraciliary row; frontoparietals separated; pretemporal single; lower eyelid with clear central disc; postsupralabial single; postmentals two (variable in *Eumeces,* hence possibly primitive in skinks); dorsal and lateral body scales with one or sometimes two (in tandem) minute pits in central posterior part of scale; digits 4/3 or less and phalanges 2.3.4.2/2.3.4 or less; premaxillary teeth modally ≤ 6; presacral vertebrae ≥ 45; sternal/mesosternal ribs $\leq 3/1$; inscriptional chevrons ≥ 7 (Table 1); thoracic and sometimes anterior lumbar ribs with dorsoanterior accessory processes.

Unusual features of *Ophiomorus latastii*.- *Ophiomorus latastii* is unique within the genus in two regards. First, it appears to have undergone a degree of truncation in the region just in front of the eye (Fig. 2). This is evident as a loss of the prefrontals, the posterior loreal, the anterior supraciliary, the anterior part of the first supraocular and probably a supralabial (see character 7 of Appendix). The adaptive significance, if any, of this foreshortening is unknown.

Second, the species has also undergone truncation in the neck region. This is evident in the loss of one of the eight cervical vertebrae, leaving only seven. A reduction in the number of cervical vertebrae is rare in scincids, occurring in only eight other lineages: the acontines (5 cervicals based the generally primitive *Acontias plumbeus* AG, pers. obs.), *Davewakeum* (7, pers. obs.), *Feylinia* (7)- *Melanoseps* (6)- *Scolecoseps* (6) (AG, pers. obs. for both the relationship and the number of cervical vertebrae) and *Scelotes mossambicus* (7, AG, pers. obs.) among the non-lygosomines (Greer and Shea, 2000) and *Anomalopus brevicollis* (7, Greer and Cogger, 1985), *Eumecia* (7, AG, pers. obs.), *Isopachys anguinoides* (7, AG, pers. obs.) and the *bipes* species group of *Lerista* (7, Greer, 1986) among the lygosomines. All these species are relatively limb-reduced. *Eumecia* has two small limbs with two digits on the manus and three on the pes;

TABLE 1: Mensural and meristic characters of the species of *Ophiomorus*. Superscripts on the sternal/mesosternal rib data indicate the number of observations in cases of intraspecific variation. Data on snout-vent length (SVL), modal number of midbody scale rows (MBSR) and the number of digits are from the literature; all other data are based on personal observation. The species are arranged in a morphocline of digits (first order) and phalanges of the pes (second order).

Species	Max SVL	MBSR	Digits manus/ pes	Phalanges manus/pes	Presacral vertebrae			Sternal/ mesosternal ribs	Inscriptional chevrons		Sacral pleurapophyses meet (+)/sep.(-)
					Range	Mean	N		Range	N	
blanfordi	96	20	4/3	2.3.4.2/2.3.4	45	45	1	3/1	7	1	+
brevipes	91	22	4/3	2.3.4.2/2.3.4	48-49	48.5	2	3/1	8	2	+
chernovi	95	24	4/3	2.3.4.2/2.3.4	51	51	1	3/1	10	1	+
nuchalis	98	22	4/3	2.3.4.2/2.3.4	52	52	1	3/1	10	1	+
streeti	110	20	3/3	2.3.4.0/2.3.4	49-50	49.5	2	3/1	11	1	+
tridactylus	95	22	3/3	2.3.4.0/2.3.4	50-53	51.2	5	2/1	8-10	2	+
raithmai	99	22	3/3	2.3.3.0/2.3.4	49-51	49.7	6	2/21-2/14	11-14	5	+
persicus	82	22	3/2	2.3.4.0/0.2.4	53-58	56.4	7	2/1	9-10	4	-

TABLE 2: Snout-vent length and number of transverse scale rows in the sexes of three species of *Ophiomorus* (data from Anderson and Leviton, 1966). MW = Mann Whitney U statistic. P values < 0.05 are in bold.

	Snout-vent length (mm)								Transverse scale rows							
	Males			Females					Males			Females				
Species	Range	Mean	N	Range	Mean	N	MW	P	Range	Mean	N	Range	Mean	N	MW	P
O. persicus	56-72	64.6	7	73-82	77.1	9	0.00	**0.0008**	112-122	115.3	7	118-124	120.8	9	7.00	**0.009**
O. raithmai	64-85	77.1	7	63-99	81.6	14	36.0	0.33	105-110	107.3	7	111-114	111.8	13	0.00	**0.0002**
O. tridactylus	71-91	82.0	9	76-88	84.7	6	18.5	0.31	101-114	110.9	9	113-121	116.2	6	5.50	**0.01**

Scelotes mossambicus has no front limbs and a clawless stylar rear limb, and the remaining species are limbless. However, none of these species is unique in its degree of limb reduction. In terms of their ecology, on the basis of its unmodified head scale morphology *Eumecia* is probably surface dwelling (but perhaps in a lattice-work of near-ground stems) whereas the others are known or can be inferred to be fossorial. But these are not unique ecological associations. Hence, on present knowledge, it is difficult to explain why any of these nine skink lineages (including *Ophiomorus latastii*) has lost a cervical vertebra.

Sexual dimorphism.- In the three species of *Ophiomorus* for which the most data are available (Anderson and Leviton, 1966: table 1), a strong sexual dimorphism in snout-vent length is evident in *Ophiomorus persicus*, with females being larger than males. However, there is no significant sexual dimorphism in snout-vent length in *O. raithmai* or *O. tridactylus*, although the females tend to be larger (Table 2). In most species of skinks, females are larger than males, but in some species males are larger than females while in other species there is no significant difference (AG, pers. obs.).

A strong sexual dimorphism is evident in the number of transverse scale rows along the body, with females having more scales than males in *Ophiomorus persicus* (noted by Anderson and Leviton, 1966 on the basis of non-overlapping ranges of counts), *O. raithmai* and *O. tridactylus* (Table 2). In many skink species, including some robust-limbed forms, the number of scales along the length of the body is higher in females than in males. Hence this particular sexual dimorphism in *Ophiomorus* is not necessarily related to its limb-reduction. Other species of skinks show no significant difference between the sexes in the number of scales in a longitudinal row along the body, but in no species of skink do males have more scales than females (AG, pers. obs.).

Cladistic relationships.- A single parsimonious tree was found (Fig. 4; Appendix IV), with tree length of 59 and ensemble fit indices as follows: consistency index (CI) = 0.71, retention index (RI) = 0.68, and rescaled consistency index (RC) = 0.49. Seven steps of the tree length are added because some species bore variable (both states) characters; in these, a final change is added within the terminal.

An earlier study of the species of *Ophiomorus* identified two groups, a western one consisting of *O. latastii, O. persicus* and *O. punctatissimus* and an eastern one consisting of *O. blanfordi, O. brevipes, O. chernovi, O. raithmai, O. streeti,* and *O. tridactylus* (Anderson and Leviton, 1966). The western group was recognised on the basis of "the tendency to limb reduction finds its extreme in these species" and a dark parietal peritoneum and the eastern group was recognised on "their morphological adaptation to this mode of life [sand-burrowing]" and a pale peritoneum (Anderson and Leviton, 1966). *O. persicus* was said to "link the two groups in some morphological aspects" but it was also said to be "undoubtedly" the closest living relative of *O. punctatissimus* (Anderson and Leviton, 1966; see also Boulenger, 1887).

The cladistic analysis supports the earlier recognised eastern group (Fig. 4: node 17) but not the western group, which is paraphyletic in this analysis. The analysis does not support a sister group relationship between *Ophiomorus persicus* and *O. punctatissimus*. The western group is monophyletic in trees that are only one step longer and Bremer support in this part of the cladogram is weak, so a topology-dependent permutation tail probability (T-PTP = 0.142; Faith, 1991) does not differentiate significantly between the two possibilities (western group monophyletic or not). The analysis supports the inclusion of the most recently described species, *O. nuchalis*, as a member of the eastern group and sister to *O. brevipes*, with which it was originally thought to be closely related (Nilson and Andrén, 1978). This sister-group relationship, however, is dependent on the homoplastic character 15 so the Bremer support for this branch is only 1.

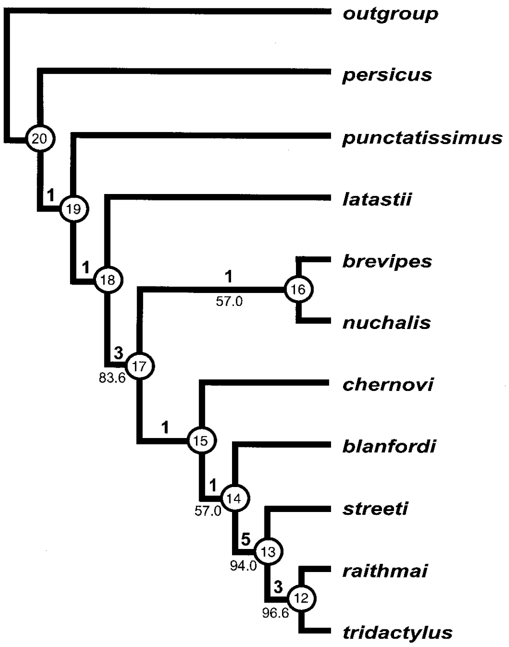

FIGURE 4: The single most parsimonious cladogram for the species of *Ophiomorus*. See text for details. Nodes numbered in circles, Bremer support values indicated above branches, and bootstrap frequency values below branches. Only branches with bootstrap values above 50% are shown.

Limb reduction.- *Ophiomorus* is one of the few limb-reduced skink lineages in which some of the species have a greater degree of digit reduction in the rear limb than in the front limb. *O. blanfordi*, *O. brevipes*, *O. chernovi* and *O. nuchalis* all have four digits on the manus and three on the pes while *O. persicus* has three on the manus and two on the pes. The remaining species have the same number of digits on the front and rear limbs (3/3 or 0/0)(Table 1). Despite the differences in the number of digits on the front and rear limb, the two variables are still highly correlated ($r = 0.95$, $P < 0.001$, $N = 10$). The only other skinks with fewer digits on the rear limb than on the front are: some *Androngo trivittatus* (4/3)(Brygoo, 1979), *Anomalopus leuckartii* (2/clawless style), *A. mackayi* (3/2), *A. verreauxii* (3/clawless style)(Greer and Cogger, 1985), some *Brachymeles cebuensis* (3/2)(Brown and Alcala, 1980), *B. pathfinderi* (5/4)(Brown and Alcala, 1980), some *Larutia miodactyla* (2/1)(Boulenger, 1912; pers. obs.),

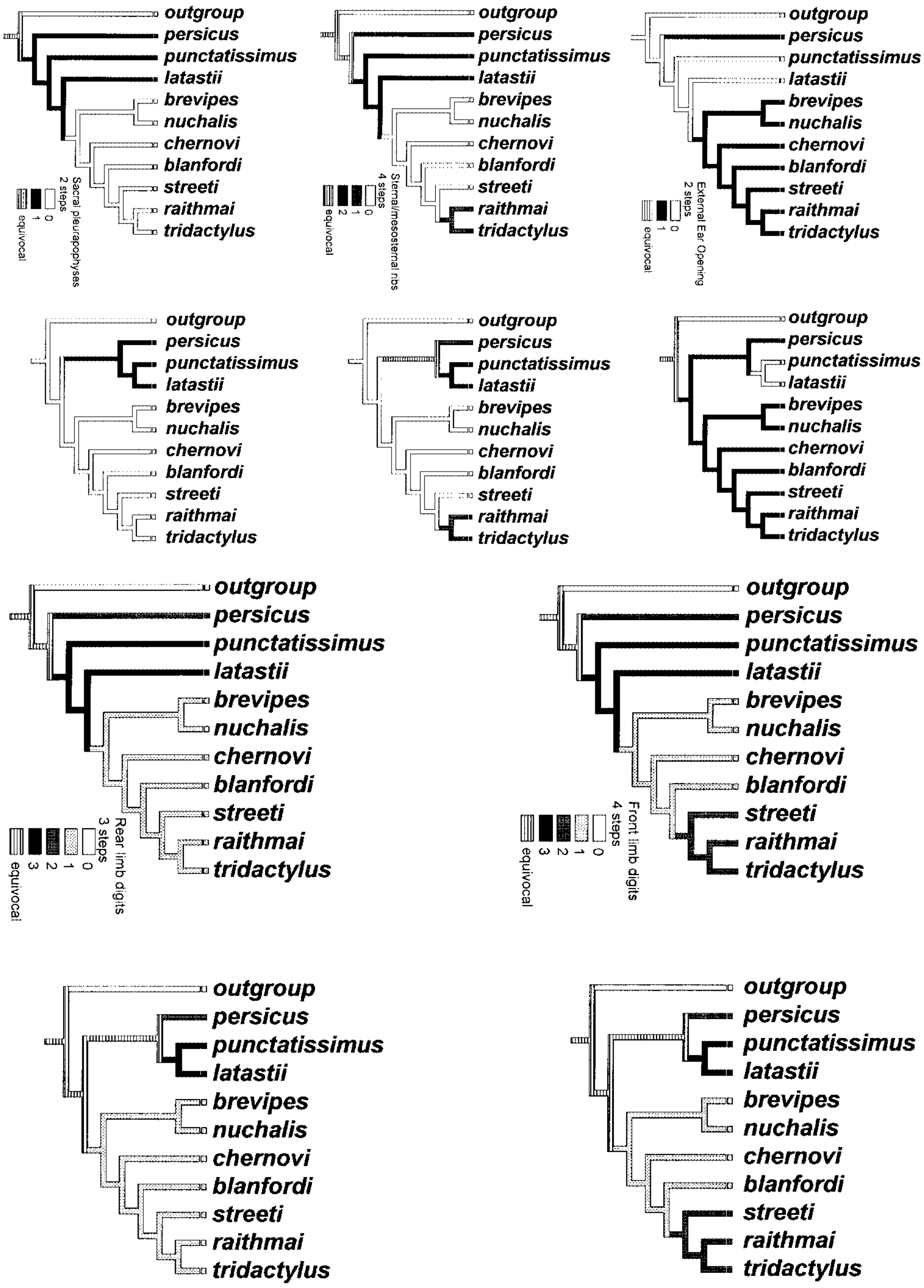

FIGURE 5: Comparison of character state changes in trees with the western group paraphyletic (left, 52 steps) and monophyletic (right, 53 steps). Characters from top to bottom are: character 13, external ear opening; character 23, sternal/mesosternal ribs; character 24, sacral pleurapophyses; character 25, front limb digits, and character 26, rear limb digits. Optimisations assume accelerated transformation.

Leptoseps poilani (5/4)(Bourret, 1937, as *Siaphos poilani*), *Lygosoma vosmaeri* (5/4)(Smith, 1935), *Panaspis luberoensis* (4/3)(Perret, 1982) and some *Sepsophis punctatus* (2/absent)(BMNH 82.5.22.156, AG, pers. obs.).

The number of phalanges in the manus and pes in *Ophiomorus* can be ordered in a morphocline; for the manus: 2.3.4.2 - 2.3.4.0 - 2.3.3.0 - 0.0.0.0 and for the pes: 2.3.4 - 0.2.4 - 0.0.0 (Table 1). In other limb reduced skink lineages, phalangeal morphoclines may be linear, e.g., *Chalcides* pes (Greer et al., 1998), *Lerista* manus (Greer, 1987), *Nannoscincus* manus and pes (Greer, 1997), *Panaspis* manus and pes (Greer, 1997) or reticulate, e.g., *Chalcides* manus (Greer et al., 1998), *Hemiergis* manus and pes (Choquenot and Greer, 1989) and *Lerista* pes (Greer, 1987). However, the cladogram for *Ophiomorus* (Fig. 4) suggests that the evolution of limb morphology may not have followed the morphocline outlined above. For example, the number of digits on the manus is hypothesized to be none (phalanges 0.0.0.0) at basal nodes 18 and 19 but then reverting to four (2.3.4.2) at node 17, and the number of digits on the pes is hypothesised to be none at basal nodes 18 and 19 but then reverting to three (2.3.4) at node 17. Hence, the relationships in the cladogram support the possibility of both strong saltations among the observed limb morphologies and possible reversals, that is, the re-acquisition of digits. However, the basal part of the cladogram is only weakly supported and a topology that has a monophyletic western group (1 step longer) could support a basal digital configuration of 4/3 and hence be compatible with the morphoclines of the phalanges for the manus and pes suggested above (although saltations would still be possible)(Fig. 5). The same argument applies to other characters generally associated with limb reduction that show apparent reversals under the most parsimonious tree (Fig. 4), such as the lower number of sternal and mesosternal ribs and the separation of the sacral pleurapophyses' distal ends.

The most parsimonious tree suggests that the external ear opening was lost twice independently in *Ophiomorus*: once in *O. persicus* and once in the eastern group (node 17) (Fig. 4). However, the topology that recognises a monophyletic western group (1 step longer) suggests that the external ear opening was absent in the ancestor of the genus but then re-acquired in the ancestor of *O. punctatissimus* and *O. latastii* (Fig. 5).

The species of *Ophiomorus* show a strong correlation between the modal number of longitudinal scale rows at midbody and the number of digits on the front limb ($r = 0.84$), the rear limb ($r = 0.82$) and both limbs combined ($r = 0.84$) ($P < 0.005$, $N = 10$ in all three cases). Assuming that scale size remains isometric with body circumference, these relationships suggest that as the number of digits decreases, the trunk becomes more attenuated and vice versa. In the Australian sand swimming genus *Lerista,* seemingly both ecologically and morphologically similar in many ways to *Ophiomorus*, the correlation between the modal or mid-range number of longitudinal scale rows at midbody, although not significant for the number of digits on the front limb ($r = 0.19$, $P > 0.12$), is significant for the rear limb ($r = 0.35$, $P < 0.01$) and both limbs combined ($r = 0.26$, $P < 0.05$, $N = 66$ in all cases).

Among species, the mean number of ventral scales and the mean number of presacral vertebrae in females (the more common sex) are highly correlated ($r = 0.94$, $P < 0.001$, $N = 10$). This result is not too surprising because both variables reflect trunk segmentation.

Ophiomorus persicus is unusual in terms of limb reduction in that despite having a rear limb with two digits, the sacral pleurapophyses' are separated widely at their distal ends ($N = 6$). Usually, only skinks with much more reduced rear limbs, such as the two limbless species of *Ophiomorus*, have the sacral pleurapophyses separated.

The relationship between the type of substrate and the degree of limb reduction in *Ophiomorus* is clouded by a lack of information for some species, especially the limbless species, *O. latastii* and *O. punctatissimus*. We know (above) or can infer from their general morphology (Anderson and Leviton, 1966) that species with the lesser degrees of limb development (digits 4/4 to 3/3) inhabit loosely consolidated sands, mainly dunes, but only the most tenuous inference for only one of the limbless species, *O. punctatissimus* (introduction) suggests that limblessness may be associated with firmer substrates. Unfortunately, the substrate type of the "intermediate" species in terms of limb reduction, *O. persicus* (digits 3/2), is unknown but critical. Like the limbless species, this species lacks the typical sand-swimming morphology seen in the other species. The beguiling possibility arising out of the available data is that, in *Ophiomorus,* intermediate and advanced degrees of limb reduction may not have evolved in association with dry, loosely consolidated substrates.

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APPENDIX I

Specimens of *Ophiomorus* examined. Those specimens examined as dried skulls are indicated with an asterisk.

O. blanfordi: FMNH 43437

O. brevipes: CAS 86593, 10979, FMNH 141550*

O. chernovi: CAS 100806

O. latastii: AMS 156215-156217; NMW 10406

O. nuchalis: NHMG 4418

O. persicus: FMNH 141555, 141557*, 141559-141561, 41563, 141565, 141577-141580, 141582

O. punctatissimus: AMS Palmer 5154; AMNH 17819; CAS 12752; MCZ 38517*, 112210, UMMZ 65579 (N = 3)

O. raithmai: AMNH 85846*; CAS 99835-99836, 99838, 99842, 99846, 121127

O. streeti: CAS 100024; FMNH 141551

O. tridactylus: AMNH 71622, 75610*; CAS 84679; UMMZ 121999, 122619

APPENDIX II

Characters used in the phylogenetic analysis of the species of *Ophiomorus.*

1) Snout rounded (0), bluntly spatulate (1) or spatulate-shaped (2).
2) Infralabials smoothly rounded (0) or with a distinct bevel (1).
3) Supraoculars three (0) or two (1).
4) Preoculars present (0) or absent (1).
5) Presubocular present (0) or absent (1).
6) Supraciliaries posterior to first present (0) or absent (1).
7) Supralabials posterior to subocular two (0) or one (1). Four species of *Ophiomorus* have six supralabials instead of seven and hence appear to have lost a supralabial. However, the supralabial has apparently been lost in two different ways. In *O. punctatissimus*, a supralabial anterior to the subocular supralabial has been lost, whereas in the ancestor of *O. raithmai, O. tridactylus* and *O. streeti* the subocular supralabial has fused with the one just posterior to it. The supralabial count as made here preserves this important distinction among the species that are "similar" in having only six supralabials.
8) Prefrontals large (0) or small (1).
9) Prefrontals separated from supralabials (0) or in contact (1).
10) Nuchal pairs > one (0) or one (1).
11) Upper secondary temporal and pretemporal in contact (0) or separated by primary temporal and parietal contact (1).
12) First pair of large chin scales in contact (0) or separated (1).
13) External ear opening present (0) or absent (1).
14) Parietal peritoneum dark (0) or pale (1).
15) Midbody scale rows modally 24 (0), 22 (1), 20 (2), 18 (3) or 16 (4)
16) Ventrolateral body wall rounded (0) or ridged (1).
17) Premaxillary teeth six (0) or 5 (1).

18) Pre- and postfrontal separated above orbit (0) or in contact (1).
19) Stapedial shaft projects below quadrate (0) or abuts quadrate (1).
20) Hypohyal present (0) or absent (1).
21) CB II present (0) or absent (1).
22) Presacral vertebrae mean falls in range of 48-52 (0) or 53-58 (1).
23) Sternal/mesosternal ribs 3/1(0), 2/1 (1) or 2/0 (2).
24) Sacral pleurapophyses contact (0) or separated (1). The distal ends of the two sacral vertebrae's pleurapophyses either contact (usually without fusing) or are widely separated at their distal ends.
25) Front limb with digits 5 (0), 4 (1), 3 (2) or limb absent (3).
26) Rear limb with digits 5 (0), 3 (1), 2 (2) or limb absent (3).

APPENDIX III

Character matrix for the analysis of the cladistic relationships of the species of *Ophiomorus.*

characters 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2
1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6
outgroup 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0 0 0 0 0 0 0
blanfordi 2 1 0 0 1 0 0 0 0 1 1 0 1 1 2 1 1 1 ? ? ? 0 0 0 1 1
brevipes 1 0 0 0 1 0 0 0 0 1 1 0 1 1 1 0 B 1 1 ? ? 0 0 0 1 1
chernovi 1 0 0 0 1 0 0 0 0 1 1 0 1 1 0 1 1 1 ? ? ? 0 0 0 1 1
latastii 1 0 0 0 1 1 0 B B 0 1 0 0 1 4 0 0 1 0 1 1 1 2 1 3 3
nuchalis 1 B 0 0 1 0 0 0 0 1 1 0 1 1 1 0 1 1 ? ? ? 0 0 0 1 1
persicus 0 0 0 0 0 0 0 1 0 0 0 0 1 0 2 0 1 0 0 1 0 1 1 1 2 2
punctatissimus 0 0 0 0 0 0 0 1 0 0 1 0 0 0 3 0 B 1 ? 1 1 0 2 1 3 3
raithmai 1 1 1 1 1 1 1 0 1 B 0 1 1 1 1 1 1 1 1 1 1 0 1 0 2 1
streeti 2 1 1 1 1 1 0 0 0 0 1 1 1 1 2 1 1 1 ? 0 0 0 0 0 2 1
tridactylus 2 1 1 1 1 1 1 0 1 B 1 1 1 1 1 1 1 1 1 1 0 0 1 0 2 1

A "B" indicates both states are present. A "?" indicates the state of the character is unknown.

APPENDIX IV

Apomorphy lists for the nodes in the cladogram of *Ophiomorus* Species (Fig. 4). A double lined arrow indicates an unambiguous change, and a single lined arrow indicates a change that could optimise on a different branch. Optimisations assume accelerated transformation (ACCTRAN). Consensus index (CI) is shown for each character state transition. See character list above for details of numbered characters. Transitions internal to the terminals are not shown.

Branch	Character	CI	Change
Outgroup to node 20	8	0.667	0 <-> 1
	15	0.667	0 <-> 2
	17	0.750	0 <-> 1
	20	0.500	0 <=> 1
	23	0.500	0 <-> 1
	24	0.500	0 <=> 1
	25	0.750	0 <-> 2
	26	1.000	0 <-> 2
node 20 to node 19	11	0.500	0 ==> 1
	18	1.000	0 ==> 1
	21	0.333	0 —> 1
	23	0.500	1 —> 2
	25	0.750	2 —> 3
	26	1.000	2 —> 3
node 19 to node 18	1	0.667	0 ==> 1
	5	1.000	0 ==> 1
	8	0.667	1 —> 0
	14	1.000	0 ==> 1
node 18 to node 17	10	0.750	0 ==> 1
	13	0.500	0 ==> 1
	19	1.000	0 ==> 1
	21	0.333	1 —> 0
	23	0.500	2 —> 0
	24	0.500	1 ==> 0
	25	0.750	3 ==> 1
	26	1.000	3 ==> 1
node 17 to node 15	16	1.000	0 ==> 1
node 15 to node 14	1	0.667	1 ==> 2
	2	1.000	0 ==> 1
node 14 to node 13	3	1.000	0 ==> 1
	4	1.000	0 ==> 1
	6	0.500	0 ==> 1
	10	0.750	1 —> 0
	12	1.000	0 ==> 1
	25	0.750	1 ==> 2
node 13 to node 12	7	1.000	0 ==> 1
	9	1.000	0 ==> 1
	15	0.667	2 ==> 1
	23	0.500	0 ==> 1
node 12 to *raithmai*	1	0.667	2 ==> 1
	11	0.500	1 ==> 0
	21	0.333	0 —> 1
node 13 to *streeti*	20	0.500	1 ==> 0
node 15 to *chernovi*	15	0.667	2 —> 0
node 17 to node 16	15	0.667	2 ==> 1
node 18 to *latastii*	6	0.500	0 ==> 1
	15	0.667	2 ==> 4
	17	0.750	1 —> 0
	22	0.500	0 ==> 1
node 19 to *punctatissimus*	15	0.667	2 ==> 3
node 20 to *persicus*	13	0.500	0 ==> 1
	22	0.500	0 ==> 1

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PHYLOGENETIC RELATIONSHIPS AMONG THE ASIAN TORTOISES OF THE GENUS *INDOTESTUDO* (REPTILIA: TESTUDINES: TESTUDINIDAE)

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(with two text-figures)

ABSTRACT.– **Based on variation in 1094 bp of the mitochondrial cytochrome *b* gene among members of the genus *Indotestudo* from southern Asia (*I. elongata*), south-western India (*I. travancorica*), and eastern Indonesia (*I. forstenii*), *I. travancorica* is most similar genetically to *I. elongata* (3.7% divergence), and strongly divergent from *I. forstenii* (5.5 to 5.9%). Individuals of *I. forstenii* with and without a nuchal scute differ genetically at less than 0.7%. Our analysis offers no support for the hypothesis that Indonesian populations of *I. forstenii* represent introductions of *I. travancorica* from India. The recognition of three nominal species (*I. elongata, I. forstenii* and *I. travancorica*) in the genus is thus warranted.**

KEY WORDS.– ***Indotestudo, I. elongata, I. forstenii, I. travancorica*, turtle, systematics, DNA.**

INTRODUCTION

Schlegel and Müller (1840: 30) first described *Testudo forstenii* from Halmahera Island, in the Molucca Islands (now Maluku) in eastern Indonesia and it is now known only from the islands of Halmahera and Sulawesi. Although Schlegel and Müller did not explicitly designate a type specimen, Hoogmoed and Crumly (1984) determined that the description was based on a specimen (RMNH 3811) in the Rijksmuseum van Natuurlijke Histoire (at present Nationaal Natuurhistorisch Museum) in Leiden. Blyth (1853: 639) described *Testudo elongata* from "Arakan" (= Rakhine Yoma, a mountain range along coordinates ca. 18-21° N, 93-95° E) in western Myanmar (Burma), apparently based on four syntypes (ZSI 796, 798, 799, and 800) in the collection of the Zoological Survey of India in Calcutta (Das et al., 1998). Fifty-four years later, Boulenger (1907:560; pl. I-II) described *Testudo travancorica* from the Western Ghats of south-western India, based on two specimens in the British Museum (Natural History) (now, The Natural History Museum, London, BMNH 1906.7.18.6-7).

Lindholm (1929) first recognized the distinctiveness of *Testudo elongata* and designated it as the type species of his new subgenus *Indotestudo* (genus *Testudo*), but he did not mention the placement of the other two species. However, Williams (1952) supported the recognition of the subgenus Indotestudo (under *Testudo*), and included *elongata, forstenii*, and *travancorica* therein. Williams (p. 220 in Loveridge and Wil-

TABLE 1: Uncorrected ("p") distance matrix for samples of *Indotestudo* and outgroup taxa.

Species	*picta*	*agassizii*	*emys*	*elongata*	*travancorica*	*forsteni* A
Chrysemys picta	–					
Gopherus agassizii	0.156	–				
Manouria emys	0.170	0.129	–			
Indotestudo elongata	0.170	0.138	0.142	–		
Indotestudo travancorica	0.172	0.141	0.138	0.037	–	
Indotestudo forstenii A (with nuchal)	0.174	0.144	0.138	0.060	**0.055**	–
Indotestudo forstenii B (without nuchal)	0.174	0.144	0.136	0.062	**0.059**	**0.005**

liams, 1957) partitioned the all-inclusive tortoise genus *Testudo*, placing *elongata, forstenii* and *travancorica* in the subgenus *Indotestudo* of the genus *Geochelone*, the arrangement followed by Auffenberg (1974). Bour (1980) subsequently elevated *Indotestudo* to full generic rank (including the same three species), a position supported by the cladistic analyses of Crumly (1982, 1984), and adopted by nearly all subsequent authors.

Although the monophyly of *Indotestudo* (whatever its rank) has not been questioned for 50 years, Auffenberg (pers. comm.; mid-1970's) and Pritchard (1979: 319) first speculated that the Indonesian populations of *I. forstenii* might represent an introduction of *I. travancorica* from India. Hoogmoed and Crumly (1984) examined specimens of all three species of *Indotestudo*, could not distinguish *I. forstenii* from *I. travancorica*, synonymized the two taxa under the older name *I. forstenii*, and could not reject the hypothesis that *I. forstenii* represented an introduced population of *I. travancorica*. This arrangement has been followed by nearly all subsequent authors (e.g., Groombridge and Wright, 1982; Das, 1991, 1995); however, Bour (in David, 1994: 87) and McCord et al. (1995) speculated that this synonymy might be premature.

Pritchard (2000) recently reopened the controversy by examining the morphology of all three species of *Indotestudo*. He concluded that *I. travancorica* was distinguishable from *I. forstenii* and *I. elongata*, and hence should be resurrected from the synonymy of *I. forstenii*. However, neither Pritchard nor any other author has hypothesized a phylogenetic relationship among the populations of *Indotestudo*. Therefore, in order to address the taxonomic and evolutionary relationships among these species from a molecular perspective, we examined mtDNA sequence variation in these and related tortoises.

MATERIALS AND METHODS

Blood samples were obtained from two pet trade specimens of *Indotestudo forstenii* in the collection of A. Weinberg, and known to have come from Sulawesi (McCord, pers. comm.), one with a nuchal (hereafter, *I. forstenii* A) and one without (hereafter, *I. forstenii* B); a captive specimen of *I. travancorica* from Chalakudy (10° 06' 23"N; 76° 09' 53"E), Kerala State, south-western India, now in the live collection of the Centre for Herpetology at the Madras Crocodile Bank Trust, which will be deposited in the collection of the Zoological Survey of India, upon its death; and a pet trade specimen of *I. elongata*, believed to have come from Myanmar, in the live collection of WPM. Tissue samples from *Manouria emys* (considered as representing the most "primitive" living genus of tortoises; Crumly, 1982, 1984), *Gopherus agassizii* (representing another early tortoise genus), and *Chrysemys picta* (an emydid turtle; Gen Bank accession #5902189) were included as our outgroup.

Whole genomic DNA was extracted from blood via SDS/protease K digestion, followed by phenol/chloroform extraction (Shaffer et al., 1997). Most (1094 of 1140bp) of the mitochondrial cytochrome *b* gene was amplified using Taq-mediated PCR and sequenced on an ABI 377 (Applied Biosystems, Foster City, CA) automatic sequencer using primers developed by PQS and HBS (available on request). Overlapping sequences within individual samples were aligned and edited using SeqED (Applied Biosystems), and complete sequences were aligned across samples using ClustalW (Thompson et al., 1994). Alignments were unambiguous, with no insertions or deletions present. All sequences will be deposited in Gen Bank. Phylogenetic analyses were conducted using PAUP* 4.0b3a (Phylogenetic Analysis Using Parsimony; provided by David L. Swofford; www.lms.si.edu/PAUP).

RESULTS AND DISCUSSION

Within the 1094 bp fragment of the cytochrome *b* gene, 152 nucleotide sites were phylogenetically informative and 788 were constant across all taxa. An heuristic search of equally weighted characters (with 100 bootstraps) using maximum parsimony produced two shortest trees differing only in the placement of two of the outgroup taxa. (Fig. 1). An analysis by the neighbour-joining method (HKY 85 model; 100 bootstraps; unweighted characters) produced identical results (Fig. 1). Maximum likelihood analysis of the same data produced a slightly different arrangement of the ingroup taxa (Fig. 2).

Although these analyses suggest some ambiguity in the placement of *I. elongata, I. travancorica* is clearly more similar genetically to *I. elongata* (3.7% distant; Table 1) than to *I. forstenii* (5.5 to 5.9%). In addition, the terminal position of *forstenii*, its high divergence from its congeners, and the low variation within *I. forstenii* (even between individuals with versus without a nuchal scute) all argue that *Indotestudo forstenii* represents a distinct species native to Indonesia. Furthermore, there is no genetic support (nor historical data) for the hypothesis that *I. forstenii* represents an introduced population of *I. travancorica*. As a consequence, we follow Pritchard (2000) in recommending that *Indotestudo travancorica* be resurrected from the synonymy of *I. forstenii*. Three nominal species in the genus *Indotestudo* are therefore recognisable: *I. elongata* from the mainland of southern and south-eastern India, *I. forstenii* from the islands of Sulawesi and Halmahera in eastern Indonesia and *I. travancorica* from the Western Ghats of south-western India.

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FIGURE 1: Strict consensus tree of phylogenetic relationships among species of the genus *Indotestudo* based on parsimony and neighbour-joining analyses of the cytochrome *b* gene sequence data. Numbers above nodes are bootstrap percentages for the parsimony analysis; numbers below are bootstrap percentages for the neighbour-joining analysis. Length = 430 steps; consistency index = 0.83. Branch length is proportional to number of nucleotide changes by the neighbor-joining analysis.

FIGURE 2: Strict consensus tree of phylogenetic relationships among species of the genus *Indotestudo* based on maximum likelihood analyses of the cytochrome *b* gene sequence data. Branch length is proportional to the number of nucleotide substitutions per site.

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AMPHIBIAN FAUNA OF KAMRUP DISTRICT, ASSAM, WITH NOTES ON THEIR NATURAL HISTORY

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(with one text-figure)

ABSTRACT.– **The amphibian fauna of Assam state, north-eastern India has been poorly evaluated and so far, 30 species have been reported. Kamrup District of Assam with an area of 4,345 km² shows a great diversity of habitats. In the present study, we report 20 species of amphibian from the District. This includes two species (*Philautus garo* and *Ichthyophis garoensis*) that are being reported for the first time from the state.**

KEYWORDS.– **Amphibian diversity, Kamrup District, Assam, India.**

INTRODUCTION

At present, 210 species of amphibians are known from India (Das and Dutta, 1998) and the Western Ghat shows the richest expression of amphibian diversity, with 117 species. In north-eastern India, Meghalaya has the highest number of species (Pillai and Chanda, 1976; 1979; 1981; Chanda 1990; 1991; 1992; 1994; 1995; Roy et al., 1998). Recently, Pillai and Ravichandran (1999) reported two new species of caecilians from the Garo Hills. Assam with its varied topography was known to support a single species of caecilian (Alcock, 1904) and 29 species of anurans (Smith, 1929; Romer, 1949; Chanda, 1994; Bordoloi and Bora, 1998, Dutta et al., 2000).

STUDY AREA

Assam State's Kamrup District (90° 58' - 92° 10'E and 25° 44' - 26° 48'N; area: 4,345 km²) is bounded along its southern border by Meghalaya and has an international boundary with Bhutan at its north-eastern end. It lies in the Brahmaputra river basin and has diversified topography from low-lying swamp (40–45 m above msl) to hills (500 m above msl). The eastern and southern parts are especially hilly, and are intersected by a number of streams, which flow into the Brahmaputra River. The climate is moist tropical with annual rainfall averaging 1,020 mm. Several perennial and seasonal water bodies (Anon., 1997) with varied vegetation (semi-evergreen to reed beds) provide favourable conditions for amphibians.

METHODOLOGY

The study was conducted between February 1997 to October 1999. Specimens were collected by hand and in pitfall traps in association with drift fences. Ecological and morphometric data were collected for all specimens. Voucher specimens were preserved, assigned museum number and housed in the Museum of Arya Vidyapeeth College (AVC). Representative specimens have been deposited in the Zoological Survey of India (ZSI), Kolkata.

NATURAL HISTORY NOTES

Family: Megophryidae

1. *Leptobrachium smithi* Matsui et al., 1999: This was observed in semi evergreen forest at 60-150 m altitudes above msl. Eleven were collected from forest floor with matted grass (*Agrostis*); three from leaf litters; and two from scrub jungle, all near perennial stream. Breeding call was recorded from April to July. Metamorphosed frog was obtained in February. This frog was originally reported from India as *L. hasselti* and a recent revision of the group restricted *L. hasselti* to Java (Matsui et al., 1999). Sengupta et al. (2001) reported *L. smithi* from Meghalaya and Assam.

2. *Megophrys parva* (Boulenger 1893): This was observed in semi evergreen forest floor at 90-110 m above msl. Four were collected from leaf litters and two from mesic vegetation. Calling male was observed on broad-leafed herbs and shrubs at a height of ca.1 m from the ground. *M. parva* was reported from Kaziranga (Assam) and from parts of Meghalaya (Chanda, 1994). Our record confirms the presence of this species on the southern bank of Brahmaputra.

Family: Bufonidae

3. *Bufo melanostictus* Schneider, 1799. This species is common throughout and was found both in human habitation and forest. This was collected from a variety of habitat, six from open field, three from paths, three from paddyfields, two from undergrowth of semi-evergreen forests, two from mesic vegetation, one from under a log and one from under a tree.

Family: Microhylidae

4. *Microhyla ornata* (Duméril and Bibron, 1841). *M. ornata* was noted at altitude ranges from 40 to 300 m above msl. Twelve specimens were collected from leaf litter, three from moist grass blade (*Agrostis*) and two from side of ephemeral water pool. Calling males were observed on the sides of ephemeral water bodies and also on floating leaves, grass blades of water bodies. Breeding coincides with monsoon period. This is a common microhylid occurring in most part of south-east Asia.

5. *Microhyla berdmorei* (Blyth, 1856). This is an occupant of moist semi evergreen forest at an altitude ranges between 110-430 m above msl. Four were collected from wet grass (ca. 60 cm high), two from walkway of forest, two from riparian vegetation and one from ground story of moist semi evergreen forest near stream. This species was reported from Garo Hills in Meghalaya (Pillai and Chanda, 1981) and Goalpara, Dudhnoi and Deoripathar in Assam and Namdapha Biosphere Reserve in Arunachal Pradesh (Chanda 1994).

6. *Uperodon globulosus* (Günther, 1864). This is a burrowing microhylid, observed only during/after heavy rain. Three were collected from waterlogged agricultural field and one from walkway of human habitation. A pair in amplexus was observed in May and August. *U. globulosus* is restricted to India and Bangladesh (Inger and Dutta, 1986; Khan, 1982) In Assam, this species was reported from Kamrup District (Bhaduri and Saha, 1980, Chanda 1994) and Biswanath Plain (Sonitpur District) (Choudhury et al., 1999).

Family: Rhacophoridae

7. *Philautus garo* (Boulenger, 1919). This species occurs at an elevation between 90-140 m above msl in moist semi evergreen forest. All collections (five calling males) were from leaves and twigs of shrub at a height of 0.97-1.88 m from the ground. The species was observed only in June – July, apparently the peak breeding period. This species was described by Boulenger (1919) from Garo Hills and after the original description no collection could be made despite intensive search carried out in and around the type locality (Chanda, 1994). The present study reveals its presence in Garbhanga R.F. and Kulsi R. F., with a range extension of ca. 175 km to the north-east.

8. *Polypedates leucomystax* (Gravenhorst, 1829). The species is commonly encountered in human habitation. In addition, the species is also found in moist evergreen forest at an elevation ranges from 40-300 m above msl. Of the specimens collected, nine were from shrubs (at a height of 1.2-1.8 m), two from trees (at 2.56-3.12 m height), three from wet ground near drain and three from well (at 1.07 m depth). Breeding was observed from April to August. The only record of *P. leucomystax* prior to our work was from Kaziranga National Park (Chanda, 1994). However, it is found to be extensively distributed in Kamrup, the breeding localities being listed by Hussain et al. (1999).

Family: Ranidae

9. *Amolops gerbillus* (Annandale, 1912). An inhabitant of wet semi evergreen forest (elevation 60-140 m above msl) *A. gerbillus* occurs near perennial stream. Seven were collected from streambed, five from riparian zone, two from

moist grass (*Agrostis*) and two from talus (rocks collected at the base of slopes). This frog was reported from Arunachal Pradesh, Meghalaya (Khasi Hills), Assam (Dibrugarh) and West Bengal (Darjeeling) (Chanda, 1994; Sarkar et al., 1992). The present record is the second from Assam and confirms its wide distribution in the north-eastern state of India.

10. *Euphlyctis cyanophlyctis* (Schneider, 1799). This species is a common aquatic frog observed to occur round the year. In all, 36 specimens were collected from waterlogged paddy fields, 19 from perennial lentic water bodies, 18 from ephemeral bodies, 10 from swamps and two from stream at elevation ranges between 40-55 m above msl. Breeding observed from March to November. The frog prefers shallow water.

11. *Hoplobatrachus crassus* (Jerdon, 1853). The species has been recently reported from Assam (Bordoloi and Bora, 1999). Collections were made from agricultural land and swamps. The species shares common habitat with *Hoplobatrachus tigerinus*. Breeding call was recorded in May to August. Saikia et al. (2000) reported wide distribution of this species in flood plain of Brahmaputra river system in Assam.

12. *Hoplobatrachus tigerinus* (Daudin, 1859). This is a common semi aquatic frog of different habitats. Of the collections made, 12 were from seasonal puddles, eight from waterlogged agricultural fields and four from paths. Breeding observed from April to July and noted to occur in both day and night. Chanda (1994) reported it as common frog of north-eastern India.

13. *Limnonectes laticeps* (Boulenger, 1882): *Limnonectes laticeps.* This semi-aquatic ranid of moist evergreen forest, was found at altitudes between 80-105 m above msl. Three specimens were collected from slow flowing stream, three from leaf litters of moist rocky streambed and one from riparian vegetation. On water, it floats, head out, rest of body obliquely positioned underwater. Mating was observed in June. In India, *L. laticeps* is known from Kaziranga National Park, Assam and Khasi Hills and Garo Hills, Meghalaya (Dutta, 1997). The westernmost specific locality of the species is Pantan R.F.

14. *Fejervarya* cf. *limnocharis* (Gravenhorst, 1829): This is a common frog collected from various habitats of altitude ranges from 40-360 m above msl. In all, 22 examples were collected from moist open land near water edges, 10 from moist leaf litter of semi evergreen forest floor, seven from human habitation, five from riparian vegetation, three from grassland, two from under log and two from stream bed. Five morps were noted: a) Size small, with a thin light yellow line extending from temporal to vent, b) Size small, with a thick broad band of yellow to dark red extending from snout to vent, c) Size large, smooth bodied, without a midline, d) Size large, grey coloured, with numerous tubercles on dorsum, the toe IV has two digits free from webbing and e) Size large, smooth bodied parrot green coloured form with more than two digits free from webbing on the toe IV.

These morphs are sympatric; the first three were more abundant The fourth closely resembles *Limnonectes keralensis,* from southern India. Dutta (1987) opined that *Rana verrucosa* (current name *L. keralensis*) reported from eastern India by Mallick and Mallick (1981) and Sarkar et al. (1992) are misidentified specimens of this morph.

Dubois (1984) reported *Limnonectes limnocharis* as a species complex. One of the major morphological characters, mid-dorsal stripe is variable both among and within species included in the species complex. Mohanty et al. (1995) reported the population of the morph with the narrow stripe as more abundant than the other three morphs. However, in the present study, the non-striped morph was found to be the most abundant.

15. *Rana alticola* (Boulenger, 1882). This is a semi-aquatic ranid found along the banks of stream from 70-430 m above msl. In the present collections, two were from stream at a depth of 0.86 m, three from sandy banks of stream and three from moist grass patches. This frog hides during the day under stones of moist stream beds. It exhibits sexual dimorphism in colouration, males with a brown dorsum with lateral black

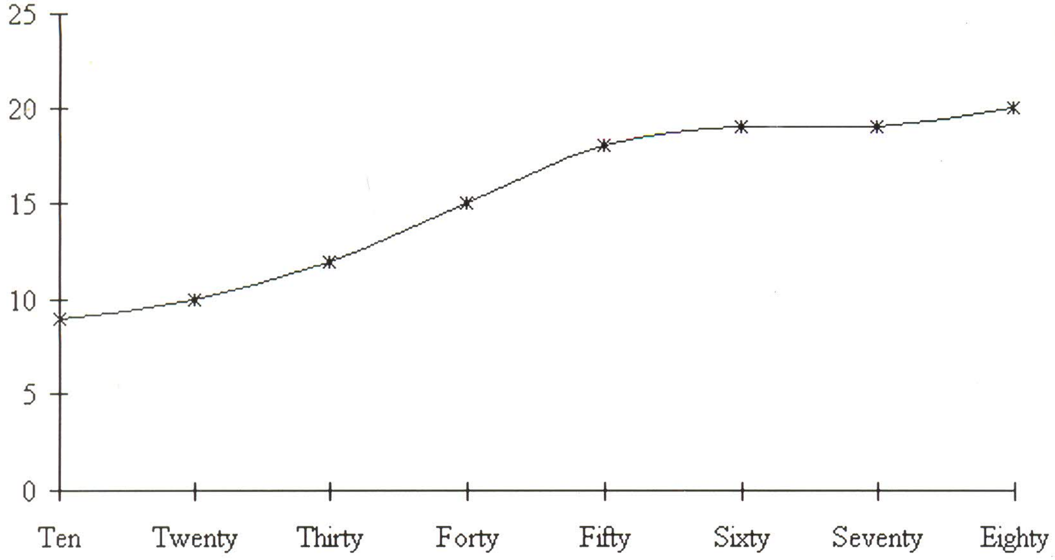

FIGURE 1: Species accumulation curve for amphibians from Kamrup District during the present study.

patch; females golden yellow. Mature males and females were collected from May to August. However, breeding was not observed. Larvae were found throughout the year. *Rana alticola* was recorded originally by Boulenger (1882) from the Khasi Hills, Meghalaya. Subsequently, Smith (1929) and Pillai and Chanda (1979) recorded the species in Meghalaya and Chanda (1994) in Assam and Tripura. This species is found from most hill streams of Kamrup, especially on the south bank of Brahmaputra.

16. *Rana danieli* Pillai and Chanda, 1977. In the present study no collection could be made. However, Chanda (1994) reported this species from Guwahati.

17. *Rana taipehensis* Van Denburgh 1909. A common species of the District that is restricted to urban centres. Six examples were collected from water hyacinth (*Eichhornia*), three from water logged paddy field and two from moist grass (*Agrostis*). Breeding was observed only in April and May. *R. taipehensis* is abundant in Kamrup. However, as this was confused with *R. erythraea* no valid record of this was available till Ahmed and Goswami (1999) and Dey and Gupta (1999) reported the species as rare from Guwahati and Barak Valley, respectively.

18. *Rana* sp (I). A species of the subgenus *Silvirana* that occurs in marshes and waterlogged paddy field of the plains. In all, 12 examples were collected from banks of puddles, three from water, two from moist grass (*Agrostis*), Seven from paddy field, three from moist leaf litter and five from aquatic vegetation. Calling males were observed on banks of pools, on mud or on leaves of aquatic vegetation. Peak breeding period is between April to June.

19. *Rana* sp (II). This species is found in moist areas near edges of marshes and other shallow water bodies. A single specimen was collected from waterlogged grass (0.38 m high). Breeding call was observed during the collection. The peak breeding period is April to July.

GYMNOPHIONA

Family: Ichthyopidae

20. *Ichthyophis garoensis* Pillai and Ravichandran, 1999: This species has been recently described from the Garo Hills, Meghalaya. We observed the species in

Garbhanga R.F. and one specimen was collected from moist leaf litter on rocky substratum near stream. It comes out in numbers after heavy showers. This is an extension of range by 170 km to the north-east.

DISCUSSION

The present inventory of amphibian fauna of Kamrup District, Assam State, north-eastern India, reveals the presence of 20 species. The species accumulation curve shows that survey efforts approach the upper asymptote level (Fig 1) and the total Kamrup fauna is likely to be around 25 species. It is therefore almost certain that we have not encountered all species that occur in the district, and more intensive and longer studies would presumably unearth the rare species.

In Assam State, no studies have been conducted to evaluate the amphibian species richness. Therefore, the Kamrup District fauna cannot be compared with other parts of the State. The closest localities, which have been surveyed include the Garo Hills (Pillai and Chanda, 1981) and the Khasi Hills (Pillai and Chanda, 1979). Although they are located at higher altitudes, they share overall climatic and floral similarities with the present study area, especially at low altitudes, with strong seasonal rainfall. Pillai and Chanda (1981) recorded 11 species of amphibian from the Garo Hills and Kamrup District shares eight species (*Bufo melanostictus, Microhyla ornata, M. bermorei, Fejervarya* cf. *limnocharis, Limnonectes laticeps, Polypedates leucomystax, Euphlyctis cyanophlyctis, Rana danieli*) with the former. Previously, Boulenger (1919, 1920) recorded four species (*Pedostibes kempi, Philautus garo, P. kempiae* and *Rana garoensis*) from the Garo Hills. We observed *P. garo* in Kamrup District, which was discovered after a period of ca. 80 years. Chanda (1994, 1995) added *Megophrys parva, Rana alticola, Rana malabarica* (erroneous identification, see Dutta, 1997) and *Rhacophorus maximus* in the faunal component of Garo Hills. The first two species were recorded in the present study. In all, of the 19 species described from Garo Hills, 11 were recorded from Kamrup.

The Khasi Hills have a rich amphibian fauna, represented by 32 species (Chanda and Pillai, 1979; Chanda, 1994, 1995; Roy et al., 1998). With an amphibian fauna x 1.6 larger than Kamrup, Khasi Hills shares 12 species with the latter. However, the intensity of collection at Garo Hills and Khasi Hills exceeded that performed at Kamrup. It appeared that Kamrup has greater faunal similarities with Garo Hills than Khasi Hills.

In summary, the Kamrup amphibian fauna consists of 19 anurans and one caecilian. The taxa represent an admixture of amphibian fauna of Myanmar and India. It appeared that Kamrup acts as a component of "biogeographic gateway" of India for amphibians of Myanmar and the far south-east region.

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APPENDIX

Data on materials referred to in text

Abbreviations: SVL = snout-vent length, HL = head length, HW = head width, TL = tibia length, R.F. = Reserve Forest.

Leptobrachium smithi: 16 examples; measurements– SVL: 38.4–68.3, HL: 13.0–25.0, HW: 15.5-20.5, TL: 13.0–24.4. Observed locations– Garbhanga R.F., Kulsi R.F., Mayeng Hill R.F. Mus. No. – ZSI A9102.

Megophrys parva: 6 examples; measurements– SVL: 49.0-67.5, HL: 16.5-21.0, HW: 20.5-28.3, TL: 20.0-21.3. Observed locations– Garbhanga R.F., Mayeng Hill R.F. Mus. No.– AVC-CND/7979.

Bufo melanostictus: 25 examples; measurements– SVL: 35.0-39.0, HL: 10.0-11.5, HW: 13.0-13.5, TL: 11.30-14.5. Observed locations– Throughout. Mus. No.– AVC-GHY/7984.

Microhyla ornata: 17 examples; measurements– SVL: 16.8-20.5, HL: 3.0-4.5, HW: 3.9-5.5, TL: 7.1-11.0. Observed locations– Throughout. Mus. No. – ZSI A9101.

Microhyla berdmorei: 9 examples; measurements– SVL: 24.30-31.0, HL: 5.4-7.5, HW: 7.0-10.0, TL: 18.4-25.0. Observed locations– Jarasal R.F., Garbhanga R.F., Mayeng Hill R.F. Mus No – AVC-BSW/8971.

Uperodon globulosus: 4 examples; measurements– SVL: 39.0-67.0, HL: 6.3-10.5, HW: 10.0-18.0, TL: 10.0-17.0. Observed locations- Mandakata, Goreswar, Boko. Mus. No.– AVC-MND/6981.

Philautus garo: 5 examples; measurements– SVL: 19.50-20.20, HL: 5.3-6.0, HW: 6.0-7.2, TL: 7.6-9.4. Observed locations– Garbhanga R.F. Mus. No. – ZSI A9097.

Polypedates leucomystax: 15 examples; measurements– SVL: 34.0-68.5, HL: 10.50-21.00, HW: 12.0-23.2, TL: 18.0-38.0. Observed locations– Throughout. Mus. No.– AVC-BSW/7977.

Amolops gerbillus: 16 examples; measurements– SVL: 23.0-35.0, HL: 8.0-13.0, HW: 8.1-12.0, TL: 12.5-20.0. Observed locations– Garbhanga R.F., Mayeng Hill R.F., Aprikhola R.F., Pantan R.F. Mus. No. – ZSI A9103.

Euphlyctis cyanophlyctis: 84 examples; measurements– SVL: 22.30-46.70. HL: 6.3-14.0, HW: 8.0-15.7, TL: 11.0-18.0. Observed locations– Throughout. Mus. No.– AVC-MK/8974.

Hoplobatrachus crassus: 3 examples; measurements– SVL: 62.3-74.0, HL: 20.2-24.0, HW: 26.4 –27.0, TL: 25.0-28.0. Observed locations– Chaygaon. Mus No.– AVC-CHG/6991.

Hoplobatrachus tigerinus: 24 examples; measurements– SVL: 31.5-64.3, HL: 14.0-36.5, HW: 11.4-38.0, TL: 15.0-55.3. Observed locations– Throughout. Mus No.– AVC-CND/79733.

Limnonectes laticeps: 7 examples; measurements– SVL: 31.4-33.0, HL: 9.3-9.5, HW: 12.0-12.5, TL: 17.0-18.5. Observed locations– Garbhanga R.F., Mayeng Hill R.F., Jarasal R.F., Pantan R.F., Aprikhola R.F. Mus No.– ZSI A9104.

Fejervarya cf. *limnocharis*: 51 examples; measurements– SVL: 15.0-49.0. HL: 7.5-14.5, HW: 6.0-18.5, TL: 8.3-20.5. Observed locations – Throughout. Mus No.– ZSI A9105.

Rana alticola: 9 examples; measurements– SVL: 36.3-59.8, HL: 14.2-21.9, HW: 12.0-18.1, TL: 21.2-34.3. Observed locations– Aprikhola R.F., Amchang R.F., Rani R.f., Garbhanga R.F., Borduar, R.F., Mayeng Hill R.F., Kulsi R.F., Pantan R.F., Borjuli R.F., Jaipur R.F. Mus. No.– AVC-GR/3987.

Rana danieli: Not collected, cited by Chanda (1994).

Rana taipehensis: 11 examples; measurements– SVL: 30.0-35.8, HL: 10.0-13.4, HW: 7.3-11.0, TL: 12.1-17.0. Observed locations– Hajo, Madankamdev, Mandakata, Guwahati, Mirza, Palasbari, Rampur, Boko, Chandubi, Digaru, Borduar.. Mus. No.– AVC-RAM/5985.

Rana sp (I).: 32 examples; measurements: SVL: 27.0-57.2, HL: 9.6-14.3, HW: 8.3-17.3, TL: 14.0-29.0. Observed locations– Guwahati, Mayeng Hill R.F., Madankamdev, Kulsi R.F. Mus No. AVC-CND/7978

Rana sp (II): 1 example; measurements– SVL: 72.45, HL: 19.15, HW: 22.5, TL: 39.35. Observed locations- Bichannala (Rangia). Mus. No.– AVC-BN/6983.

Ichthyophis garoensis.: 1 example; measurements– SVL: 283.0, HL: 8.5, HW: 7.3, BW: 10.3, Annuli: 284. Observed location– Garbhanga R.F. Mus No. AVC-GRB/7599

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A REVISION OF THE BEVELNOSED BOAS (*CANDOIA CARINATA* COMPLEX) (REPTILIA: SERPENTES)

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(with nine text-figures)

ABSTRACT.– **On the basis of observations in captivity of 35 live snakes from various populations, and external morphological data taken on them and 359 museum specimens, *Candoia carinata* auctorum is regarded as a complex of three species, in turn comprising two subcomplexes. The *C. carinata* subcomplex consists of two species, each with two subspecies: *C. s. superciliosa* and *C. s. crombiei* subsp. nov., and *C. c. carinata* and *C. c. tepedeleni* subsp. nov. The *C. paulsoni* subcomplex consists solely of *C. paulsoni*, with six subspecies: *C. p. paulsoni*, *C. p. mcdowelli* subsp. nov., *C. p. rosadoi* subsp. nov., *C. p. sadlieri* subsp. nov., *C. p. tasmai* subsp. nov. and *C. p. vindumi* subsp. nov. All species and subspecies are allopatric, except for marginal sympatry of *C. c. tepedeleni* with both *C. p. paulsoni* and *C. p. mcdowelli*. Intergrade populations are known to occur between *C. p. paulsoni* and *C. p. vindumi*.**

KEY WORDS.– **South Pacific islands; boid snakes; *Candoia carinata* complex; species; subspecies.**

INTRODUCTION

Candoia carinata (Schneider, 1801; Böhme et al., 1998) is a member of the genus of three species of relatively small boas of the South Pacific. The only other boas in the Eastern Hemisphere are three species of *Boa* in Madagascar and Runion islands. Both genera are placed in the infraorder Macrostomata, superfamily Booidea, family Boidae, and subfamily Boinae with five extant genera (Dowling, 1985; McDiarmid et al., 1999).

Abundant in many places, this species is popular in herpetocultural circles. Certain populations are extremely docile, others unpredictably aggressive at times.

The present study of the *Candoia carinata* complex was initiated through observations on live animals provided by one of us (KT) from various localities. Variation in size, diet and behavior made it apparent that more than one species was involved.

The only previous comprehensive study of geographic variation in *Candoia carinata* (McDowell, 1979) concluded that only one species, and no subspecies, was represented. Stull (1956) had earlier described a subspecies, *C. c. paulsoni*, which had generally been accepted (e.g., Stimson, 1969) and even yet is often recognized (e.g., O'Shea, 1996) or mentioned, especially in the popular and herpetocultural literature (e.g., Walls, 1994). However, Stull's distinctions were in high ventral count and pattern, whereas McDowell found no clearcut differences in those features. Nevertheless McDowell came close to the same basic conclusions reached here, as indicated by his statement that "I cannot prove, with the evidence available to me, that "Long-tails" are not specifically distinct from "Short-tails", at least in the Lae region of New Guinea" (McDowell, 1979: 48), where we recognize *C. c. carinata* and *C. paulsoni mcdowelli*.

A variety of common names for *Candoia* and its constituent taxa has been adopted in various works (e.g. Frank and Ramus, 1995; O'Shea, 1996; Walls, 1994), but without consensus. The name "Pacific boas" has commonly been used for the genus as a whole, and is more appropriate than "Ground boas," because arboreality is usual in several populations. "Viper boa" is often used for *C. asper*, and is an apt name for that species, with its stout body, non-prehensile tail and aggressive disposition. Walls (1994) dubbed *C. carinata* as the "Square-snouted ground boa," and we too think it is appropriate to focus its name on its flat, bevel-like, overhung snout, to which we allude with the name "Bevelnosed boa," which is more precisely descriptive of the shape of the snout (Fig. 5). We apply it to all taxa collectively of the *C. carinata* complex, which is moderately to highly arboreal, unlike the terrestrial *C. asper*. "Bibron's boa" for *C. bibronii* is a distinctive name and avoids the ambiguity of other suggested names for that species.

TAXONOMIC CATEGORIES

We are aware that our recognition of subspecies in the *Candoia carinata* complex may be regarded as controversial, particularly in view of the widespread rejection of them at the present time.

It is our philosophy that the subspecies category serves an important, designatory function in certain considerations (e.g., diversity contexts, intraspecific geographic variation and phylogeny, conservation problems, etc.) in those species in which subspecies are recognizable. They therefore should not be regarded as categorically unacceptable.

We have here recognized subspecies in species where there is a consistent difference at least at a 70% level over a significant and/or discrete geographic area. In general, such areas may be either parapatric, with a zone of freely interbreeding intergrades between them, or dichopatric, with no or discreet (restriction to intervening peaks or islets) interbreeding. In the *Candoia carinata* complex, every subspecies is dichopatric, although discrete intergrades on intervening islets occur between the ranges of *C. p. paulsoni* and *C. p. vindumi*. Dichopatry adds to the probability of validity because of the absence of opportunity for interbreeding that might break down the perceived differences.

It is likely that isolation, genetic drift and/or the founder effect are responsible for the evolution of all of the subspecies of the *Candoia carinata* complex, because there are few or no discernible differences in habitat where these animals commonly occur that might lead to adaptive differences. The three species as well may have originated in the same way, at a much earlier time. Ample opportunities for the effects of isolation existed over the some 40 million years that this complex occurred in the South Pacific (Austin, 2000: 348).

Obviously the subspecies we here recognize have evolved from ancestral populations, and therefore can be treated phylogenetically. They are not imaginary; they are real entities because of their consistent independence and anatomical differentiation. They give handles for analyses of stabilized intraspecific variation that failure of subspecific recognition would not permit, except by some other sort of label.

In the present complex, recognition of subspecies has been particularly helpful in detection of the strange, mutual split in the ranges of *Candoia paulsoni* and *C. carinata*.

MATERIALS, CHARACTERS AND THEIR VARIATION

Our present review of what we now regard as the *Candoia carinata* complex is based on external morphological data taken on 359 preserved specimens of various sources, including most museums in the United States, as well as one each in France, New Guinea and Australia (symbols from Leviton et al., 1985, insofar as possible). Data were also taken on 35 live specimens, and their behavior in captivity was observed.

Standard data taken on all specimens of the complex, insofar as possible, were as follows. Minimum anterior scale rows (24-37); maximum midbody scalerows (31-43); minimum posterior scale rows (20-30); ventrals (Dowling method) (165-202, only one less than the minimum in *Candoia bibronii*); subcaudals (36-58, anterior one almost always divided; Fig. 5); ventrals plus subcaudals (206-249); ventrals minus subcaudals (121-156); umbilicus position from ventral 132 to 153; anal spurs (always present in males, small ones present in females on both sides of one *C. c. carinata* [CAS 132236] and one *C. p. paulsoni* [USNM 119725], and on one side in one *C. s. superciliosa* [USNM 521651]); preanals (always at least one, rarely two, that are as narrow as the anal, and sharply narrower than the preceding ventrals; Fig. 5); supralabials (9-16 on each side); subocular supralabials (1-3, involving labials 5-9, except one with none on one side [USNM 561640], thus on that side agreeing with the condition in both other species of the genus); frequency of split (Fig. 5) in 2nd, 3d and 4th supralabials (rare in 2nd, except in *C. s. crombiei*, 8-82% of 3rd, 35-100% of 4th); infralabials (10-17); circumorbitals (7-14, excluding infralabials but including preocular and subpreocular; Fig. 5); enlarged supraoculars (0-6; Fig. 3), entering orbit (0-4); minimum interorbitals in one row (4-11); postrostrals (3-5, normally 3; Fig. 3); internasals between nasals posterior to postrostrals (2-5; Fig. 3); tiny scales between internasals and postrostrals (0-7, typically 2; Fig. 3); postnasals between postrostral and 2nd supralabial (2-5, usually three, exceptions most frequent in *C. carinata* and *C. superciliosa*); prefrontals posterior to internasals (2-7; Fig. 3); minimum interpreoculars in a row anterior to circumorbitals (5-11).

The total length varied 156-1365 mm, but 187 mm was the minimum for a wild-caught specimen (*Candoia p. mcdowelli*); the lower measurements of 156 and 158 mm were on captive-born neonates (*C. p. tasmai*) that were anomalous in various ways, including subminimal subcaudals and ventrals. It is not clear that size at birth differs significantly among the taxa of the complex, but it is quite obvious that maximum length differs greatly between the two subcomplexes. Males of all subspecies of *C. paulsoni* reach a recorded maximum of at least 592 mm, and as much as 840 mm, whereas in the other four taxa the maxima vary 505-576 mm. Maxima for females of *C. paulsoni* subspecies are 801-1365 mm, but only 627-722 mm in the other four taxa, except for *C. s. superciliosa* at 885 mm. The female maxima are no lower than 940 mm in *C. paulsoni* subspecies except in *C. p. mcdowelli* with 849 mm (n = 17) and *C. p. rosadoi* with 801 mm (n = 7).

The tail/total length ratio varied .10-.19, with mean ratios in the 10 taxa varying .13-.16.

Measurements were also taken of the width of head at anterior border of eye; length of snout from level of anterior border of eyes; eye to rictus oris; length of eye; width of eye; av. eye diameter; minimum distance, eye to lip; ratio, lip/av. eye diameter. The head measurements were taken to objectivize perceived differences in length and width of head.

Although notes were taken on dorsal and ventral pattern of body and tail, the variability was so great that we did not find any useful taxonomic correlation.

For place names in the Belau (Palau) archipelago, we follow Motteler (1986).

ANALYSES

The *Candoia carinata* Subcomplexes

The *Candoia carinata* complex, sensu lato, appears to consist of two different subcomplexes. The one to which the oldest name, *Boa carinata* Schneider (1801), applies (Böhme et al., 1998), here designated the *C. carinata* subcomplex, is a relatively small, exceptionally placid stock which rarely or never bites, is highly prehensile (a distinctive behavior involving a tenacious gripping of any support within reach, especially with the tail but also with the body), and preys almost exclusively on ectotherms (e.g. geckos, skinks, and frogs). In addition, a postanal white spot is invariably present (Fig. 2); the anterior scale rows are not known to reach 29 or more (0 in 129); usually the maximum number of midbody scale rows is 35 or fewer (85%); the posterior scale rows are seldom 25 or more (9%, 12 in 128); the ventrals minus subcaudals are seldom 136 or more (6%, 8 in 124); the tail/total length ratio is usually .15 or more (71%, 86 in 121); seldom do two or more enlarged supraoculars enter the orbit (5%, 6 of 125); and the lip/eye diameter ratio tends to be less than .61 (79%). The maximum S-V length in females is 722 mm except for *C. s. superciliosa* with 885 mm, and in males 576 mm; the mean T/TTL ratio is .14-.16.

We propose that the *carinata* subcomplex contains two species: *Candoia carinata* and *C. superciliosa* (Günther, 1863), each with two subspecies. On the basis of its central position geographically, splitting the range of *C. paulsoni* (Figs. 6, 7), it appears that the *C. carinata* subcomplex is less derived than the *C. paulsoni* subcomplex, as in effect was concluded by McDowell (1979: 49) and also by Austin (2000: 346) on molecular grounds.

Members of the second subcomplex, for which the only name available is *Enygrus carinata paulsoni* Stull (1956) and hence is here termed the *Candoia paulsoni* subcomplex, with but one species and six subspecies, attain at least twice the length or bulk of members of the other subcomplex, are easily excited (balling or fleeing when disturbed, quick to become defensive), bite freely, are weakly or not prehensile (do not tenaciously grip support at all times), and feed primarily on endotherms at least as adults. In addition, there is no postanal white spot; the anterior scale rows are usually 29 or more (88%, 208 of 237); usually the maximum scale rows are 36 or more (86%, 208 of 234); the posterior scale rows are usually 25 or more (74%, 174 of 236); the ventrals minus subcaudals are usually 136 or more (93%, 207 of 222); the tail/total length ratio is usually .14 or less (85%, 185 of 217); two or more enlarged supraoculars usually enter the orbit (77%, 178 of 231); and the lip/eye diameter ratio tends to be .61 or more (57%, 128 of 223). The maximum S-V length in females is 1365 mm, in males 840 mm; the recorded maximum in males of all six subspecies of *C. paulsoni* exceeds the maxima recorded in all males of the *C. carinata* subcomplex, and in only two subspecies of *C. paulsoni* (*C. p. mcdowelli*, *C. p. rosadoi*) are the recorded maxima for females less than the maxima for the *C. carinata* subcomplex. The T/TTL ratio is .13 in all subspecies except for *C. p. rosadoi* (McDowell's [1979] enigmatic Misima Island population), with .15.

The review of molecular phylogeny of *Candoia* (Austin, 2000) substantiates the recognition of three species, as here proposed, in the *C. carinata* complex, although it sheds no light on the subspecies. The phylogram depicted in that work first segregates what we would identify as *C. carinata* (sensu stricto), from West Sepik Province, Papua New Guinea, sister to two separate entities identifiable as (1) *C. superciliosa* from Belau and *C. p. paulsoni* from Choiseul Island, Solomon Islands, and (2) *C. p. mcdowelli* from Milne Bay Province, Papua New Guinea. That proposed phylogeny conforms with McDowell's (1979) and our own deductions on the basis of morphology, except that Austin's (2000) phylogram places *C. superciliosa* as sister to *C. paulsoni*. On the contrary, we place *C. superciliosa* and *C. carinata* in one subcomplex, *C. paulsoni* in the other. Austin's phylogram, however, belies the statement (p. 346) that the Belau population (*C. superciliosa*) "shows a relatively large degree of sequence divergence (12%) from the New Guinea and Solomon Islands populations [*C. paulsoni*] sampled." At least he regarded his "data as compatible with species-level divergence".

CANDOIA CARINATA SUBCOMPLEX

1. *Candoia superciliosa* (Günther)
Belau Bevelnosed Boa

Enygrus superciliosus Günther, 1863: 360. Two syntypes, BM(NH) 1946.1.16.47 (formerly 63.10.2.7) and 1946.1.16.50 (formerly 63.10.2.8). Type locality "Pelew Islands." Presented by G. L. King. Date unknown.

Enygrus carinatus var. *superciliosus*: Kinghorn, 1928: 142 (notes that 5 specimens from "Ysabel Island," Solomon Islands, "could be placed nearest the variety *superciliosus*").

Enygrus carinatus (*nec* Schneider): Boettger, 1898: 111 (part; "Palau," 1 specimen); Sternfeld, 1920: 423-430 (part; 5 from "Angaur"); Dryden and Taylor, 1969: 271 (one specimen from "Koror," one from "Angaur").

TABLE 1: Variation in non-cranial characters differentiating members of the *Candoia carinata* complex. Taxa are designated by acronyms of their scientific names. For scale row, ventral and subcaudal counts, and for tail/total length ratios, means are given in the second line, followed parenthetically by sample size. Ect. = Ectotherm, end. = Endotherm; the symbol ~ implies "mostly."

Taxon	Csc	Css	Cct	Ccc	Cpv	Cpt	Cpm	Cpr	Cps	Cpp
Min. Anterior-scale rows	25-28 26.3 (8)	24-28 26.5 (53)	26-28 27.3 (20)	24-28 26.3 (47)	32-37 34.5 (37)	27-31 29.5 (39)	27-32 29.4 (74)	28-33 29.8 (20)	29-32 31.6 (9)	27-35 31.3 (67)
Max. Midbody scale rows	31-36 33.3 (8)	32-36 33.5 (53)	34-38 35.7 (20)	32-36 33.9 (47)	40-43 41.5 (37)	32-40 36.6 (38)	32-39 36.3 (72)	34-38 36.3 (20)	37-41 38.6 (9)	34-42 38.0 (69)
Min. Posterior scale rows	20-23 21.7 (8)	21-25 23.1 (53)	23-25 23.9 (19)	20-25 23.4 (47)	27-30 28.6 (37)	23-28 25.7 (38)	23-27 24.7 (72)	22-26 24.5 (20)	25-27 26.6 (9)	22-28 25.4 (69)
Ventrals	183-192 188.0 (8)	165-178 173.4 (53)	178-187 182.6 (20)	165-182 174.2 (48)	180-188 183.9 (36)	177-188 183.3 (38)	167-187 178.6 (72)	184-195 189.7 (20)	191-198 194.2 (9)	184-202 191.1 (67)
Subcaudals	44-49 46.7 (6)	41-49 44.5 (57)	50-58 53.1 (20)	45-53 49.4 (47)	38-44 40.1 (35)	36-43 39.6 (35)	36-43 40.0 (69)	47-51 49.6 (19)	45-51 46.8 (9)	40-48 43.0 (63)
Ventrals + subcaudals	230-237 234.0 (6)	202-226 217.4 (51)	229-245 235.4 (19)	212-232 223.5 (47)	219-229 223.9 (34)	214-230 222.9 (36)	207-229 218.7 (69)	235-245 239.2 (19)	238-248 241.0 (9)	225-249 234.5 (62)
Ventrals - subcaudals	136-144 141.1 (6)	121-135 130.8 (51)	123-133 128.3 (19)	116-135 124.7 (47)	140-148 143.6 (34)	140-152 144.2 (38)	127-148 138.5 (70)	133-145 140.0 (19)	144-152 147.4 (9)	139-156 148.0 (61)
Umbilicus	144-151	137-140	143-150	132-139	138-147	142-144	136-152	145-146	–	143-153
Total length, Max.♀♂	722/505	885/546	595/564	715/576	1200/726	940/642	849/680	801/655	952/695	1365/840
Tail-length ratio	.13-.15 .14 (6)	.12-.16 .14 (50)	.14-.18 .161 (17)	.13-.17 .160 (47)	.10-.16 .128 (33)	.11-.14 .127 (35)	.10-.18 .128 (67)	.13-.16 .146 (19)	.12-.15 .132 (9)	.11-.18 13.5 (64)
Keels 2nd row dorsals	0%	0%	100%	100%	0%	0%	0%	0%	0%	0%
Postanal white spot	100%	100%	100%	100%	0%	0%	0%	0%	0%	0%
Behaviour	docile	docile	docile	docile	irritable	irritable	irritable	irritable	irritable	irritable
Prehensility	++++	++++	++++	++++	++	++	++	++	++	++
Diet	~ ect.	~ ect.	~ ect.	~ ect.	~ end.	~ end.	~ end.	~ end.	~ end.	~ end.

TABLE 2: Labial scale characteristics differentiating members of the *Candoia carinata* complex. Taxa are indicated by acronyms of their scientific names. Means are in second lines, sample sizes in parentheses.

Taxon	Csc	Css	Cct	Ccc	Cpv	Cpt	Cpm	Cpr	Cps	Cpp
Supralabials	10-12 11.1 (16)	10-14 12.0 (106)	11-14 12.3 (40)	10-15 12.5 (94)	12-16 13.8 (74)	9-14 11.3 (78)	10-15 11.9 (145)	9-12 10.5 (39)	11-12 11.4 (18)	10-15 12.2 (134)
No supralabial in orbit	0	1 (106)	0	0	0	0	0	0	0	0
Supralabials 5-6 in orbit	7 (16)	14 (106)	1 (40)	4 (94)	0	15 (78)	13 (143)	16 (39)	1 (18)	12 (133)
Supralabials 5-6-7 in orbit	0	2 (106)	1 (40)	0	0	1 (78)	2 (143)	0	0	0
Supralabials 6-7 in orbit	7 (16)	71 (106)	22 (40)	45 (94)	23 (74)	58 (78)	115 (143)	23 (39)	17 (18)	107 (133)
Supralabials 6-7-8 in orbit	0	9 (106)	11 (40)	19 (94)	0	3 (78)	10 (143)	0	0	4 (133)
Supralabial 6 in orbit	2 (16)	1 (106)	0	0	0	0	0	0	0	0
Supralabial 7 in orbit	0	1 (106)	0	0	0	0	0	0	0	0
Supralabials 7-8 in orbit	0	7 (106)	5 (40)	26 (94)	49 (74)	1 (78)	3 (143)	0	0	9 (133)
Supralabials 7-8-9 in orbit	0	0	0	0	2 (74)	0	0	0	0	0
Supralabials 8-9 in orbit	0	0	0	0	0	0	0	0	0	1 (133)
3rd supralabial split	14 (16)	66 (106)	22 (36)	33 (92)	68 (76)	4 (78)	36 (146)	6 (40)	8 (18)	84 (134)
4th supralabial split	15 (16)	101 (106)	31 (36)	87 (96)	76 (76)	32 (78)	138 (146)	39 (40)	14 (18)	127 (136)
Infralabials	11-13 11.8 (16)	10-15 12.8 (126)	11-15 13.2 (40)	11-15 13.0 (92)	13-17 14.9 (74)	11-15 13.1 (78)	11-16 12.9 (143)	11-14 11.9 (40)	12-14 12.6 (18)	11-16 13.5 (132)

TABLE 3: Non-labial cranial characteristics differentiating members of the *Candoia carinata* complex. Taxa are indicated by abbreviation of their scientific names. Means are in second lines, sample sizes in parentheses.

Taxon	Csc	Css	Cct	Ccc	Cpv	Cpt	Cpm	Cpr	Cps	Cpp
Circumorbitals	10-13 11.4 (16)	10-14 11.0 (107)	9-12 10.9 (40)	9-14 11.2 (94)	10-13 11.3 (74)	7-11 9.8 (78)	8-12 10.2 (136)	9-12 10.2 (39)	10-13 11.3 (18)	7-13 10.3 (135)
Minimum interorbitals in one row	4-6 5.3 (8)	4-8 5.9 (53)	7-11 8.8 (20)	5-11 7.5 (46)	6-9 7.8 (37)	5-7 5.8 (39)	5-9 6.5 (72)	7-10 8.4 (20)	6-9 7.8 (9)	5-9 6.7 (67)
Greatly enlarged supraocular each side, minimum ≤ 3 scales in row between	+	+	–	–	–	–	–	–	–	–
One enlarged supraocular reaching orbit	6 (16)	34 (106)	3 (34)	10 (96)	0	17 (78)	32 (144)	8 (40)	2 (18)	41 (134)
Two or more enlarged supraoculars reaching orbit	0 (16)	4 (106)	0 (34)	1 (96)	50 (62)	61 (78)	109 (144)	23 (40)	16 (18)	82 (134)
No enlarged supraoculars reaching orbit	10 (16)	68 (106)	31 (34)	85 (96)	12 (62)	0	3 (144)	9 (40)	0	11 (134)
Minimum interpreoculars	6-8 6.9 (8)	6-8 7.4 (53)	8-10 8.7 (20)	6-10 8.0 (46)	7-11 8.9 (36)	5-10 8.1 (39)	6-10 8.3 (69)	7-10 8.8 (18)	8-10 8.6 (9)	6-11 7.5 (67)
Prefrontals	2-5 3.6 (8)	2-5 2.5 (53)	2-5 3.3 (20)	2-7 4.0 (47)	2-5 3.1 (37)	2-6 2.6 (39)	2-5 3.1 (68)	2-3 2.7 (20)	2-4 2.3 (9)	2-5 2.9 (68)
Scales between postrostrals and internasals	1 1.0 (16)	0-2 1.4 (53)	1-4 2.7 (20)	0-6 1.7 (47)	1-3 2.1 (37)	1-2 1.6 (39)	1-5 2.1 (72)	1-3 1.2 (20)	1-2 1.8 (9)	0-3 1.8 (69)
Internasals	2 2.0 (8)	2-3 2.0 (53)	2-4 2.8 (20)	2-5 2.4 (46)	2-4 2.2 (37)	2-3 2.1 (39)	2-4 2.3 (72)	2-4 2.2 (20)	2 2.0 (69)	2-3 2.1 (68)
Postrostrals	3 3.0 (8)	3-5 3.0 (53)	3-5 3.9 (20)	3-5 3.2 (49)	3-5 3.2 (37)	3-4 3.1 (38)	3-4 3.0 (70)	3 3.0 (20)	3 3.0 (9)	3 3.0 (70)
Ratio, lip/av. Eye diameter	.52-.71 .58 (5)	.40-.86 .54 (53)	.41-.70 .50 (18)	.38-.79 .51 (43)	.50-.97 .69 (35)	.49-1.00 .67 (37)	.47-.93 .68 (64)	.47-.65 .56 (18)	.50-.72 .54 (7)	.44-1.0 .62 (65)

Candoia carinata (*nec* Schneider): McDowell, 1979: 27-51 (part; includes 5 specimens from "Koror").

Diagnosis and definition (based on 62 specimens examined and less than a dozen others in the literature). A member of the *Candoia carinata* complex, differing from other complexes of the genus in having a broad, flat, slanted, bevel-like, overhung snout, supralabials entering orbit, subcaudals 35 or more, and ventrals less than 203.

Unique among all members of the *Candoia carinata* complex in the combination of presence (Fig. 2) of a distinct postanal white spot (100%); absence of keels on the 2nd row of dorsals (100%); presence of a greatly enlarged supraocular on each side (Fig 3), with a minimum of 3 or fewer scales in a row between those on the two sides (100%); anterior scale rows fewer than 29 (100%); total length not exceeding 885 mm, seldom reaching 700 mm; temperament retiring, withdrawing, not aggressive under any circumstance; and diet consisting almost exclusively of ectotherms.

Comparisons. Species other than those of the *carinata* complex have a more or less rounded snout, not flat and overhung, and the supralabials are separated from the orbit; in addition, in *Candoia asper* the subcaudals are in the tens or twenties, on a very short tail, and in *C. bibronii* the ventrals are 203 or more.

Within the *Candoia carinata* complex, the distinct postanal white spot, docile temperament, ectotherm diet and small size are shared only with populations from the South Moluccas (topotypes of *C. carinata*, see Böhme et al., 1998), and their relatives in Sangihe, Irian Jaya and northern Papua New Guinea, almost invariably with keels on the 2nd scale row at least on neck. In all populations, the enlarged supraoculars are smaller, usually there is a minimum of 4 or more scales in a row between them, and usually 2 or more border the orbit. The anterior scale rows number 29 or more in 94% of the material from the Solomon Islands, 100% of Bougainville material, 82% from Papua New Guinea, and 79% from Halmahera. Total lengths of 900 mm or more, up to 1375 mm, are known from Halmahera, Bougainville and the Solomon Islands, the largest from the latter area.

Variation. See tables. Exceedingly polymorphic in colour and pattern in life, "with everything from lemon yellow to charcoal occurring, including bright brick red, and with striped, spotted or zigzag patterns, dull to brightly contrasted" (Crombie, pers. comm.). The striped individuals have a unique, irregular dorsolateral white line on each side (Fig. 5); no other species of the *carinata* complex exhibits that variation in the striped phase.

Range. Limited (Fig. 4) to the Belau Islands, where it appears to occur on "all islands within the fringing reefs, including Ngeaur, except possibly the low sand-cays with only haline shrubs for vegetation. Ngcheangel atoll to the north has been collected well enough in the past (1944-5) and also recently that it might be safe to conclude that the species does not occur there, although at least three of the four islets appear to be acceptable habitats" (Crombie, pers. comm.).

Etymology. The name *superciliosa* presumably refers to the much enlarged supraocular scales, characteristic of the species.

Remarks. The Belau Islands support a healthy population of the bevelnosed boas. Because that population is isolated by about 800 airline km from the nearest populations of the same complex on the Kepulauan Talaud Islands and Morotai Island (Fig. 1), and is the northernmost outlier of the *Candoia carinata* complex, it is not surprising that we find a correlated taxonomic differentiation, although the double endemism that we found would not have been anticipated.

Crombie (pers. comm.) reports that he has found *Candoia* "most often arboreally, but frequently terrestrially, active diurnally as well as nocturnally." Their intrinsic arboreality is reflected in their strong tendency to latch onto anything available, especially with the tail but also with the body; they are often difficult to release from the hand. It is a behavior shared with the related *C. carinata*, but not by any others of the genus.

According to Crombie (pers. com.), "Since the species is still quite abundant in backyard banana and taro patches in Koror town itself, and on almost completely deforested islands like Ngemelachel, it certainly is not a forest obligate, but adapts very well to disturbed habitats. If its abundance on Ngemelachel is typical, it may be more common in disturbed habitats than in forests, due perhaps to the greater abundance of prey.

"They feed most often on frogs and geckos, occasionally skinks. They are small compared with other "*C. carinata*" [i.e., *C. paulsoni*], and are exceptionally placid; I've never been able to induce a Belauan *Candoia* even to strike close-mouthed, much less to bite. On several occasions I have taken one to local show-and-tells for staff and clients, usually finding the snake on the way, but it is passed around with no apparent distress. While dancing and socializing, women have worn them as bracelets, and the snake stays seemingly comfortably coiled where placed. When I left on one occasion a young lady with reluctance parted with the snake which rested in her navel ring. Paradoxically, Belauans fear *Candoia* far more than the other, nervous and vicious snakes of the islands. It appears to be assumed that because it is so placid and cryptic, *Candoia* must be untrustworthy and likely to attack without warning. Belauan children nevertheless quickly learn to enjoy handling them, although their parents commonly assume that I have drugged the snake or performed some other magic to keep it under control."

Representatives of the *Candoia paulsoni* complex, on the contrary, bite freely, struggle to escape or ball up, commonly accept small endotherms as food, attain a larger size, and tend to be more terrestrial.

Content. Two subspecies: *Candoia s. superciliosa* and *C. s. crombiei.*

1a. *Candoia superciliosa crombiei* Smith and Chiszar, subsp. nov.

Ngeaur Bevelnosed Boa

Enygrus carinatus (*nec* Schneider): Sternfeld, 1920: 425-430 (part; from "Angaur;" first report from that island); Dryden and Taylor, 1969: 271 (part; one specimen from "Angaur").

Holotype. USNM 521718, juvenile male with everted hemipenes, from Ngeaur Island, at the intersection of the west coast road and the road to Our Lady of the Rosary church (just N cemetery turnoff), S Ngaramasch village. Taken 31 July 1996 by Ronald I. Crombie.

Paratypes. Seven: BPBM 1744-6, NE point, Ngeaur Island; CM 29084, Saipan (= Ngaramasch), a village on Ngeaur Island; CM 29085, center of Ngeaur Island; CM 29086, Ngeaur Island; FMNH 189962, Ngeaur Island (specimen reported by Dryden and Taylor, 1969).

Diagnosis and definition. A subspecies of *Candoia superciliosa* differing primarily from the nominotypical subspecies by having more than 180 ventrals (183-192, M = 188.0, n = 8), vs fewer than 180 (165-178, M = 173.4, n = 53). See Comparisons for other differences.

Description of holotype. In preservative April 1998, 462 mm TTL, TL 67 mm (in life, 467 mm and 71 mm, 23.4 gm). Scale rows 25-33-20, 2nd row nowhere keeled; ventrals 188; anal entire; a single preanal, as narrow as anal, narrower than preceding ventrals; umbilicus at ventrals 150-151; subcaudals 49, the first one divided, an additional terminal spine; 10-11 supralabials, 5-6 entering orbit on each side; 12-12 infralabials; 10-11 circumorbitals; 3 postrostrals; 2 internasals; one scale between postrostrals and internasals; a minimum of 7 scales in a row between preoculars anterior to the circumorbitals, 6 between orbits; 2-2 very large supraoculars, none extending to orbit; 3 scales contacting nasal between postrostral and 2nd supralabial; both 3rd and 4th supralabials split, compared with 2nd; 2nd supralabial split on one side (a very rare variant); 2 prefrontals.

Horizontal and vertical diameters of eye each 2.1 mm; minimum eye-lip distance 1.1 mm; eye-snout distance 6.3 mm; eye-rictus oris distance 6.0 mm.

Postanal spot involving 11 subcaudals; light grey-brown above, on sides and encroaching on venter; middle of venter mostly white; a broken zigzag streak on dorsum, the lateral, staggered angles of which are darker than most of the rest of the streak, and are mostly light-edged; parts between the dark angles are but faintly discernible; the angles are fused as single dorsal dark blotches on rear of body and on tail, where the largely white ventral surface is sharply delineated by an irregular dark line (Fig. 2).

Variation. See tables.

Comparisons. The 8 specimens examined from Ngeaur were compared with 55 of the nominotypical subspecies, listed in the following account. Comparisons were also made with some 250 other specimens of *Candoia carinata* auctorum.

The major difference between the two subspecies is in number of ventrals, *Candoia s. crombiei* having 183-192, vs 165-178 in *C. s. superciliosa*. There is likewise no overlap in either ventrals plus subcaudals (230-237 vs 202-226) or ventrals minus subcaudals (136-144 vs 121-135), or in position of the umbilicus (144-151 vs 137-140). *C. s. superciliosa* may possibly reach a larger size, 885 mm TTL having been recorded for it (FMNH 121599), and also it more frequently has the 3rd supralabial entire (not split), at 38% vs 13%. The supralabials are usually (63%) 10 or 11, the infralabials usually (94%) 12 or fewer in *C. s. crombiei*, 25% amd 41% respectively in *C. s. superciliosa*. The modal number of interpreoculars is 8 (25 of 53) in the latter, 7 (5 in 8) in the former. The prefrontals are usually 3-5 (75%, 6 of 8) in *C. s. crombiei*, only 17% (9 in 53) in *C. s. superciliosa*. All *C. s. crombiei* have a single scale between postrostrals and internasals, whereas 40% (22) of 55 *C. s. superciliosa* have two, and one has none. Three of the five examined for the character have the 2nd supralabial split on one or both sides, but in only one of 53 *C. s. superciliosa*.

Range. Limited to Ngeaur Island, Belau Archipelago (Fig. 4).

Etymology. The name *crombiei* honors the collector, Ronald I. Crombie, of the holotype and also of the bulk of the comparative material from elsewhere in Belau. As an authority on the history and biology of Belau, he has provided much background and natural history information for us.

Remarks. The holotype was, according to field notes provided by Crombie, found "inactive at 10:35 hrs under a large flake of exfoliating bark 1.9 m high on a Casuarina tree along the dirt coastal road about one km south of Ngaramasch (= Saipan). The tree is on the NE corner of a dead-end road leading to a house about 80 m inland, and a missionary school is at the intersection. On the other side of the road from the tree is strand vegetation, and the rocky coast is only 30 m distant. Although most of the interior of the island is forest or swamp, this particular piece of the coast road is the most developed part of the island other than downtown Ngaramasch, not forested at all."

Wm. Llewellen noted that one of the specimens he took on Ngeaur (CM 29085) was found in a tent on the center of the island, and another (CM 29086) "appeared to be sleeping, tail hooked on a loose piece of bark, the head pressed against the tree, making a perfect camouflage, resembling a vine."

As well defined as *Candoia s. crombiei* is, it is surprising that no other evidence of extant endemism on Ngeaur is known. We expect that, as its fauna becomes better known, other examples will be discovered. Skeletal remains of several specimens of an agamid, tentatively assigned to *Hypsilurus godeffroyi* Peters (1867) (based on two specimens labelled "Pelew Inseln"), suggest that this species may be endemic to Ngeaur (Crombie and Pregill, 1999). No live specimens have been observed on the island, but it has not been explored thoroughly.

Sternfeld (1920: 426) recorded data on three specimens from Ngeaur, all conformant with ours: 185, 188 and 192 ventrals, 46-47 subcaudals, and 32, 33 and 35 maximum scale rows. He even suggested (p. 429) that two taxa of *Candoia* may occur on the Belau Islands. He mentioned ventral counts of 178, 183 and 190 in his discussion of other Belau material, without clarifying more precisely their geographic origin.

Although Günther (1863) gave 180 ventrals for the syntypes of *Candoia s. superciliosa*, and Boulenger (1893) gave 178 and 183 for them, Dr. Colin McCarthy recounted them and reported (pers. comm.) 175 and 178; they thus fall within the established range of the subspecies and therefore could not have come from Ngeaur. Indeed, no records exist that Ngeaur was visited by any Europeans prior to 1863, when the species was described. "Traffic from the main part of Belau was minimal because it has always been and still is a hazardous trip, even though Beliliou is clearly visible from Ngeaur. The channel between is narrow and very scary in a small boat, with treacherous currents and unpredictable winds. Most of Ngeaur's coastline is precipitous and rocky, with huge surf. Except for the battle in WWII, Ngeaur has been little visited" (Crombie, pers. comm.).

The only previous comparative treatment of Belau *Candoia* is in McDowell (1979), who regarded it as "intermediate" between his "Long-tailed" and "Short-tailed" morphotypes. He concluded that these categories are not taxonomic, however, and we agree that length of tail (or number of subcaudals) is not by itself a valid taxonomic criterion in the *Candoia carinata* complex.

1b. *Candoia superciliosa superciliosa* (Günther), comb. nov.

Northern Belau Bevelnosed Boa

Diagnosis. A subspecies of *Candoia superciliosa* most conspicuously differing from *C. s. crombiei* by having fewer than 180 ventrals (165-178, M = 173.4, n = 53). See Comparisons of the latter account for further details.

Variation. See tables.

Comparisons. See account for *Candoia s. crombiei*.

Range. All of the Belau Islands that are inhabited by the species, except for Ngeaur. In addition to the islands listed below, Crombie and Pregill (1999) list the species (hence this subspecies) also from Ngercheu, Ngerduais, Ngerukeuid and Pkulaklim.

Specimens Examined. The 55 specimens examined of *Candoia s. superciliosa* are from the following localities (old spelling in parentheses). *Belau* (Palau): MCZ 177140-2, UMMZ 65619, 65779. *Babeldaub* (Babeldaob): N-C Sect., Ngiwal Mun., upper Ngeromeshong River, 7 32 50N, 134 35 37E (CAS 19046); 16 rd km N Ngerubar (UF 62041); Airai village, Airai state (USNM 301534); 1 rd km W Airai village, Airai state (USNM 521643-4); Nekkeng Forestry Camp, Aimeliik state (USNM 521640); S Ulimang village, Tim Taunton's property, Ngaraard state (USNM 521641-2); 1.5 air mi E Ngermetengel village, stream valley midway betw Ngermetengel and Ngeruach (rock outcrop), trail to Malat's cave, Ngeremlengui state (USNM 521645). *Beliliou* (Peleliu): Ngalkol village (BPBM 1743); Akalokul (BPBM 1742). *Ngemelachel* (Malakal): E slope Radio Tower Hill, SW of E side of Commercial Port, just above Paradise Club (USNM 521646-54). *Ngerechur* (N of N end of Babeldaob, northernmost locality for the species): SE end (USNM 521655); W side (USNM 521656). *Ngerekebesang*: The Carolines Resort, SW Meyungs village, just NE of turnoff to Echang village (USNM 521639). *Ngeruktabel* (Urukthabel): SE tip, N side, trail to German lighthouse, trail above 2nd bunker (USNM 521663). *Ngetmeduch* (a tiny islet in the Oreor-Babeldaob channel at the interinsular bridge, just offshore of Oreor): top of central rock outcrop (USNM 521657). *Oreor* (Koror): AMNH 70645-50, FMNH 121599, MVZ 41965); rd below Koror Hospital and Trust Territory Entomological Lab, 7 20 09N, 134 28 49E (CAS 19031); vic Ngetkedam, 7 20 00N, 134 28 50E (CAS 19032); vic Ngesekes, 7 20 14N, 134 28 57E (CAS 19033); Ngarbaged, 7 19 50N, 134 29 03E (CAS 19035-7); W streamlet Aebukuru, 7 20 39N, 134 29 30E (CAS 19042); nr Biolaboratory and Belau National Museum (USNM 284570, 301533); Mandy's (Sngal) Ridge, NE end of island (USNM 521658); Commandant's Ridge, NE end of island (USNM 521659); E edge Koror town, woods betw water tank and main road (USNM 521660); Tibedul area, 0.5 rd mi W Ngermid village (USNM 521661); Hotel Nikko Palau grounds, Ngerunguiki area SW Ngermid village (USNM 521662).

2. *Candoia carinata* (Schneider)

Schneider's Bevelnosed Boa

Boa carinata Schneider, 1801: 261-263. Lectotype ZMFK 35503, designated by McDowell (1979: 28), although then thought to be lost. Type locality "Amboina," supplied by Böhme et al., 1998 (not stated in original description). Collector and date unknown.

Candoia carinata: Gray, 1842: 43; Forcart, 1951: 197 (restoration of combination); McDowell, 1979: 27-51 (description, designation of lectotype); Böhme et al., 1998: 1-6, 1-2 (fixation of type locality, redescription of lectotype).

Enygrus carinatus (part): Duméril and Bibron, 1844: 479-483; Boulenger, 1893: 107-108.

Diagnosis and definition (based on 70 specimens examined and numerous others in the literature). A member of the *Candoia carinata* complex, differing from other complexes of the genus in having a broad, flat, slanted, bevel-like, overhung snout (Fig. 5), supralabials entering orbit, subcaudals 35 or more, and ventrals less than 203.

Differing from members of the *paulsoni* subcomplex in always having a characteristic white spot (Fig. 2) immediately postanal in position (vs no such spot); scales of 2nd row of dorsals keeled at least on neck (100%, 44 of 44, vs never); in 1% (1 of 67), 2 or more enlarged supraoculars entering orbit on either side (vs 78%, 184 of 237); seldom with one or more enlarged supraoculars reaching orbit on both sides (6%, 4 in 67, vs 93%, 222 in 240); 24-28 anterior scale rows (100%, n = 70, vs 12%, 29 in 241); 32-37 maximum scale rows, only 12 of 68 (18%) 36 or more (vs 32-43, 88% [210 of 238] 36 or more); 20-25 posterior scale rows, only 8 of 67 (12%) 25 or more (vs 22-30, 73% [176 of 240] 25 or more); ventrals minus subcaudals 116-145, only 2 of 67 (3%) 136 or more (vs 127-156, 93% [211 of 226] 136 or more); tail/total length ratio .13-.18, 6 of 70 (9%) .14 or less (vs .10-.18, 85% [189 of 221] .14 or less); and only 11% (7 of 64) with a lip/eye diameter ratio of .61 or more (vs 58%, 131 of 227).

Differing from *Candoia superciliosa* in having large dark blotches (Fig. 6) low on sides (vs absent); 4-8 scales between enlarged supraoculars (vs 2-3); scales of 2nd row of dorsals usually keeled at least on neck (98%, 40 in 41, vs never); subcaudals usually 48 or more (85%, 58 of 68, vs 7%, 4 of 57); tail/total length ratio .16 or more (72%, 48 of 67, vs 16%, 9 of 55); minimum intersupraocular count 7 or more (82%, 60 of 73, vs 29%, 18 of 62).

Variation. See tables.

Range (Fig. 6). Sangihe islands and the southern Moluccas (Ambon, Banda, Ceram, Goram, Haruku); Irian Jaya (including the islands of Misool, Batanta and Salawati); most of the Bismarck Archipelago; and Papua New Guinea with its northern offshore islands, but excluding its south-eastern peninsula and the Milne Bay province islands. According to McDowell (1979: 50) and Stimson (1969: 7), it occurs also on Tanimbar Island east of the Lesser Sunda chain.

Etymology. The name *carinata* (Latin, carinate or keeled) alludes to the prominent keels characteristic of the species. At the time the name was proposed, the species was the only booid snake known with keeled scales.

Remarks. As pointed out by McDowell (1979: 48), who was aware of the existence of two groups in *Candoia carinata* s.l. in spite of recognizing no taxonomic division in the complex, this species splits the range of the *paulsoni* subcomplex (the Halmahera/Sulawesi/Talaud region to the west, Papua New Guinea and the Solomons region to the east), with a hiatus of some 2000 km between those two parts. In addition, the western part of the range of the *paulsoni* subcomplex splits the range of this species. The history of the Sangihe Islands population of *C. c. carinata* is of much interest, sandwiched as that population is between populations of the *paulsoni* subcomplex on Talaud Island and Sulawesi.

Content. Two subspecies: *Candoia c. carinata* and *C. c. tepedeleni.*

2a. *Candoia carinata tepedeleni* Smith and Chiszar, subsp. nov.

Tepedelen's Bevelnosed Boa

Enygrus carinatus (part): Werner, 1899: 373 (first confirmable record of the subspecies; Bismarck Archipelago); Hediger, 1933: 15-18 (data on 21 specimens from the Bismarck Archipelago); Hediger, 1934: 475-6 (data on 5 specimens from New Britain).

Candoia carinata carinata (part): Stimson, 1969: 7 (Bismarck Archipelago).

Candoia carinata (part): McDowell, 1979: 27-51.

Holotype. MCZ 72155, an adult male from Rabaul, New Britain, Fred Parker collector; 1963.

Paratypes. Nineteen, including FMNH 13919, topotype; FMNH 21732, New Britain; MNHN 1889-134-6, New Britain; MNHN 1900-259-261, Blanche Bay, New Britain; CAS 136606-8, Keravat, New Britain; MCZ 49472, Liki Island, off Sarmi Island, Irian Jaya; MCZ 167138, Lorengau, Manus Island; BPBM 2942, Gaulim, New Britain; BPBM 12012, 12173, Bekum, New Ireland; AMS 3151-2, New Britain; AMS 129583, Amelei (= Melei), West New Britain province (06-06S, 150-37E; nr Fulleborn, S Donnellan coll.).

Diagnosis and definition. *Candoia c. tepedeleni* is a subspecies of *C. carinata*, with which it agrees (and differs from *C. superciliosa*) in having large dark blotches on sides (Fig. 6); 4-8 scales between enlarged supraoculars; scales in 2nd row of dorsals always (20) keeled at least on neck; subcaudals always (19) 48 or more; tail/total length ratio usually .16 or more (88%, 15 of 17); and minimum interorbital count always (20) 7 or more.

Candoia c. tepedeleni differs from the nominotypical subspecies in having 179 or more ventrals (90%, 18 of 20, vs 13%, 6 of 47); ventrals plus caudals 229 or more (100% of 20, vs 11%, 5 of 47); ventrals minus caudals 128 or more (68%, 13 of 19, vs 26%, 12 of 47); caudals 52 or more (79%, 15 of 19, vs 25%, 12 of 47); posterior scale rows 24 or 25 (68%, 13 of 19, vs 31%, 15 of 47); interorbitals 9 or more (65%, 13 of 20, vs 22%, 10 of 46); anterior scale rows 27 or 28 (90%, 18 of 20, vs 49%, 24 of 47); frequently 4 or 5 postrostrals instead of the standard 3 (50% vs 12%); internasals usually 3 or more (70% vs 31%); scales between internasals and postrostrals 1-4, 45% (9 of 20) over 2 (vs 0-6, 22% [11 of 49] over 2).

Description of holotype. A contorted young male, well patterned and undamaged, 473 mm TTL, 79 mm TL. Scale rows 27-35-24; scales in 2nd row of dorsals distinctly keeled on neck, weakly keeled near anus, smooth elsewhere. Ventrals 186; anal entire, preceded by a preanal as narrow as anal, narrower than adjacent ventral (as in Fig. 1); umbilicus not discernible; subcaudals 54, the first one divided but its halves in contact; a terminal caudal spine; 12-13 supralabials, 6th and 7th entering orbit on one side, 7th and 8th on the other; 14-15 infralabials; 12-12 circumorbitals, including a large preocular and a small subpreocular on each side; 5 postrostrals; 3 internasals; 3 scales between postrostrals and internasals; a minimum of 9 scales in a row between preoculars anterior to circumorbitals, 9 between orbits; 4 moderately enlarged supraoculars on each side, none extending to orbit; 3 scales contacting nasal between postrostral and 2nd supralabial; 3rd supralabial entire on each side, like 2nd, but 4th split; 2 prefrontals.

Horizontal and vertical diameters of eye 2.3 and 2.1 mm respectively; minimum eye-lip distance 1.1 mm; eye-snout distance 7.0 mm; eye-rictus oris distance 6.0 mm.

Postanal spot involving 8 subcaudals; ground colour, a light brown above and below; large dark blotches on sides of body, 5-8 scales long, extending onto ends of ventrals, separated by spaces 2-3 times as long as the blotches; a series of 18 small, paired paravertebral, angular, closely placed zigzag dark spots, the pairs separated by distances 4-6 times their length, forming fused median blotches on the tail.

Variation. See tables.

Comparisons. The 20 specimens examined of *Candoia c. tepedeleni*, supplemented with data on 23 reported by Hediger (1933, 1934), were compared with 49 specimens examined of the nominotypical subspecies, as well as with 63 of *C. superciliosa*, and 242 of the *paulsoni* subcomplex.

Presence of the distinctive postanal white spot invariably distinguishes *Candoia c. tepedeleni* from members of the *paulsoni* subcomplex, as does also the presence of keels on anterior scales of the 2nd row of dorsals. Less categorical differences are noted in the Diagnosis and definition for the species *C. carinata* as a whole, and in the diagnoses of the *carinata* and *paulsoni* subcomplexes.

There are no categorical differences between *Candoia c. tepedeleni* and *C. c carinata* (other than position of umbilicus, with too few data to be secure), but each of at least six characters distinguish at least 70% (one is as high as 100% vs 11%) of each subspecies. Several others are different to lesser although significant degrees (see Diagnosis and definition for *C. c. tepedeleni*).

Range. Limited to islands in the north-eastern part of the range of the species, from Liki Island off the northern coast of Irian Jaya eastward through the Admiralty Islands, New Britain, New Ireland and some adjacent islands (Fig. 6).

Etymology. The subspecific name newly proposed here honors our colleague Kamuran Tepedelen, to whom we are indebted for initiation of the study of the *Candoia carinata* complex, and for providing critical live material for observation in captivity. The University of Colorado Museum is also indebted to him for donation of many exotic herpetozoa. He sets a high standard for maintenance of animals destined for herpetoculture and research. His camaraderie has expedited numerous projects at this institution and elsewhere.

Remarks. This subspecies appears to coexist with *C. p. paulsoni* on Tabar Island, just east of the middle of New Ireland. Three specimens from there were reported by Hediger (1933) to have 41-46 caudals and no white postanal spot, whereas three others had 57-60 caudals, and two of the three had a postanal white spot. All of the 16 others he reported there from elsewhere in the Bismarck Archipelago (as well as 5 he reported in 1934 from New Britain) had 52-58 caudals and a postanal white spot.

McDowell (1979: 48-49) cited the Tabar Island data provided by Hediger as evidence of polymorphy, rather than allospecificity. On the contrary, we interpret them as evidence of sympatry of two species. That *Candoia p. paulsoni* exists in the vicinity is demonstrated by three specimens (AMNH 153108, 154246, 154251) from the nearby Feni Islands (Babase and Ambittle islands) and two (UPNG 2994, 3010) from Nissan Island of the Green Islands group. One of them is a huge male (840mm TTL, tail incomplete), and another is a large female (875 mm TTL). All lack a postanal white spot, have no keels on the 2nd row of dorsals, and have 2-3 enlarged supraoculars reaching orbit on both sides, etc. We infer that the questioned Tabar Island specimens belong to the same taxon as the Feni and Green Islands specimens. Whether hybridization occurs on Tabar Island or elsewhere remains to be determined, as is the identity of the populations on other islands just east and north-east of New Ireland, which apparently have not yet been sampled. Hediger's data (1933) make it plain that *C. c. tepedeleni* occurs on the islands west and north-west of New Ireland (East Islands, including New Hanover, the St. Matthias group, and the Admiralty Islands).

In view of the apparent sympatry of *Candoia c. tepedeleni* and *C. p. paulsoni* on Tabar Island, it is not particularly surprising that sympatry also appears to exist between *C. c. carinata* and *C. p. mcdowelli* in central and western Papua New Guinea. As indicated in Fig. 6, the former taxon is widely distributed in that area, where our present data indicate occurrence of *C. p. mcdowelli* in seven localities (Fig. 9). McDowell (1979: 48) was well aware of sympatry between two morphotypes (as he interpreted them) in the Lae region, but he lacked further evidence.

In addition, specimens of *C. p. mcdowelli* from "New Britain," without more precise locality (AMS 11180-3), suggest that sympatry with *C. c. tepedeleni* may occur also on that island, where precise localities for the latter taxon are available except at the western end of the island. The distribution map for *C. p. mcdowelli* (Fig. 9) indicates possible occurrence there with a question mark.

2b. *Candoia carinata carinata* (Schneider)
Western Schneider's Bevelnosed Boa

Boa variegata Thunberg, 1807: 1-4. Lectotype ZMUU 313, designated by Bauer and Wahlgren (2001: 162). Type locality "East Indies", but probably from the "South Moluccas" (*loc. cit.*).

Enygrus carinatus carinatus: Stull, 1956: 185.

Candoia carinata carinata: Stimson, 1969: 1969: 7 (part).

Diagnosis and definition. A subspecies of *Candoia carinata* having large dark blotches on sides; 4-8 scales between enlarged supraoculars;

scales in 2nd row of dorsals always keeled at least on neck; subcaudals always 48 or more; tail/total length ratio usually .16 or more (69%); and minimum intersupraocular count always 7 or more.

Differing from *Candoia c. tepedeleni* in having 178 or fewer ventrals (87% vs 10%); ventrals plus subcaudals 228 or fewer (89% vs 0%); ventrals minus subcaudals 127 or fewer (81% vs 32%); subcaudals 51 or fewer (75 % vs 21%); posterior scale rows 20-23 (69% vs 32%); interorbitals 8 or fewer (78% vs 35%); anterior scale rows 24-26 (51% vs 10%); seldom more than three postrostrals (88% vs 50%); internasals usually 2 (65% vs 30%); scales between internasals and postrostrals 0-6, 74% two or fewer (vs 55%).

Variation. See tables.

Comparisons. See account for *Candoia c. tepedeleni.*

Range. Eastern Indonesia, on the islands of Sangihe, Ambon, Seram and Tanimbar, and on the mainland of Irian Jaya, eastward throughout most if not all of mainland Papua New Guinea except eastward from about the level of the Owen Stanley Range; Karkar Island (Fig. 6).

Specimens Examined. The 49 specimens examined of *C. c. carinata* are from the following localities. INDONESIA: SANGIHE ISLANDS: Sangihe (AMNH 71512); AMBON ISLAND (AMNH 5068-70); SERAM ISLAND (AMNH 21129-33, UCM 7 uncat., 6 live specimens); IRIAN JAYA: Bernhard Camp, Idenburg River, 75 m (AMNH 62473); Fakfak (MNHN 1909-200); Hollandia (= Jayapura) (CAS 13676); Sorong (UCM 57421). PAPUA NEW GUINEA: EAST SEPIK PROVINCE: Wewak (AMS 95593; AMNH 74509, 75240); 9 mi S Wewak, Passam, Brandi High School (AMNH 107141). GULF PROVINCE: Kerema (AMS 14479); Port Romilly, delta sawmills (AMNH 59682). MADANG PROVINCE: Karkar Island (AMNH 107139; FMNH 191339); Wanuma, Adelbert Mts., 2200 ft (AMNH 120458). MOROBE PROVINCE: Lae (AMNH 66747, 95139); 19 rd mi NW Lae (AMNH 95138); SOUTHERN HIGHLANDS PROVINCE: Waro (AMS 122345-6, 122349); WESTERN PROVINCE: Derongo (CAS 121233); Lake Murray (CAS 135504, 133810); Sturt Island (AMNH 59876); Togo (CAS 132236); Wipim (AMNH 107240; CAS 135503); Yongtau No. 1 (CAS 121218).

Remarks. The existence of the long-neglected name *Boa variegata* Thunberg was first noted in herpetological works since its description by Bauer and Wahlgren (2001). They thoroughly analyzed the probable source of the two specimens originally described (one paralectotype now lost), and redescribed the lectotype, leaving no doubt of its conspecificity with *Boa carinata* Schneider.

CANDOIA PAULSONI SUBCOMPLEX

3. *Candoia paulsoni* (Stull)

Paulson's Bevelnosed Boa

Enygrus carinatus paulsoni Stull, 1956: 185-186. Holotype MCZ 14521. Type locality "Ugi Island, Solomon Islands."

Candoia carinata paulsoni: Stimson, 1969: 7.

Diagnosis and definition. A member of the *Candoia carinata* complex, differing from other complexes of the genus in having a broad, flat, slanted, bevel-like, overhung snout, supralabials entering orbit, subcaudals 35 or more, and ventrals less than 203.

Differing from members of the *Candoia carinata* subcomplex in always lacking a distinctive postanal white spot; scales in second row of dorsals never keeled; usually one or more enlarged supraoculars reaching orbit on both sides (92%); anterior scale rows usually (88%) 29 or more; maximum scale rows usually (89%) 36 or more; posterior scale rows usually (74%) 25 or more; ventrals minus caudals usually (93%) 136 or more; tail/total length ratio usually (85%) .14 or less; usually (77%) two or more enlarged supraoculars reaching orbit on one or both sides; lip/eye diameter ratio usually (57%) .61 or more.

Variation. See tables.

Range. Fragmented in three main divisions (Fig. 7), eastern, central and western. The eastern division includes the Solomon Islands, the extreme eastern Admiralty Islands, and the northern Santa Cruz Islands; the central division includes part of mainland Papua New Guinea, north of the Highlands but not south of the Owen

Stanley Range in or near the National Capitol District, but Umboi Island and most of the islands of the Milne Bay District; and the western division includes Halmahera, Morotai, Ternate and Talaud Islands as well as the tip of the north-eastern arm of Sulawesi.

Etymology. The species-group name, according to Stull (1956), honors "Mr. John Paulson, of Gothenburg, the Swedish herpetologist who has been particularly interested in snakes of the family Boidae for many years, and has collected them and studied their habits in many parts of the world."

Remarks. The curious fragmentation of the range of *Candoia paulsoni* is complemented by the equally fragmented range of the *C, carinata* subcomplex, resulting in very little overlap of the ranges of those two subcomplexes. Competitive exclusion of the two subcomplexes is perhaps likely. See Remarks in the account for the species *C. carinata*.

Content. Six subspecies: *Candoia p. vindumi, C. p. tasmai, C. p. mcdowelli, C. p. rosadoi, C. p. sadlieri, and C. p. paulsoni.*

3a. *Candoia paulsoni vindumi* Smith and Chiszar, subsp. nov.

Vindum's Bevelnosed Boa

Enygrus carinatus (part): Sternfeld, 1913: 385 (first report for Bougainville).

Candoia carinata (part): McDowell, 1979: 27-51 (comparisons in an analysis of variation in the species as a whole).

Holotype. AMNH 92064, from the Kunua coastal area, Bougainville Island, taken by Fred Parker May 15, 1962. Paratypes. Thirty-six, all from Bougainville Island except for one (MCZ 72166) from Buka Island, about 1 km N of Bougainville: AMNH 90109-10, 92063, 92065, CAS 94026, MCZ 72167-9, topotypes; AMNH 42036, 42038, 42044-5, no specific locality; AMNH 89435-9, Kieta; AMNH 101221, CAS 113543, 113563, 113575-6, 113580-1, 118991, Turiboiru; BPBM 2936, between Borioco and Mumari; CAS 113587, Melilup, 3000 ft; CAS 113586, Pamauita, 1200'; CM 91825-6, betw Empress Augusta Bay and Emperor Mts.; FMNH 44808, 44815, Empress Augusta Bay; USNM 120224, 120233, Cape Torokina.

Diagnosis and definition. A member of the *paulsoni* subcomplex, reaching a relatively large size (at least 1200 mm TTL), and lacking a postanal white spot or keels anywhere on second row of dorsals; ventrals minus caudals 140-148; tail/total length ratio usually .14 or less (88%, 29 of 33); 2 or more enlarged supraoculars usually reaching eye on both sides (83%, 30 of 36); and lip/eye ratio usually (78%, 28 of 36) .61 or more.

Differing from all others of the *paulsoni* subcomplex (as well as those of the *carinata* subcomplex) in usually having 34 or more anterior scale rows, 40 or more maximum scale rows, and 27 or more posterior scale rows; usually 13 or more supralabials, 14 or more infralabials; 3rd supralabial usually split on both sides; and usually supralabials 7-8, 7-8-9, or 8-9, entering orbit.

Description of holotype. A young, well preserved female with one short abdominal slit. Scale rows 34-43-28; keels present on all dorsal scales except in 1st and 2nd rows. Ventrals 187; anal entire, preceded by a preanal as narrow as anal, narrower than adjacent ventral; umbilicus on ventrals 145-7; subcaudals 39, the 1st divided but its halves in contact; an additional, terminal caudal spine. Supralabials 14-14, 7th and 8th entering orbit on both sides; 14-15 infralabials; 12-13 circumorbitals, including a large preocular on each side and one small subpreocular on one side, two on the other; 3 postrostrals; 2 internasals; 2 scales between postrostrals and internasals; a minimum of 11 scales in a row between preoculars anterior to circumorbitals, 9 between orbits; 3-3 enlarged supraoculars, 2-2 entering orbit; 3 scales contacting nasal between postrostral and 2nd supralabial; 3rd and 4th supralabials split on both sides, as compared with 2nd; 3 prefrontals.

TTL 627 mm, TL 75 mm; horizontal and vertical diameters of eye 3.2 and 2.5 mm resp.; minimum eye-lip distance 1.9 mm; eye-snout distance 10.8 mm; eye-rictus oris distance 9.0 mm.

Ground colour, a light grey-brown, lighter on venter; a vertebral darker streak about four scales wide, with lateral extensions onto four or more scale rows on each side, usually alternating so as to produce a somewhat zigzag pattern; under side of head mostly dark, of about same shade as top of head and the dark marks on body. Tail dark brown, almost black, sharply contrasted with body, its pattern an expansion of the dorsal pattern of body, but with equally dark blotches on lower surface separated from each other and from dorsal markings by irregular white areas.

Variation. See tables. Eleven females (of 26) exceeded the TTL of the largest male. Only 11 of the total of 37 examined were males.

No specimens examined exhibited the striped morph that is so common in members of the *carinata* subcomplex, and occurs also in *Candoia p. mcdowelli;* all had a zigzag pattern much like the holotype. However, four had a very bright pattern because of a light, almost white ground colour and nearly black markings. The tail is distinctly darker than the body in all except the four brightly marked specimens, in which the body markings are about as dark as those on the tail.

Comparisons. *Candoia p. vindumi* is readily distinguished from the rest of the *paulsoni* subcomplex by its high number of scale rows, as well as by a few other characters. In 92% of *C. p. vindumi* the anterior scale rows are 34 or more (vs 11% in *C. p. paulsoni*, 0% in the other subspecies of *C. paulsoni*); maximum scale rows 40 or more in 100% (vs 21% in *C. p. paulsoni*, 0-5% in the other subspecies); posterior scale rows 27 or more in 100% (vs 22% in *C. p. paulsoni*, 1-12% in the other subspecies).

In addition, the supralabials are 13 or more in 96% of *Candoia p. vindumi*, 30% of *C. p. paulsoni*, and 2-13% in others of the subcomplex. Concomitantly, only the 7th and/or higher numbers of supralabials enter the orbit in 69% of *C. p. vindumi*, only 0-8% in the others. The 3rd supralabial is split on both sides in 81% of *C. p. vindumi*, in 54% of *C. p. paulsoni* and 0-16% of the rest. The infralabials are 14 or more in 91% of *C. p. vindumi*, in 48% of *C. p. paulsoni*, and in 4-33% of the others.

Range. Limited to Bougainville and Buka islands so far as is known, although probably occurring also on small offshore islands (Fig. 8).

Relationships. As is obvious from the preceding Comparisons, *Candoia p. vindumi* exhibits greater character-state overlap with *C. p. paulsoni* than with any other member of the *paulsoni* subcomplex. It is therefore likely that *C. p. paulsoni* is its closest relative.

Two specimens from Shortland Island (CAS 113588, AMNH 42065), only 10 km S of Bougainville Island, we tentatively regard as intergrades between *C. p. vindumi* and *C. p. paulsoni*. Conformant with the latter are 32 anterior scale rows of one, and 39 maximum scale rows of the other, but conformant with *C. p. vindumi* are 34 anterior scale rows of one, 40 maximum scale rows of the other, and 27 or 28 posterior scale rows of each. Both have 188 ventrals, whereas only 2 (of 36) *C. p. vindumi* have that many (its maximum); numerous *C. p. paulsoni* have 188. No specimens from Ovau or Fauro islands, which are about as distant from Bougainville as Shortland Island, have been available, but the populations there may also represent intergrades.

The more distant Treasury and Choiseul islands, about 50 km from Bougainville, have typical *C. p. paulsoni*. Intergradation with any other member of the *paulsoni* subcomplex seems unlikely because of the great distances between them.

Etymology. The subspecific name here proposed honors Jens V. Vindum, collections manager for herpetology in the California Academy of Science, to whom we are indebted for his encouragement at a critical time, for his counsel, and for his cooperation in making available vital material for study.

Remarks. The only known occurrence of *Candoia p. paulsoni* outside of the Solomon Islands is on some extreme eastern islands (Tabar, Feni, Green) of the Bismarck Archipelago (Fig. 8), isolated from southern populations of the subspecies by *C. p. vindumi* on Bougainville and Buka islands. We hypothesize that *C. p. paulsoni* may occur, or have occurred, on the small islands of the Solomons east of Bougainville, thus providing insular continuity of the northern and southern parts of the range of the subspecies.

3b. *Candoia paulsoni tasmai* Smith and Tepedelen, subsp. nov.

Tasma's Bevelnosed Boa

Enygrus carinatus (part): Peters and Doria, 1878: 405 (first report of specimens referable to *C. p. tasmai*, from Ternate and Halmahera).

Candoia carinata carinata (part): Stimson, 1969: 7.

Candoia carinata (part): McDowell, 1979: 27-51.

Holotype. USNM 215917, from Kampung Loloba, Wasile District, Halmahera; Habei Singou, collector; 3 October 1978.

Paratypes. Thirteen, including USNM 215915, 215919, 215921-3, topotypes; CM 25534-6, Morotai Island; MCZ 45767, Karelkelong, Talaud Island; MNHN 1996-187, Batu Lubang, Halmahera; UCM 58967, 60040, between Sidangola and Tobelo, Halmahera; and USNM 237673, Ternate Island.

Diagnosis and definition. A member of the *paulsoni* subcomplex of *Candoia*, reaching a relatively large size (at least 940 mm TTL), and lacking a distinctive postanal white spot, or keels anywhere on 2nd row of dorsals; ventrals minus caudals 140-152; TL/TTL ratio .14 or less (100%); usually (92%, 36 of 39) 2 or more enlarged supraoculars reaching orbit on one or both sides; and lip/eye ratio usually (51%, 19 of 37) .61 or more.

Differing from other members of the *paulsoni* complex as follows. From *C. p. paulsoni* primarily in having fewer caudals (91% 41 or fewer, vs 27%) and fewer ventrals plus caudals (92% 227 or fewer, vs 10%). From *C. p. vindumi* in having fewer anterior scale rows (100% fewer than 32, vs 0%), fewer maximum scale rows (95% 39 or fewer, vs 0%), and fewer posterior scale rows (95% 26 or fewer, vs 0%). From *C. p. mcdowelli* by having more ventrals (79% 182 or more, vs 18%), and having the 4th supralabial entire on one or both sides (67% vs 7%). From *C. p. rosadoi* and *C. p. sadlieri* by having fewer subcaudals (100% fewer than 44, vs 100% more than 44), and fewer ventrals plus subcaudals (100% fewer than 231, vs 100% more than 234).

Description of holotype. A mature, well-preserved male with well developed spurs, venter with an 8 cm slit (sewed shut), mouth widespread. Scale rows 30-38-26; keels present on all dorsal scales except those in 1st and 2nd rows. Ventrals 184; anal entire, preceded by a preanal as narrow as anal, narrower than adjacent ventral; subcaudals 38, the 1st divided but its halves in contact; an additional, terminal caudal spine. Supralabials 11-12, 6th and 7th entering orbit on both sides; 12-14 infralabials; 10-10 circumorbitals, including a large preocular and a small subpreocular on each side; 3 postrostrals; 2 internasals; 2 scales between postrostrals and internasals; a minimum of 8 scales in a row between preoculars, anterior to circumorbitals, 6 between orbits; 2-2 enlarged supraoculars, 2-2 entering orbit; 3 scales contacting nasal between postrostral and 2nd supralabial; neither 3rd nor 4th supralabial split on either side as compared with the 2nd; 2 prefrontals.

TTL 496 mm, TL 66 mm; horizontal and vertical diameters of eye 3.0 and 2.1 mm, respectively; minimum eye-lip distance 1.4 mm.; eye-snout distance 8.5 mm; eye-rictus oris distance 7.9 mm.

Ground colour, a moderately dark brown above and on sides; a darker brown vertebral streak 2-4 scales wide from which triangular, dark brown, light-edged lateral extensions reach 3-5 scale rows beyond the vertebral streak; most of the triangular extensions alternate in position from side to side, producing a zigzag appearance, but on neck and rump they coincide in position, forming blotches; about 40 triangular extensions on each side on body, 5 on tail, where they are enlarged and irregularly encircle the tail. Venter uniformly densely pigmented on head and neck, but on most of body with alternating, poorly defined, darker and lighter areas of irregular size; markings on tail somewhat darker than those on body.

Variation (based on 23 live adults or captive-born neonates in addition to the 14 types). See tables. Thirteen females exceeded the maximum TTL of the largest male. Fifteen of the total of 38 sexable specimens were males.

No specimen of *Candoia p. tasmai* exhibited a striped morph, which so far has been reported only in *C. carinata* (both subspecies), *C. superciliosa* (but not yet in *C. s. crombiei*, of which only 8 specimens are known), and in *C. p.*

mcdowelli. All specimens examined from Halmahera were relatively dark; none were brightly marked like, for example, some *C. p. vindumi*. Thus the tail is not conspicuously darker than the body, unlike typical *C. p. paulsoni* and *C. p. vindumi*. However, the specimen from Talaud Island has a relatively light ground colour, and the tail markings are much brighter than those on body.

Three neonates (UCM 60041-3) born in captivity 25 February 1997 from a female captured June-August 1996, at the same locality as the UCM paratypes, exhibit striking anomalies, possibly due to unfavorable developmental conditions. One appears to be more or less normal, having a TTL of 225 mm, TL 27 mm, 182 ventrals, 38 subcaudals, and the umbilicus at ventrals 142-4. The others, on the contrary, have the umbilicus located at ventrals 133-4 and 124-6; the subcaudals are 25 and 27, ventrals 169 and 177 (although the latter is within the normal range of variation, it has 23 ventrals split or partially split, in addition to umbilicals); and their TTL and TL are abnormally short, at 156 and 158 mm and 12 and 13 mm, respectively.

Comparisons. See Diagnosis and definition.

Range. Halmahera, Morotai, Ternate and Talaud islands, and (fide McDowell, 1979, and others) the tip of the north-eastern arm of Sulawesi (Fig. 7).

Remarks. This is the most isolated population of *Candoia paulsoni*, at the western limit of the range of the species, where it is separated by about 800 km from the central population (Fig. 7). The eastern and central populations are separated by considerably less- at least about 350 km. The gaps between the three populational clusters coincide with major oceanic depths, hence are topographically and biogeographically consistent. However, the absence of categorical distinctions (i.e., the existence of some character-state overlap) among the numerous morphological differences between the six recognizable taxa of the subcomplex leads us to assign them all to subspecific rank, although eventual molecular studies may indicate species-level distinctions in some cases.

Much like all races of *Candoia paulsoni*, *C. p. tasmai* appears to be a locally differentiated population, no more closely related to one than to another except as dictated by distance. Of considerable interest is its allopatry with *C. c. carinata*, so far as known at present. Sympatry may occur where their ranges are most closely approximated. The interdigitation of their ranges on the east side of the Sulawesi Sea is puzzling, with *C. c. carinata* on Sangihe (AMNH 71512), sandwiched between records of *C. p. tasmai* on the adjacent arm of Sulawesi (McDowell, 1979) and on Talaud Island (MCZ 45767).

Behaviour. We have had the opportunity through KT to observe 23 live *Candoia p. tasmai* in captivity. They were uniformly nervous animals, given to sudden jerky movements or, on the contrary, to balling up defensively, head hidden from view. When not balled up, they were likely to bite suddenly. They fed without hesitation on neonate rats.

KT collected some of the live specimens himself, during a heavy rainstorm at night along a road where the snakes were very abundant. Most were lying stretched out straight, and were often mistaken for fallen twigs. They appeared to be moving rectilinearly, with sharp angles if not straight, rather than moving sinuously. Probably a dozen were observed in one evening.

Etymology. The genitive-case subspecific name here proposed honors Mr. Budiyanto Tasma of Jakarta, Indonesia, who has been of prime importance in providing many specimens with reliable locality data.

3c. *Candoia paulsoni mcdowelli* Smith and Chiszar, subsp. nov.

McDowell's Bevelnosed Boa

Boa carinata: Schlegel, 1872: 53 (part; *nec* Schneider; first record for Papua New Guinea, on islands, hence not likely true *C. carinata*; fide McDowell, 1979: 28).

Candoia carinata: Forcart, 1951: 197; McDowell, 1979: 27-51 (part).

Candoia carinata paulsoni: O'Shea, 1996: 68-69, 202 (part; first reference of New Guinea material to *paulsoni*).

Holotype. MCZ 111795, a spurless, well-preserved female with the entire ventral surface slit longitudinally and some viscera emergent, from Sogeri, Central Province, Papua New Guinea, taken by Fred Parker in 1969.

Paratypes. Seventy-four, all from Papua New Guinea: NATIONAL CAPITOL DISTRICT: McDonald's Corner, Port Moresby Subprovince (USNM 213395). MADANG PROVINCE: Bostrem Bay (AMNH 107140). MILNE BAY PROVINCE: Menapi, Cape Vogel, sea level (AMNH 73936, 73944, 73947-8, 73950, 73953, 73955, 73966, 73981); Samarai, sea level (AMNH 73938, 73984); Biniguni, 175-190 m (AMNH 73969); Biniguni, Gwariu River (AMNH 73977); Bolubolu, Goodenough Isl., sea level (AMNH 73965, MCZ 146064-5); Agamoia, 2.5-3 mi S Lake Ruaba, Fergusson Isl., 200 m (AMNH 76634, 76638); Rambuso, Sudest Isl. (AMNH 76649-50); Rossel Isl. (= Yela Isl; MCZ 153109-10); Jinja, Rossel Isl. (AMNH 76667-8); Waikaiuna, Normanby Isl. (AMNH 76714); Guasopa, Woodlark Isl. (AMS 124892); Guleguleu, Normanby Isl. (AMS 129719, 129723, 129726, 129740); Dataona, Normanby Isl. (AMS 129735); Wamula, Sugunaki River, Normanby Isl. (AMS 129745); Ilaila, Fergusson Isl. (AMS 137981, 137995); Imalele, Fergusson Isl. (AMS 137996); Rossel Isl. (MCZ 153109-10); Trobriand Isl. (MCZ 145928); Paneati Isl. (UPNG 4363); Ahoima (10.19.50S, 150.31.20E)(USNM 118040); Kuia Isl., Trobriand Isls. (USNM 192986-7). MOROBE PROVINCE: Water Rice, Upper Markham Valley, 450 m (AMNH 85662-3); Pependango, 3200 ft (AMNH 95516); Lae (AMNH 95518, 103635; BPBM 6517); 22 mi W Lae, Oomsis creek, 100 m. (AMNH 85665); Pindiu, 3000 ft (AMNH 95517); Finschhafen (AMNH 95519-20; CAS 13677; USNM 118822, 159895); Garaina, 2300 ft (AMNH 95589-90, 95592, 95595, 103634, 104078); Awelcom, Umboi Isl., 600 m (BPBM 5456); 8 km WNW Lablab, Umboi Isl., 300 m (BPBM 5466); Gusika, 15 mi NE Finschhafen (USNM 119502). NORTHERN PROVINCE: Jumbora Plantation, Popondetta (BPBM 3808); 11 mi S Popondetta (MCZ 140738); 10 mi N Popondetta on Killington rd (USNM 195596). WEST SEPIK PROVINCE: Aitape (AMS 8888); Telefomin forest, 6000 ft (BPBM 4188). WEST NEW BRITAIN PROVINCE ?: New Britain (AMS 11180-3).

Definition and diagnosis. A member of the *Candoia carinata* complex, differing from other complexes of the genus in having a broad, flat, slanted, bevel-like, overhung snout, supralabials entering orbit, subcaudals 35 or more, and ventrals less than 200.

A member of the *paulsoni* subcomplex, differing from the members of the *carinata* subcomplex by having the combination of absence of a distinctive postanal white spot; absence of keels on any scales of the 2nd row of dorsals; usual (97%) contact of one or more supraoculars with the orbit on both sides; anterior scale rows usually (96%) 28 or more; ventrals minus subcaudals usually (92%) 134 or more.

The other five subspecies of *Candoia paulsoni* differ from *C. p. mcdowelli* as follows. *C. p. vindumi* has (1) 32 or more anterior scale rows (100% vs 3%); (2) 40 or more maximum scale rows (100% vs 0%); (3) 27 or more posterior scale rows (100% vs 1%); (4) 182 or more ventrals (83% vs 18%); (5) 222 or more ventrals plus subcaudals (82% vs 21%); (6) 142 or more ventrals minus subcaudals (79% vs 21%); (7) 13 or more supralabials (96% vs 13%); (8) the 3rd supralabial split on both sides (81% vs 23%); (9) 14 or more infralabials (91% vs 24%); (10) 11 or more circumorbitals (76% vs 29%); and (11) supralabials usually 7-8 or higher entering orbit (68% vs 3%).

Candoia p. paulsoni differs in having (1) 185 or more ventrals (99% vs 6%); (2) 42 or more subcaudals (73% vs 24%); (3) 227 or more ventrals plus subcaudals (94% vs 3%); (4) ventrals minus subcaudals 144 or more (92% vs 14%); and (5) usually 7 or fewer interpreoculars (61% vs 14%).

Candoia p. tasmai differs in having (1) 182 or more ventrals (79% vs 18%); (2) 221 or more ventrals plus subcaudals (72% vs 24%); (3) ventrals minus subcaudals 142 or more (87% vs 21%); (4) 4th supralabial usually entire on both sides (67% vs 7%); and (5) prefrontals usually 2 (62% vs 19%).

Candoia p. rosadoi and *C. p. sadlieri* differ in having (1) 187 or more ventrals (96% vs 3%); (2) 45 or more subcaudals (100% vs 0%); (3) 234 or more ventrals plus subcaudals (100% vs 0%); and (4) eye-lip distance/eye diameter ratio usually .60 or less (70% vs 37%).

Description of holotype. Scale rows 31-37-26; no keels anywhere on scales of 2nd row of dorsals; ventrals 178; anal entire, preceded by an entire preanal of like size, narrower than preceding ventral; 41 subcaudals; a terminal caudal spine; supralabials 10-11, 5th and 6th entering orbit on both sides; infralabials 13-13; 10-10 circumorbitals, including a large preocular and small subpreocular; 3 postrostrals; 8 interpreoculars anterior to circumorbitals; 3 internasals; 3 prefrontals; 2 scales between internasals and postrostrals; a minimum of 5 scales in a row between orbits; 3 scales on each side contacting nasal between postrostral and 2nd supralabial; 3rd supralabial split on one side, not the other; 4th supralabial split on both sides; 2 enlarged supraoculars, 1 entering orbit on each side.

Total length 675 mm; tail 91 mm; eye-snout distance 10.3 mm; eye-rictus oris distance 8.8 mm; horizontal and vertical diameters of eye 2.9 and 2.5 mm respectively; minimum eye-lip distance 2.0 mm.

Ground colour, a moderately dark grey-brown on dorsum; venter heavily stippled, with numerous, irregular, lighter areas; a dark brown middorsal streak covering 2-3 median scale rows, with about 45 more or less triangular lateral extensions on each side onto 3-4 additional scale rows, producing a generally zigzag pattern; sides with vaguely darker vertical blotches, poorly defined and of irregular shape, more or less alternating with the lateral extensions of the medial stripe; the dorsal and lateral markings encircle the tail, producing 5 irregular, very dark rings separated by very irregular white areas ventrally, by grey-brown areas dorsally; a narrow, irregular light streak on sides of neck, scarcely reaching beyond angle of mouth anteriorly; no lip markings; head more or less uniform dark brown above, on sides and below.

Variation. See tables. TTLs of 600 mm or more occur in 31 of 71 specimens; only 6 of that number are males, a significant difference from frequency of females ($c^2 = 9.14$, df = 1, $p < 0.01$). Of the 73 sexable individuals, 47 are females.

Most specimens possessed variations on the typical zigzag middorsal, brown stripe. Three were noted as especially dark, almost melanistic, and three were very light coloured, with pattern difficult to distinguish. Six were predominantly straight-striped – a variant pattern occurring in no other subspecies of *Candoia paulsoni*. Since it occurs rather commonly in the partially sympatric *C. carinata*, some introgression appears possible.

Comparisons. See Definition and diagnosis.

Range. North of the Papua New Guinea Highlands, except south of the Owen Stanley Range in or near the National Capitol District; Umboi Island and most of the islands of the Milne Bay Province (Fig. 10).

Relationships. *Candoia p. mcdowelli* is separated by at least 350 km from its geographically nearest recognized conspecifics, *C. p. paulsoni* and *C. p. vindumi*, in the Solomon Islands, across the nearly 10,000 m deep New Britain trench and associated trenches. There are more differences from that eastern cluster than from the more distant (800 km) *C. p. tasmai*, to the west in the northern Malukus. *C. p. rosadoi* and *C. p. sadlieri* are allopatric with *C. p. mcdowelli*, occuring on two eastern Milne Bay Province islands, and are most similar to the latter subspecies, although still sharply distinguishable.

As pointed out by McDowell (1979: 48), this taxon is sympatric with *Candoia c. carinata* in the region of Lae, although McDowell did not distinguish the two as species; he regarded them as "long-tailed" and "short-tailed" morphotypes. As he was well aware, tail length does not differ categorically among the various populations of the *C. carinata* complex, but he did not observe or placed little emphasis on other character-states that do differ categorically. Actually, it appears likely that *C. c. carinata* and *C. p. mcdowelli* are sympatric in West Sepik, East Sepik and Madang provinces of Papua New Guinea, as indicated by the overlapping, although not identical, locality records in those provinces indicated by comparison of the accompanying maps (Figs. 7, 10).

Etymology. The subspecies here described honors Dr. Samuel B. McDowell for his epochal study of variation in the *Candoia carinata* complex, as well as for his other taxonomic and anatomical studies setting new high standards of scholarship.

3d. *Candoia paulsoni rosadoi* Smith and Chiszar, subsp. nov.

Rosado's Bevelnosed Boa

Candoia carinata (*nec* Schneider): McDowell, 1979: 27-51 (part only; Misima material); O'Shea, 1996: 68-69, 202 (part; Misima material).

Holotype. AMS 124945, nr Bwagaoia village (10.40S, 152.50E), Misima Island, Milne Bay Province, Papua New Guinea, taken by Gregory A. Mengden 8 August 1987. Paratypes (19, all from Misima Island). N slope Mt. Sisa, 350 m (AMNH 76686-8); Narian, mouth Cornwall Creek, 25 mi W Bwagaoia village, 0-50 m (AMNH 76699-76700); nr Bwagaoia village (AMS 124943-4, 124946-8, 124956-61, 124975); Umuna mine site (10.40S, 152.50E; AMS 124981-2).

Definition and diagnosis. A member of the *Candoia carinata* complex, having supraoculars contacting orbit, subcaudals 35 or more, ventrals fewer than 203, and a broad, flat, slanted, bevel-like, overhung rostral.

A member of the *Candoia paulsoni* subcomplex, differing from members of the *C. carinata* complex in lacking a distinctive postanal white spot, in the absence of keels on any scales of the 2nd row of dorsals, in the rare presence (4%) of as few as 28 anterior scale rows (vs 100%), in usually (85%) having 36 or more maximum scale rows (vs 15%), and in usually having 136 or more ventrals minus subcaudals (95% vs 0% except for *C. superciliosa crombiei* with 100%).

Differing from other subspecies of *Candoia paulsoni* as follows.

From *Candoia p. paulsoni* by having (1) 47 or more subcaudals (84% vs 6%); (2) 237 or more ventrals plus subcaudals (82% vs 28%); (3) 144 or fewer ventrals minus subcaudals (85% vs 18%); (4) 3rd supralabial split on neither side (85% vs 28%); (5) minimum scales in a row between orbits 8 or more (90% vs 30%); and (6) minimum interpreoculars in a row anterior to circumorbitals 9 or more (95% vs 39%).

From its nearest relative, *Candoia p. mcdowelli*, by having (1) 187 or more ventrals (95% vs 3%); (2) 45 or more subcaudals (100% vs 0%); and (3) ventrals plus subcaudals minimum 235 (vs maximum 229).

From its most distant relative, *Candoia p. tasmai*, by having (1) over 44 subcaudals (vs fewer than 44); and (2) ventrals plus subcaudals minimum 235 (vs maximum 230).

From its most dissimilar relative, *Candoia p. vindumi*, by having (1) 33 or fewer anterior scale rows (100% vs 8%); (2) maximum scale rows fewer than 40 (100% vs 0%); (3) posterior scale rows fewer than 27 (100% vs 0%); (4) subcaudals 45 or more (100% vs 0%); (5) ventrals plus subcaudals minimum 235 (vs maximum 229); (6) supralabials 12 or fewer (100% vs 4%); (7) 3rd supralabials entire on one or both sides (90% vs 29%); (8) infralabials 13 or fewer (95% vs 10%); and (9) 6th supralabial (along with 5th or 7th) entering orbit (100% vs 14%).

From *C. p. sadlieri* by having fewer than 192 ventrals (75% vs 11%); fewer than 144 ventrals minus subcaudals (95% vs 0%); fewer than 32 anterior scale rows (95% vs 22%); fewer than 38 maximum scale rows (95% vs 22%); fewer than 26 posterior scale rows (95% vs 11%); scales between internasals and postrostrals seldom two (10% vs 78%); prefrontals seldom two (25% vs 78%); TL/TTL ratio usually .14 or more (79% vs 22%).

Description of holotype. A mature, coiled male with spurs, posterior half of venter slit longitudinally, hemipenes partially everted. Scale rows 30-37-26; ventrals 187; anal entire; a preanal, as narrow as anal; 50 subcaudals excluding conical tip but including a basal pair, its two halves separated. Supralabials 12-12, 6th and 7th entering orbit; infralabials 12-12; circumorbitals 11-12, including a preocular and subpreocular; 3 postrostrals; two internasals; one scale between internasals and postrostrals; 3 prefrontals; a minimum of 10 scales in a row between preoculars,

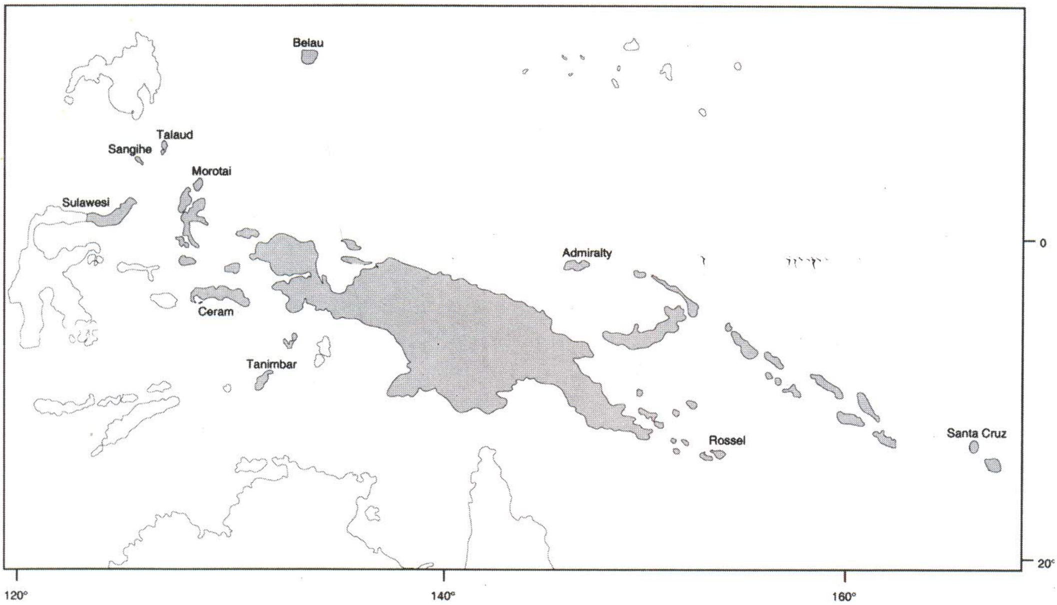

FIGURE 1: Distribution of the *Candoia carinata* complex (shaded), with peripheral limits of distribution identified. Adapted from Crombie and Pregill (1999: 63).

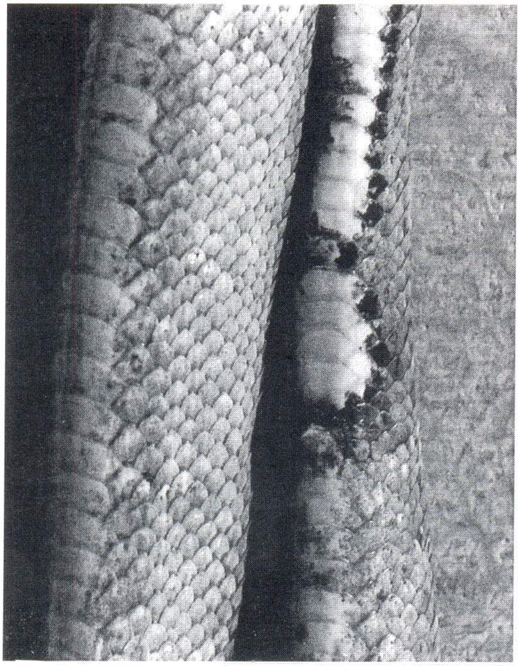

FIGURE 2: Lateral view of base of tail (showing the postanal white spot characteristic of members of the *Candoia carinata* subcomplex), and a section of the body of *C. s. superciliosa*, USNM 521661, Oreor Island, Belau.

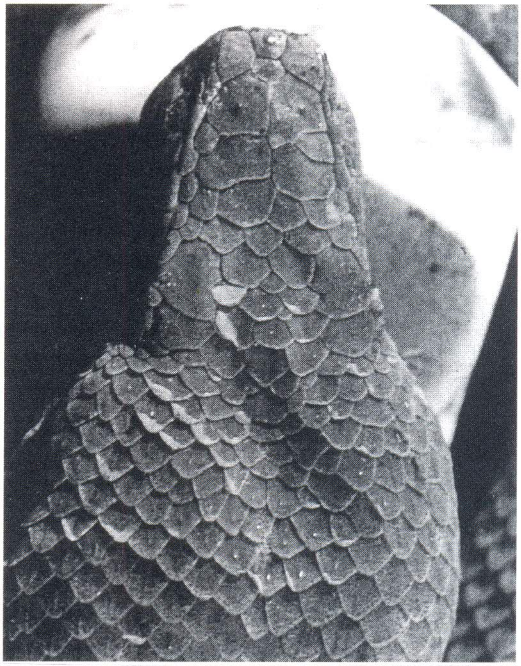

FIGURE 3: Dorsal view of head scales of *Candoia s. superciliosa* (USNM 521661, Oreor Island, Belau); note the enlarged supraoculars, large paired internasals, paired prefrontals, three postrostrals, single scale between internasals and postrostrals, etc.

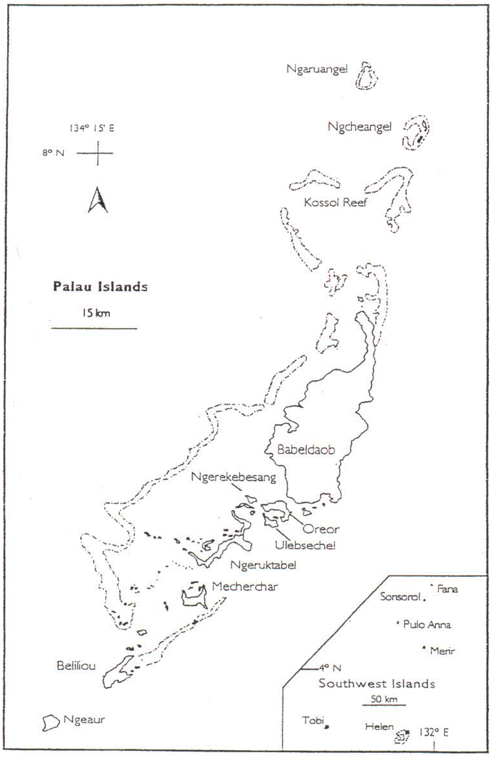

FIGURE 4: The main islands of Belau, from Crombie and Pregill (1999: 32). *Candoia superciliosa* occurs only on islands from Babeldaob southward; *C. s. crombiei* is limited to Ngeaur, the nominotypical subspecies to islands north of Ngeaur.

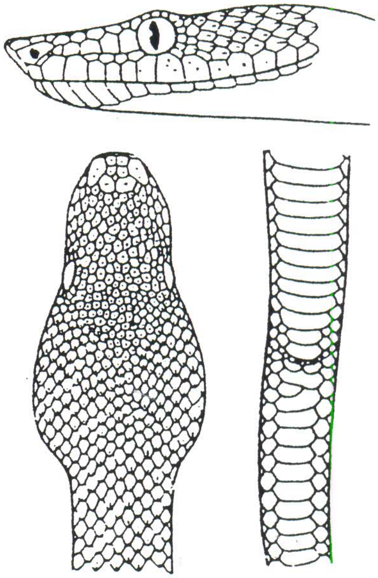

FIGURE 5: *Candoia c. carinata*, from Jan and Sordelli (1861: livr 2, pl. 2). Note the large preocular, small subpreocular, small supraoculars, undivided 3rd supralabial, divided 4th supralabial, 7th and 8th supralabials entering orbit, preanal, the small, divided first subcaudal, etc.

excluding circumorbitals; a minimum of 9 scales in a row between orbits; 3-3 scales contacting nasal between postrostral and 2nd supralabial; 3rd supralabial not divided on either side; 6-6 enlarged supraoculars, 3-3 reaching orbit; 4th supralabial divided.

TTL 583 mm, TL 87 mm; eye-snout, 10.1 mm; eye-rictus oris, 8.5 mm; horizontal and vertical diameters of eye, respectively, 3.8 and 2.6 mm; minimum eye-lip distance 1.5 mm.

Ground colour, grey-brown above and on sides, with a zigzag middorsal pattern evident mostly as dark brown, some light-edged, triangles more or less alternating on either side of, and their bases against, a poorly defined vertebral area only slightly darker than ground colour; the darker vertebral area is expanded between the dark triangles on some parts of the body, often resembling the triangles, but lighter and less sharply defined; about 34 dark triangles on each side of body. Numerous small dark blotches on sides of body, not light-edged, and not as dark as the paravertebral triangles. Midventer throughout length of body whitish, bordered by numerous dark brown, diffuse spots on ends of 1-3 ventrals, in contact with each other or separated by 1-2 ventrals; an irregular, narrow whitish streak (1-3 scales wide) extending posteriorly from rictus oris diagonally posteroventrally onto the lowermost dorsal scale rows and continuing to tail as a very irregular, broken light streak. Ventral surface of tail mostly very dark, nearly black, with a series of small, mostly whitish patches, but no distinctive postanal white patch; dorsal surface of tail patterned and coloured like body, but much darker toward tip. Lips and ventral surface of head mostly black, with a few small white marks on lips; dorsal surface of head uniform dark brown.

Variation. See tables. Only 2 of 7 females exceed the TTL of the largest male.

All specimens exhibit the basic zigzag dorsal pattern; none have a striped variant. No example

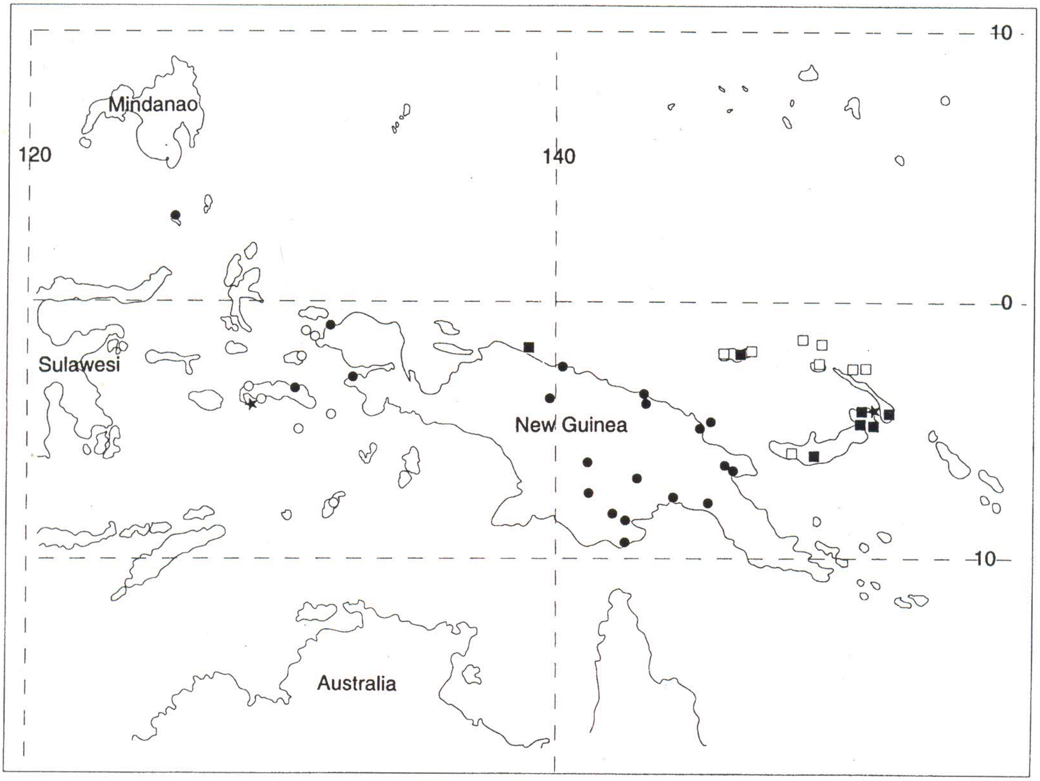

FIGURE 6: Localities of record for *Candoia carinata*. Specimens examined, solid symbols; literature records only, hollow symbols. Circular symbols, *C. c. carinata*; square symbols, *C. c. tepedeleni*. Oceanic symbols denote small islands.

has a distinctive white postanal spot. The lips are barred in most specimens.

Comparisons. See Definition and diagnosis.

Range. Known only from Misima Island (Fig. 7).

Relationships. Although *Candoia paulsoni mcdowelli* occurs throughout much of mainland Papua New Guinea, except toward the south-west (Fig. 7), and in almost all of the islands of the Milne Bay province, the populations of Misima and Woodlark islands are markedly different. McDowell (1979: 48) first reported some of those differences, but inasmuch as they appeared to link their populations with the widely separated "Long-tails" of the South Molukus, Irian Jaya, Bismarck Archipelago, etc., the picture made no geographic sense and taxonomic partition was rejected in favor of the assumption of polymorphy.

On the contrary, we conclude, on the basis of external morphology as well as behavior, that although most of McDowell's "Long-tails" represent the various members of the *C. carinata* subcomplex, the two long-tailed Misima and Woodlark populations belong to the *C. paulsoni* subcomplex, which otherwise consists mostly of McDowell's "Short-tails". Those two populations we regard as subspecifically distinct from each other and from other subspecies of *C. paulsoni*.

McDowell (1979: 49) hypothesized that the long-tailed populations of the *Candoia carinata* complex are more primitive than the short-tailed ones, have been extensively replaced by the latter, and remain largely as peripheral relicts. That hypothesis remains tenable in the present taxonomic interpretation, and in that context *C. p. mcdowelli* would appear to be the taxon most closely related to *C. p. rosadoi*, although as a de-

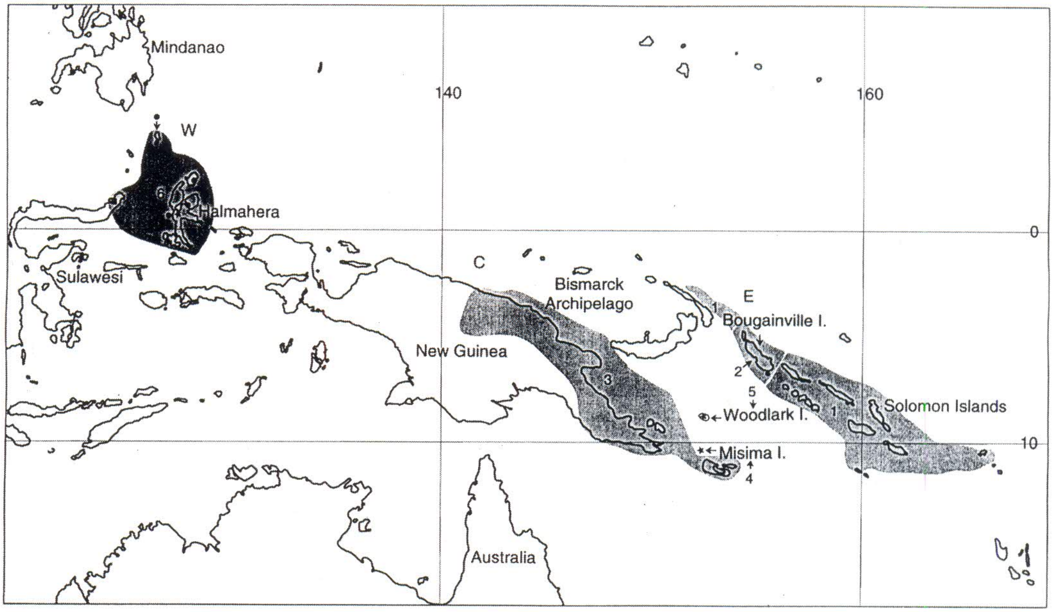

FIGURE 7: Distribution of *Candoia paulsoni,* showing its three main divisions: eastern (E), central (C), and western (W). The ranges of its six subspecies are designated as follows: 1 (in two parts), *C. p. paulsoni*; 2, *C. p. vindumi*; 3, *C. p. mcdowelli*; 4, *C. p. rosadoi* (type locality indicated by an asterisk); 5, *C. p. sadlieri* (type locality indicated by an asterisk); 6, *C. p. tasmai.* In the latter area, an asterisk indicates the type locality, and solid dots other localities from which specimens were examined.

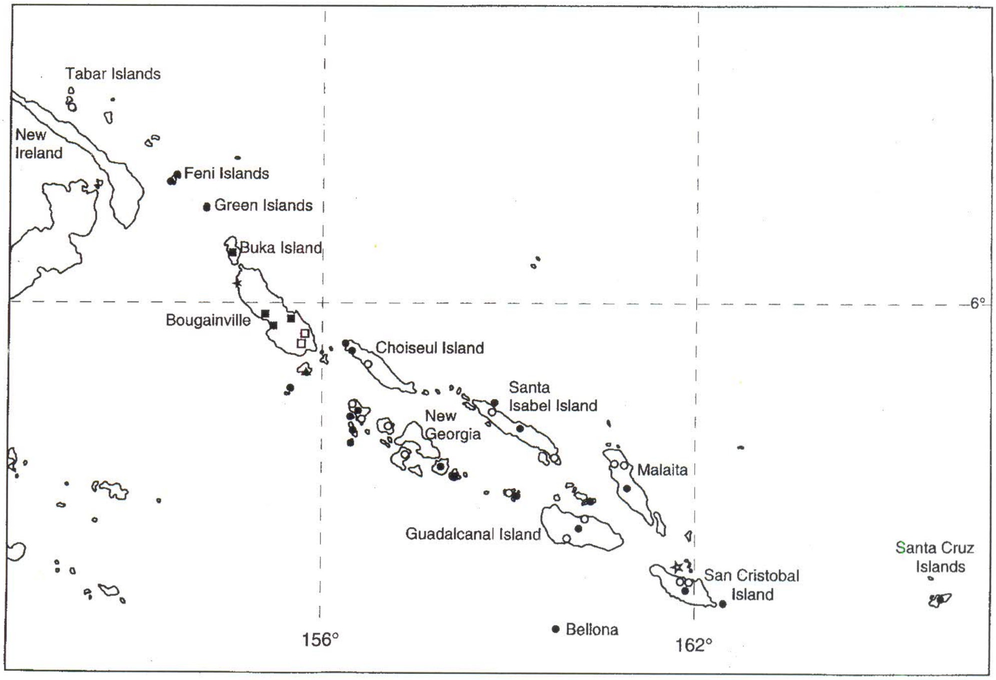

FIGURE 8: Distribution of *Candoia p. paulsoni* (dots) and *C. p. vindumi* (squares). Hollow symbols, literature records; solid symbols, specimens examined. Stars, type localities. Oceanic symbols indicate occurrence on small islands. A symbol in the center of an island indicates no specific locality. The triangle indicates an intergrade population between the two subspecies on Shortland Island. Note the literature record for *C. p. paulsoni* on Tabar Island, the northernmost known for the subspecies.

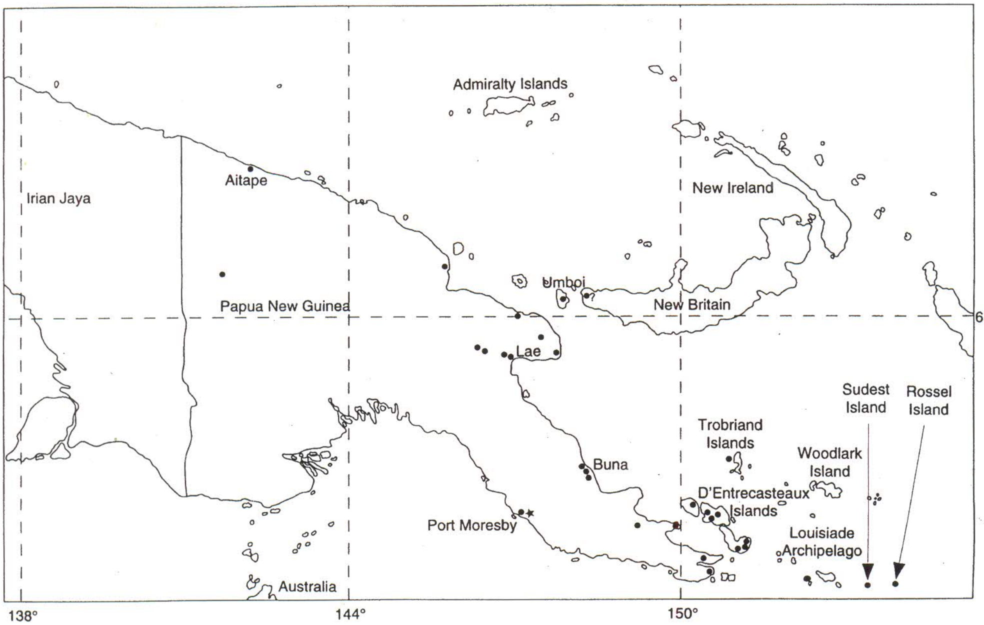

FIGURE 9: Distribution of *Candoia p. mcdowelli*. The solid dots and asterisk (type locality) indicate localities represented by specimens examined.

rivative instead of an ancestor. Both the latter subspecies and *C. p. sadlieri* appear to be relictual vestiges of a formerly more widespread taxon, presumably with a remote connection with the ancestor of the *C. carinata* subcomplex.

Etymology. The subspecific name is a patronymic noun in the genitive case honoring the venerable herpetological collections manager of Harvard University's Museum of Comparative Zoology, José P. Rosado. It recognizes our indebtedness to him for his patient, prompt and good willed provision of critical material for the present study, as he has done repeatedly over many years in the past, for ourselves and for many others.

3e. *Candoia paulsoni sadlieri* Smith and Chiszar, subsp. nov.

Sadlier's Bevelnosed Boa

Candoia carinata (nec Schneider): McDowell, 1979: 34, 48 (Woodlark Island material).

Candoia carinata paulsoni (nec Stull): O'Shea, 1996: 202 (Woodlark Island material).

Holotype. AMS 124877, from Guasopa, Woodlark Island, Milne Bay Province, Papua New Guinea, taken by Gregory A. Mengden 10 August 1987. Paratypes. Eight, all from Woodlark Island: AMS 124868, 124878, 124883-4, 124897, 125270, topotypes; AMNH 76613, 76631, Kulumadau, 0-100 m.

Definition and diagnosis. A member of the *Candoia carinata* complex and the *C. paulsoni* subcomplex, on the same grounds as *C. p. rosadoi*.

Differing from the other subpecies of *Candoia paulsoni* as follows. From *C. p. paulsoni* by having (1) 46 or more subcaudals (78% vs 17%); (2) 238 or more ventrals plus subcaudals (100% vs 28%); and (3) minimum scales in a row between orbits 8 or more (78% vs 30%).

From *Candoia p. mcdowelli* by having (1) 191 or more ventrals (vs a maximum of 187); (2) 45 or more subcaudals (100% vs 0%); and (3) ventrals plus subcaudals minimum 238 (vs maximum of 229).

From *Candoia p. tasmai* by having (1) over 44 subcaudals (vs fewer than 44); and (2) ventrals plus subcaudals minimum 238 (vs maximum of 230).

From *Candoia p. vindumi* by having (1) 33 or fewer anterior scale rows (100% vs 8%); (2) maximum scale rows fewer than 40 (100% vs 0%); (3) posterior scale rows fewer than 28 (100% vs 19%); (4) subcaudals 45 or more (100% vs 0%); (5) ventrals plus subcaudals minimum 238 (vs maximum 229); (6) supralabials 12 or fewer (100% vs 4%); (7) infralabials 13 or fewer (83% vs 10%); and (8) 6th infralabial (along with 5th [1] or 7th [17]) entering orbit (100% vs 14%).

From *Candoia p. rosadoi* by having (1) 192 or more ventrals (89% vs 25%); (2) 144 or more ventrals minus subcaudals (100% vs 5%); (3) anterior scale rows 32 or more (78% vs 5%); (4) maximum scale rows 38 or more (78% vs 5%); (5) posterior scale rows 26 or more (89% vs 5%); (6) scales between internasals and postrostrals two (78% vs 10%); (7) two prefrontals (78% vs 25%); and (8) TL/TTL ratio .13 or less (78% vs 21%).

Description of holotype. A mature female in a flat, circular coil on its side, without spurs, and with two ventral slits - one at midbody, the other posteriorly. Scale rows 32-41-27; ventrals 192; anal entire; a preanal, as narrow as anal; 47 subcaudals excluding a conical tip but including a basal, paired scale. Supralabials 11-11, 6th and 7th entering orbit; infralabials 12-13; circumorbitals 12-12, including a horizontally divided preocular and a subpreocular; 3 postrostrals; 2 internasals; 2 scales between latter and postrostrals; 2 prefrontals; a minimum of 8 scales in a row between preoculars, excluding circumorbitals; a minimum of 9 scales in a row between orbits; 3-3 scales contacting nasal between postrostral and 2nd supralabial; 3rd and 4th supralabials both split on both sides; 5-5 enlarged supraoculars, 3-3 reaching orbit.

TTL 752 mm, TL 96 mm; eye-snout, 11.1 mm; eye-rictus oris, 9.0 mm; horizontal and vertical diameters of orbit 3.7 mm; minimum eye-lip distance 2.6 mm.

A vertebral medium brown streak 3-4 scales wide on body, with more or less alternating triangular dark brown marks on each side, their tips extending laterally over 1-4 scale rows from the edge of the median streak, giving the impression of a zigzag dorsal stripe; ground colour, light brown over 5-6 scale rows lateral to median streak; 0-2 scale rows lateral to the paramedian triangles a series of about 37 short (mostly 3-6 scales), narrow (mostly two scale rows), medially black-edged dark brown spots alternating with the triangles on each side of the body; ventrad of that series, the sides are medium brown with small, diffuse, irregular, slightly darker areas; venter lighter, with small, irregular, dark spots on sides spaced generally 2-4 scales apart. The expanded, zigzag markings on the tail are darker than those on body, and are bandlike; small light areas are present on the ventral surface of the tail, but no distinctive postanal white patch. The head is relatively heavily pigmented dorsally and ventrally; the anterior infralabial region is weakly barred; a dark brown, light-edged streak passes through the orbit, except the upper part, through the temporal region and onto the sides of the neck, where it is transformed into the serial dark spots on the lower dorsal scale rows and ends of ventrals; the postocular streak is prominently light-edged below, across the posterior supralabials.

Variation. See tables. All five females are larger than the largest of four males.

Pattern and colour are much as in the holotype, although most are darker. The light streak through the rear supralabial is constant, and the supralabials are not barred. No specimens exhibit either a distinct white postanal spot or a tendency of the pattern to be striped.

Comparisons. See Definition and diagnosis.

Range. Known only from Woodlark Island (Fig. 7).

Relationships. *Candoia p. sadlieri* is distinguished from *C. p. paulsoni* by fewer characters (3) than is *C. p. rosadoi* (6), suggesting a closer relationship of the former two than of the latter two. The differences are about the same in comparison of both *C. p. rosadoi* and *C. p. sadlieri* with the othersubspecies of *C. paulsoni*.

Of special interest is a specimen (AMS 124892) from the type locality of *Candoia p. sadlieri*, taken by the same collector as, but a few days later (13 August 1987) than, the holotype, that conforms in all respects with the differential criteria for *C. p. mcdowelli*, to which we refer it, and in no respect with those for *C. p. sadlieri*. Although a paratype of *C. p. sadlieri* has the same date and locality, we regard it much more likely that the locality for AMS 124892 is in error than that both taxa occur sympatrically or that such variation occurs in *C. p. sadlieri*. The collector travelled widely the same summer in Milne Bay Province, where *C. p. mcdowelli* occurs to the exclusion of all other taxa of the *C. carinata* complex except on Misima and Woodlark islands. The ease with which specimens may be kept alive for later preservation could readily lead to erroneous designation of island source, especially when but a single taxon is thought to be involved. Character states of significance are 181 ventrals, 42 subcaudals, 139 ventrals minus subcaudals, 223 ventrals plus subcaudals, 30-36-25 scale rows, and a TL/TTL ratio of .15, all out of the known range of variation in *C. p. sadlieri*.

Etymology. The subspecific name is a noun in the genitive case honoring the herpetological collections manager of the Australian Museum in Sydney, Australia, Ross A. Sadlier, in recognition of his patient compliance with our appeal for the loan of critical material and for vital counsel.

3f. *Candoia paulsoni paulsoni* (Stull), comb. nov.

Solomon Bevelnosed Boa

Definition and diagnosis. A member of the *C. carinata* complex, differing from other complexes of the genus in having a broad, flat, slanted, bevel-like, overhung snout, supralabials entering orbit, subcaudals 35 or more, and ventrals less than 200.

A member of the *paulsoni* subcomplex, differing from the members of the *carinata* subcomplex by having the combination of absence of a distinctive postanal white spot; absence of keels on any scales of the 2nd row of dorsals; usual (97%) contact of one or more supraoculars with the orbit on both sides; anterior scale rows usually (96%) 28 or more; ventrals minus subcaudals usually (92%) 134 or more; and large size (reaching 1365 mm TTL vs 885 mm).

Distinguished from *Candoia p. mcdowelli* in having (1) 185 or more ventrals (99% vs 6%); (2) 42 or more subcaudals (73% vs 24%); (3) 227 or more ventrals plus subcaudals (94% vs 3%); (4) ventrals minus subcaudals 144 or more (92% vs 14%); and (5) usually 7 or fewer interpreoculars (61% vs 14%).

From *Candoia p. tasmai* in having more subcaudals (73% 42 or more, vs 9%), and more ventrals plus subcaudals (90% 228 or more, vs 8%).

From *Candoia p. vindumi* in seldom having supralabials 7-8 or 7-8-9 entering the orbit (8% vs 69%); usually having 33 or fewer anterior scale rows (90% vs 8%); 39 or fewer maximum scale rows (80% vs 0%); 26 or fewer posterior scale rows (77% vs 0%); 12 or fewer supralabials (70% vs 4%); 13 or fewer infralabials (52% vs 9%); and 3rd supralabial less often split on both sides 54% vs 81%).

From *Candoia p. rosadoi* by having 46 or fewer subcaudals (94% vs 16%), ventrals plus subcaudals 236 or fewer (72% vs 18%), ventrals minus subcaudals 145 or more (82% vs 15%), 3rd supralabial split on one or both sides (72% vs 15%), minimum scales in a row between orbits 7 or fewer (70% vs 10%), and minimum interpreoculars in a row anterior to circumorbitals 8 or fewer (61% vs 5%).

From *Candoia p. sadlieri* by having 45 or fewer subcaudals (83% vs 22%); 237 or fewer ventrals plus subcaudals (72% vs 0%); and minimum scales in a row between orbits seven or fewer (70% vs 22%).

Variation. See tables. Six of the 40 females exceed the maximum TTL of the 29 males. .

The pattern usually includes a typical zigzag dorsal brown stripe on a lighter brown backgroud. Three specimens were unicolour, and in four the zigzag pattern was broken into a series of blotches. No specimen exhibited the striped variant so frequent in the *Candoia carinata* subcomplex; it appears to be shared in the *C. paulsoni* subcomplex only by *C. p. mcdowelli*. A characteristic feature of the pattern of *C. p. paulsoni* is the rather distinctly darker markings on the tail than on the body.

Comparisons. See Diagnosis and definition.

Range. The Solomon Islands and outliers in the Santa Cruz Islands to the south-east, and the Green, Feni and Tabar Islands to the north-west (Figs. 7-8).

Remarks. Although we examined only 69 museum specimens of *Candoia p. paulsoni*, its wide range in the rather frequently visited Solomon Islands makes it the most widely familiar taxon of the *C. carinata* complex, and the most widely represented taxon of *Candoia* in museums, zoos and pet shops. Live specimens in the "pet" trade appear most frequently to represent that subspecies, and we maintained a few for a time in captivity. It is a serendipitous coincidence that the nominotypical subspecies is the one most familiar.

Specimens examined. Sixty-nine museum specimens, as follows. PAPUA NEW GUINEA: Ambittle I., New Ireland Prov., Nisnis Plantation, 2 km S, 2 km E Waramung Plantation (MCZ 154246); Babase I., New Ireland Prov., airstrip (MCZ 153108, 154251); Nissan I., Bougainville Prov. (UPNG 2994, 3010). SOLOMON I. (UCM 60158-9, UF 105769, 105772-83): Bagga I. (= Mbava) (AMNH 42068); Bellona I. (CAS 72205); Choiseul I.: Nukiki (BPBM 12779), Sumbisumbi (BPBM 12822-3); Fatura I. (may = Fapuhli): Papatura (?) (AMNH 42067); Guadalcanal I. (AMNH 66213-4, 66224, 66227-8; UF 88473A, B, 105770-1); Magnusaiai I., Shortland Group: Nuhu (CAS 113588); Malaita I. (AMNH 42061-2, 42341); Mbanika I., Russell Group (USNM 121396); Mono I. (AMNH 42069); Narovo (= Simba) I. (AMNH 42247-8); Nggatokae I. (BPBM 36403-4); Ranongga I. (AMNH 42240, 42242, 42244-5), Pienuna (BPBM 12854-5); San Cristobal I. (AMNH 40411, 40414, 42096, 42204); Santa Ana I. (AMNH 42214, paratype of *C. p. paulsoni*); Santa Cruz I. (= Nendo) (AMNH 40431); Santa Isabel I. (AMNH 42046); Shortland I. (AMNH 42065); Treasury I. (USNM 119725-6, 119730); Tulagi I. (UMMZ 99978); Vangunu I.: Tingge (BPBM 12948-9, 12965); Vella Lavella I. (AMNH 42055-6): Supato (BPBM 12856).

KEY TO THE *CANDOIA CARINATA* COMPLEX

The following key is based on the most salient differential character states of the ten taxa here recognized in the *Candoia carinata* complex. In most cases several other distinctive character states exist. If preliminary attempts at identification are inconsistent with the geographic ranges here delineated, the diagnoses, which give full summaries of distinctive features, should be consulted.

1A. A distinctive postanal white spot present 2
B. No distinctive postanal white spot – Paulson's bevelnosed boa – *paulsoni* 5

2A. Keels present on 2nd row of dorsals at least on neck or preanal region – Schneider's bevelnosed boa – *carinata* 3
B. No keels on 2nd row of dorsala anywhere on body – Belau bevelnosed boa – *superciliosa* 4
3A. Ventrals 178 or fewer (87%) – Schneider's bevelnosed boa .... *c. carinata*
B. Ventrals 179 or more (88%) – Tepedelen's bevelnosed boa .... *c. tepedeleni*
4A. Ventrals fewer than 180 (100%) – Belau bevelnosed boa .... *s. superciliosa*
B. Ventrals more than 180 (100%) – Crombie's bevelnosed boa .... *s. crombiei*
5A. Anterior scale rows 34 or more (92%) – Vindum's bevelnosed boa .... *p. vindumi*
B. Anterior scale rows 33 or fewer (100% in all except *p. paulsoni*, with 89%) 6
6A. Ventrals 181 or fewer (82%) – McDowell's bevelnosed boa .... *p. mcdowelli*
B. Ventrals 182 or more (100% in *p. paulsoni*, *p. sadlieri*, and *p. rosadoi*, 79% in *p. tasmai*) 7
7A. Subcaudals 41 or fewer (91%) – Tasma's bevelnosed boa .... *p. tasmai*
B. Subcaudals 42 or more (100% in *p. rosadoi* and *p. sadlieri*, 73% in *p. paulsoni*) 8
8A. Ventrals plus subcaudals 236 or fewer (72%) – Paulson's bevelnosed boa .... *p. paulsoni*

B. Ventrals plus subcaudals 237 or more (89% in *p. rosadoi*, 100% in *p. sadlieri* 9

9A. Ventrals minus subcaudals 144 or more (100%) – Sadlier's bevelnosed boa .... *p. sadlieri*

B. Ventrals minus subcaudals 143 or fewer (95%) – Rosado's bevelnosed boa .... *p. rosadoi*

ZOOGEOGRAPHIC AND PHYLOGENETIC IMPLICATIONS

The relatively precise distributional picture that has emerged with this study of the *Candoia carinata* complex provides fascinating raw material for zoogeographic correlation, as for example with the numerous reviews in Keast and Miller (1996). Origin of *Candoia* from the Oriental Region is generally agreed (e.g., Allison, 1996), and *Boa* (formerly *Sanzinia) manditra* of Madagascar is apparently its closest relative (Austin, 2000). The most peripheral and highly arboreal member of the genus, *C. bibroni*, is regarded by Austin (2000) as basal, and *C. asper*, the most terrestrial, as the most derived. Following the same line of thought in the *C. carinata* complex, the less arboreal species, *C. paulsoni*, would likely be the more derived, and indeed Austin's (2000: 346) data suggested "that the colonization of the Solomon Islands was from ...populations from southern New Guinea ... rather than from northern populations via the Bismarck archipelago." That suggests the long-tailed Misima and Woodlark island populations (*C. p. rosadoi* and *C. p. sadlieri*, especially the latter) as ancestrally related to *C. p. paulsoni*, much as we have concluded on morphological grounds. In turn we hypothesize that *C. carinata* is ancestrally related to the Misima and Woodlark taxa.

Thus the *Candoia carinata* complex, limited as it is to the heart of diversification in the South Pacific and appearing there over 40 million years ago (Austin, 2000: 348), was little or not affected by the rapid stowaway dispersals that took place in the eastern Pacific (e.g., Austin, 1999). Humans did not reach New Guinea until some 40,000 ybp, or the Admiralty, Bismarck and Solomon islands until some 20,000 ybp (Cann and Lum, 1996). Stowaway dispersal cannot be ruled out since then in several cases of peripheral occurrences, such as in Talaud and Sulawesi for *C. paulsoni tasmai*, in Sangihe for *C. c. carinata*, and in Tabar for *C. p. paulsoni*. A combination of stowaway or waif dispersal and the founder effect are possibly responsible for *C. s. crombiei*, but all other taxa of the *C. carinata* complex appear to be products of ancient vicariance.

The strange distribution of *Candoia carinata* from the Malukus (Moluccas) and Irian Jaya along the northern border and eastern half of New Guinea and into the Admiralty and Bismarck archipelagoes finds some parallelism in the distribution of water striders (Polhemus, 1996), cicadas (Boer and Duffels, 1996), frogs and lizards (Allison, 1996: 429), which in turn reflect to some degree the vicissitudes of island arcs associated with movements of the Pacific and Australian plates (see Boer and Duffels, 1996: 310-312, for a summary).

We hypothesize that comparable movements at different times were responsible for the extraordinary interdigitation of the geographic ranges of *Candoia carinata* and *C. paulsoni* (Figs. 6-7). We reject the alternative that the distributions observed of the three enclaves of *C. paulsoni* are a product of independent origin from different populations of *C. carinata*. The concordance of morphology and behavior among all subspecies of *C. paulsoni* precludes their independent origin. Neither historical zoogeography nor molecular techniques are sufficiently refined to provide definitive answers to that question at present, but may do so in the future.

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KINEMATIC MODULATION OF THE STRIKE OF THE WESTERN DIAMONDBACK RATTLESNAKE (*CROTALUS ATROX*)

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ABSTRACT.– **High-speed digital videography, and frame-by-frame quantification, was used to explore the kinematics of the strike in *Crotalus atrox*. One group of freshly caught adult *C. atrox* was used for predatory trials in which each snake struck at four small (14-16 gm) and large (24-26 gm) live unrestrained mice. A second group of freshly caught *C. atrox* was used for defensive trials in which each snake struck at a large stuffed doll, pre-killed adult (mean mass = 27.1 gm) mice, and a mouse-sized stuffed doll. Analyses of the predatory strike revealed little difference between the strikes launched at the two size classes of mice, and low levels of correlation among the kinematic variables. No significant differences were found between defensive strikes directed at a mouse or a mouse-sized stuffed doll. Defensive strikes directed at either small target were significantly different from those directed at the large stuffed doll. Collectively, there was a rather high level of correlation found among the kinematic variables of the defensive strikes. Significant differences were found between predatory and defensive strikes directed at similar-size mouse targets. Collectively the results suggests that *C. atrox* can modulate its strike depending on target size and behavioural context, but that predatory strikes are more stereotypic than defensive strikes.**

KEY WORDS.– **Feeding, reptiles, prey capture, serpentes, teeth, defense, behaviour.**

INTRODUCTION

The feeding system of snakes has long been recognized as a highly specialized form/function complex, yet large gaps remain in our understanding of the functional morphology, ecological plasticity, and phylogeny of this system. In part these gaps have arisen from a historical emphasis on intraoral transport, and the technical challenges of studying the strike (Cundall and Greene, 2000). Quantitative descriptions of the snake strike based on high-speed motion analysis exist for only a few species. Though these studies have documented considerable variation in prey capture kinematics (e.g., Coleman et al., 1993; Alfaro, 1999; Kley and Brainard, 1999), there is undoubtedly additional structural and kinematic diversity to ophidian feeding.

The behavioural repertoire of prey capture in venomous snakes has been widely studied, particularly in pit-vipers (see Greene, 1997, Cundall and Greene, 2000). These studies generally focus on either the stimuli which trigger the strike (e.g., Hayes and Duvall, 1991; Kardong, 1992; Alving and Kardong, 1996; Haverly and Kardong, 1996), the relocation of released envenomated prey (e.g., Chiszar et al., 1977, 1992), or the kinematics of the strike. The speed of the viper strike has proven prohibitive to detailed analyses without special equipment for high resolution, high-speed recording. Several previous studies have included only a few kinematic variables or have experimental designs which complicate interpretation of their data. The most detailed studies of prey capture kinematics in vipers were conducted by Kardong (1986a) and Kardong and Bels (1998) who provided a detailed quantitative description of the predatory strike of *Crotalus viridis oreganus*.

The kinematics of the rattlesnake strike can potentially be influenced by, among other things, the size of the target, the behavioural context of the strike, the method of presentation, and intraspecific differences (particularly in regard to snake size). The general kinematic differences in rattlesnake strikes directed at small and large targets have been known for some time (Mitchell, 1861), yet many studies (e.g., Kardong, 1986a; LaDuc, 2000) have failed to control for target size. Controlling the behavioural context of the strike is particularly important when attempting to compare the kinematics of predatory and defensive strikes (e.g., Kardong, 1986a; LaDuc, 2000). While behavioural context can be readily gauged in rattlesnakes due to the presence of distinctive suites of defensive (e.g., Klauber, 1956; Minton, 1969; Gove, 1979; Kardong, 1986a; Kinney et al., 1998) and predatory (e.g., Klauber, 1956; Minton, 1969; Chiszar et al., 1977; Kardong, 1986a,b; Hayes and Duvall, 1991; Kardong, 1993). Behaviors like these are influenced by target presentation. For example, a freely moving rodent will evoke predatory strikes from rattlesnakes but rarely defensive strikes; similarly, artificially presented rodents can evoke defensive strikes but add an element of artifice to any predatory trial.

The current study was undertaken to provide a detailed, quantitative description of the kinematics of the strike in the western diamondback rattlesnake, *Crotalus atrox*. In the present study we attempt to control intraspecific variation by using snakes from a restricted size range and with similar histories in captivity. Strikes will be recorded during both predatory and defensive encounters, with suites of behavioural characteristics- including head orientation, body posture, defensive sound production, and tongue flicking- used to document the behavioural context of the strike. Within each behavioural context, the snakes will be presented with two different size classes of targets. One target, adult mice, will be common to both the defensive and predatory strikes, enabling a comparison of the influence of behavioural context on the kinematics of the strike. Controlling these aspects required a compromise on presentation technique, but our results suggest that this compromise did not influence our results.

MATERIALS AND METHODS

Animals.- The kinematics of the strike were investigated using adult western diamondback rattlesnakes (*Crotalus atrox*) which were wild caught in Texas. To minimize any impact of long-term captivity, defensive strikes were examined using five specimens (snout-vent lengths = 74-104 cm) and five other specimens (snout-vent lengths = 78-112 cm) were used for the predatory strikes. The snakes were maintained at Lafayette College in a specially designed venomous snake room; data recording began between 30 and 60 days post capture. For the duration of the study the snakes were maintained at 26-31° C, with a 12:12 photoperiod, wa-

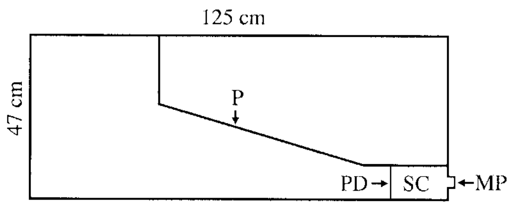

FIGURE 1: Schematic of the filming cage. Note how the partition (P) reduced the free area of the cage to form the strike chamber (SC). Access to the strike chamber for the prey was via a mouse portal (MP) in the wall, and for the snakes was via removal of a sliding Plexiglas divider (PD).

FIGURE 2: Two targets used to elicit defensive strikes. Note how the large vertical surface on the doll contrasts the smaller cylindrical surface of the mouse.

ter ad libitum, and a diet of pre-killed mice. All animal maintenance and experimental procedures comply with existing guidelines for both live reptiles and venomous snakes, and were approved by the Lafayette College Institutional Animal Care and Use Committee.

Filming cage.- The specimens were placed individually in a 125cm x 47cm x 48 cm tall filming cage (Fig. 1). The front of the filming cage was glass and the floor was roughened plywood which provided reliable contact points for the snake. The filming cage was located in a quiet room which was maintained at 26°C.

To prevent the snake from becoming defensive during the predatory experiments the filming cage was surrounded with a floor to ceiling drape which visually isolated the snake. A partition in the filming cage limited the area in which the snake could strike the mouse. The partition gradually narrowed the available area in the cage, reducing one end of the cage to a 16 x 10 cm strike chamber. A clear Plexiglas sliding door which extended the height of the cage prevented the snake from entering the strike chamber before presentation of the live mouse, but allowed visual stimulation when the mouse was in the chamber (Fig. 1). Five mm holes drilled near the bottom edge of the door provided the snake thermal and olfactory stimulation from the mouse. A sealable portal hole in the wall of the strike chamber allowed introduction of the mouse without entering the snake's visual field. When the snake was within striking distance of the mouse the Plexiglas door was retracted by way of a pulley system, thereby allowing the snake access to the striking chamber and live mouse.

Filming.- Strikes were recorded using a MotionScope 1000S digital high-speed video camera (Redlake Instruments). All videos were taken at 500 frames per second (fps) with a shutter speed of 1/20,000 sec. Northstar lights (Photographic Analysis) were used to illuminate the filming cage. For defensive strikes the video camera was directed at the deepest portion of the filming cage, whereas for predatory strikes it was directed at the smaller strike chamber. In either location, the camera was positioned such that the field of view was level to the floor of the cage and the filming axis was perpendicular to the strike.

To maximize resolution while capturing the full range of the strike, a final recording field of approximately 30 cm was used. A printed 5 mm grid was placed in the filming cage as a reference for digitizing. The recorded strikes were streamed to a PowerMac 8500 (Macintosh) and recorded using Premiere 4.0 (Adobe). The frame counter and timer from the camera were recorded with the video image, and these counters were used during all subsequent digitizing.

Behavioural context.- A suite of behavioural characteristics were used to determine the behavioural context of the strike. For defensive strikes the snake was stimulated visually by motions of the investigators, and occasionally by contact with a padded prod. Targets were only presented once the snake was judged to be maintaining a defensive behaviour, herein defined as combining an elevated coil, continual rattling, and slow tongue flicks (see Hayes and Duvall, 1991).

Each specimen was allowed to acclimate to the filming cage for at least 16 hours prior to filming predatory strikes. Two to three minutes prior to filming a Northstar light (Photographic Analysis) was remotely activated and used to illuminate the strike chamber. The portal in the strike chamber was then opened and a single live mouse was quickly introduced to the strike chamber. When the snake was judged to be within striking distance of the mouse, a series of pulleys and cables allowed the Plexiglas partition to be retracted by the researcher behind the drape.The videocamera was located within the drape, but was remotely triggered so that the researchers remained isolated from the snake during the predatory trials.

Targets.- Defensive strikes. Three different targets were used for defensive strikes, one large and two small. The large target was a commercially available stuffed doll (Fig. 2). This doll was 23 cm tall, with an oversized head approximately 15 cm in diameter. The bottom portion of the doll was packed with heavy beads, while the upper portion and head was composed of dense foam; the large doll had a mass of 320 gm. The head of the doll was covered in a felt-like fabric

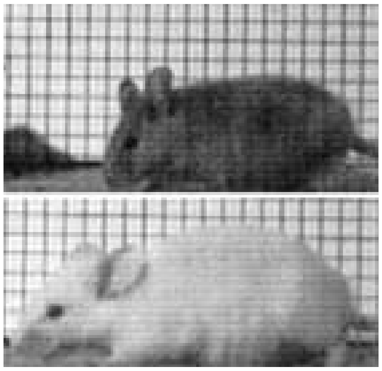

FIGURE 3: Illustration of a small (14-16 gm) mouse (top) and a large (24- 26 gm) mouse (bottom) standing against the same 5 mm grid. Note that the 10 gm difference in body mass results in a visually apparent increase in overall dimensions of the mouse.

with a low matte; initial trials indicated that the snakes were able to cleanly retract their teeth from the fabric without snagging. Prior to presentation to the snake the doll was placed in front of a radiant heater (until surface temp was over 35° C) and the front surface of the doll was rubbed with human hair.

The first small target was a previously frozen mouse. The mice used (mean mass = 27.1 gm, s.d. = 2.96 gm) were slowly thawed in hot water then placed on a small (7 x 4 cm) wooden platform. Two 1.5 cm long springs were placed loosely in 0.8 cm deep holes in the top of the platform. The ipsilateral legs of the thawed mouse were attached to these springs using small metal clips. In this way the mouse was positioned in a normal resting posture with a gap between the ventral surface of the mouse and the board (Fig. 2). The combination of metal clips and springs ensured that the mouse would separate from the platform upon contact by the snake; movements of the mouse after contact were determined by the combined mass of the mouse and inertia of the snake, rather than the attachment of the mouse to the platform. If the mouse cooled down during the filming session it was briefly heated in a microwave oven to ensure that the surface temperature was at least 35° C.

The second small target was a stuffed doll with a similar body shape and orientation as a mouse; the dimensions of the doll were slightly greater than those of the mice and it weighed 40 gm (compared to the mean mouse mass of 27.1 gm). The doll was similarly rubbed with human hair and heated with a radiant heater before being attached (via clips and springs) to the same wooden platform used for the mice. Every effort was made to present the small stuffed doll in the same manner as the mice, which normally involved a broadside presentation to the snake.

A 60 cm long pair of tongs was used to hold the top of the large target or the wooden platform of the small targets. The targets were generally positioned at ground level in the cage, although during movement they were occasionally slightly elevated (particular the small target). The targets were kept isolated from the snake, then rapidly, and forcefully, advanced toward the snake. If the snake did not strike the target it was removed and re-heated, the snake again stimulated by the investigator, and the target re-introduced. Most strikes occurred within one second of presentation of the target.

The large and small stuffed targets were washed between filming bouts. Each mouse was presented to a single snake, and was subsequently fed to that snake. The surface of each target was visually inspected for the presence of venom after each strike. Each snake was presented with only one target type per filming episode, and given a minimum of one week between filming episodes (the typical duration was over two weeks). From each rattlesnake seven strikes directed at the large target and seven strikes directed at mice were digitized. A total of 10 strikes directed at the small stuffed target were digitized, with at least two strikes recorded from each snake.

Predatory targets.- The targets for the predatory strikes were live, unrestrained laboratory mice. Only mice with a mass of 14-16 gm (small) or 24-26 gm (large) were used. These size classes ensured that the interclass difference (minimum of 8 gm) was far greater than the variation within either size class (2 gm), and that both size classes would be accepted as prey items by all of the rattlesnakes in the study (Fig. 3).

Snakes were allowed to strike only a single mouse, and were only fed during these filmed strikes. Each specimen was given at least 8 days between strikes, but vagaries in scheduling and shedding cycles forced intervals of up to 31 days. The mean duration between strikes was 11.5 days. From each snake, data were analyzed from strikes at four small and four large mice.

Data culling.- Many of the recorded strikes, particularly during the defensive encounters, were not analyzed. Strikes were rejected based on one of three criteria: indistinct behavioural context, oblique strikes, or missed strikes. Any predatory strike in which the snake exhibited a defensive behaviour (e.g., rattling) was rejected, as were defensive strikes in which the snake exhibited a delayed response to the target, or a diminution of the defensive behaviours. The video camera was positioned to provide a lateral perspective of the strike, strikes in which the snake moved sharply obliquely to the filming plane were rejected; this was particularly common in defensive strikes which were filmed in the deeper portion of the cage. Since the purpose of this study was, in part, to explore the interaction between the snake and the target, we eliminated all strikes in which the snake missed the target .

Data collection.- Linear and angular measurements were taken on a frame-by-frame basis using Image 1.6.2 (N.I.H.). Stable scalation points on the head (e.g., the cranial border between the first and second postocular) and lower jaw (e.g., the dorsal border between the fourth and fifth infralabial scales) were used for the linear measurements. Angular measurements were taken as defined below.

From each strike seven linear variables (distance to target at onset of strike, horizontal distance from onset to first contact with target, vertical distance from onset to first contact with target, horizontal distance after contact with target, vertical distance after contact with target, total horizontal distance from onset to fang withdrawal, total vertical distance from onset to fang withdrawal), and five angular variables (angle of gape at first contact with target, angle of gape at fang withdrawal, maximum angle of gape, fang angle at penetration of target, maximum fang angle) were recorded. Gape was measured as the angle at the corner of the mouth formed by the ventral border of the supralabial scales and the dorsal border of the infralabial scales. Fang angle was defined as the angle between the ventral surface of the supralabial scales and the leading edge of the fang sheath.

By recording the frame number and timer readings, three temporal variables (duration from initial fang erection to fang penetration, duration from first contact with target to fang penetration, and total duration of fang penetration) were calculated. Using an EXCEL spreadsheet and these same temporal, linear, and angular values, the maximum velocity of the strike and the maximum rotary velocity of fang erection were calculated. Since we were more concerned with issues of inertia and momentum, we concentrated on the velocity of the strike, rather than the acceleration.

The site of contact between the snake and the target was classified from each strike. For the snakes, four contact sites were defined: closed mouth (denoting contact with the nasal or mental regions of the head), the fang, the lower jaw, and the roof of the mouth (caudal to the fang). The contact sites on the mice were classified into five cranial-caudal zones (head, thorax, abdomen, pelvis, and legs) and three dorsal-ventral regions (dorsal, middle, and ventral).

Statistical analysis.- Each strike produced 18 variables including the classification of contact site on the snake; the defensive and predatory strikes directed at the mice produced two additional variables representing the contact region and zone on the mouse. Given the high degree of variability exhibited by each specimen, and the inherent variation in “motivation”, every strike (including those from the same snake) was considered an independent event. Early analyses (using ANOVA and least-squares regression) revealed little influence of body size on the strike kinematics. Intraspecific variation, where it was pronounced, resulted from a single specimen rather than a trend across the specimens. For this reason, the influence of body size and

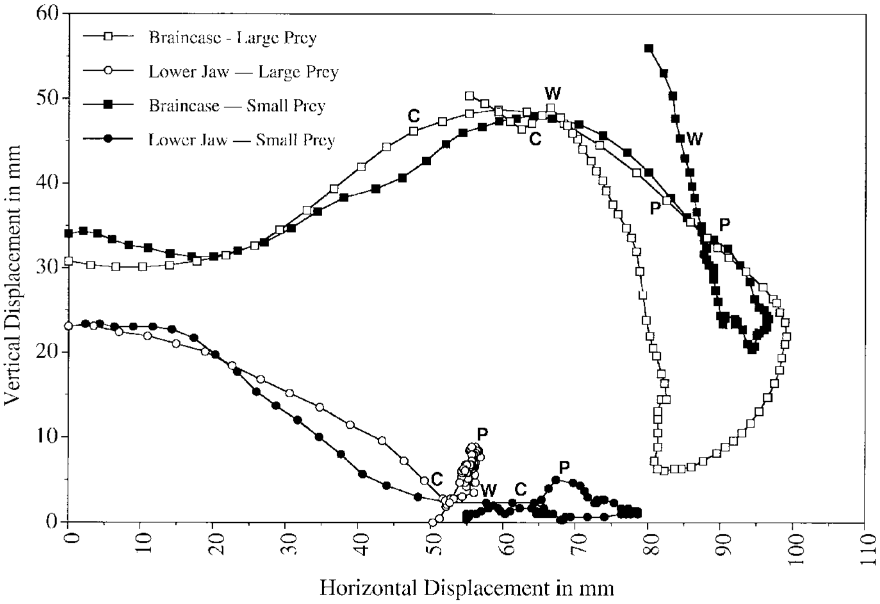

FIGURE 4: Frame by frame displacement of the braincase (squares) and lower jaw (circles) during predatory strikes at small (solid symbols) and large (open symbols) prey. The limited motion of the lower jaw following contact is evident, as is the rotation of the braincase over the prey item. Since each frame represents a constant time interval (2 msec), velocity and acceleration can be determined by the distances between successive points. Note the general kinematic similarity between the two strikes. C- frame of first contact with the prey (in both strikes first contact was made with the lower jaws); P- frame of fang penetration; W- frame of fang withdrawal.

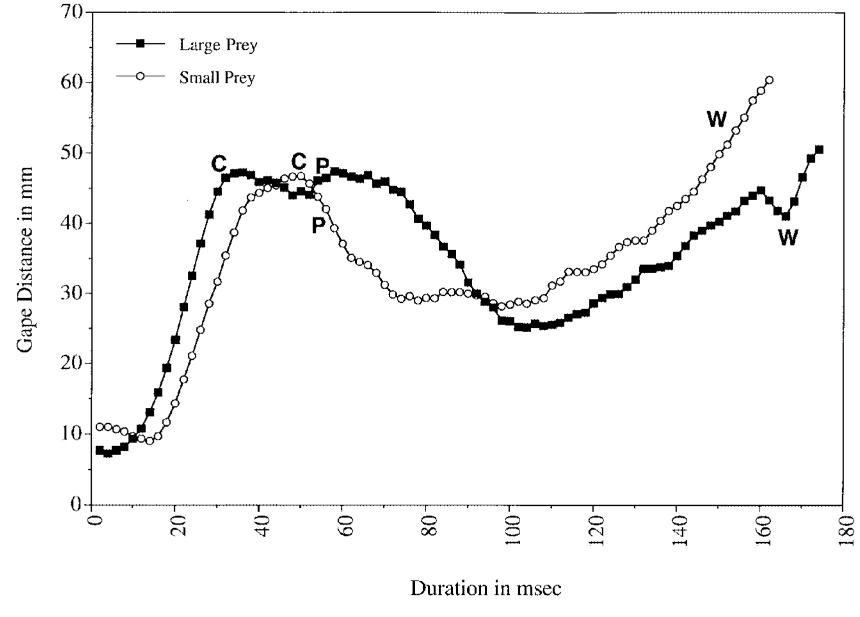

FIGURE 5: Magnitude of gape during the predatory strike. Gape was determined as the linear distance between a stationary point on the lower jaw and braincase. C- frame of first contact; P- frame of fang penetration; W- frame of fang withdrawal. Note the limited change in gape between contact and fang penetration, the period of relatively constant gape (around 90 msec) following fang penetration, and the relative similarity between these two strikes.

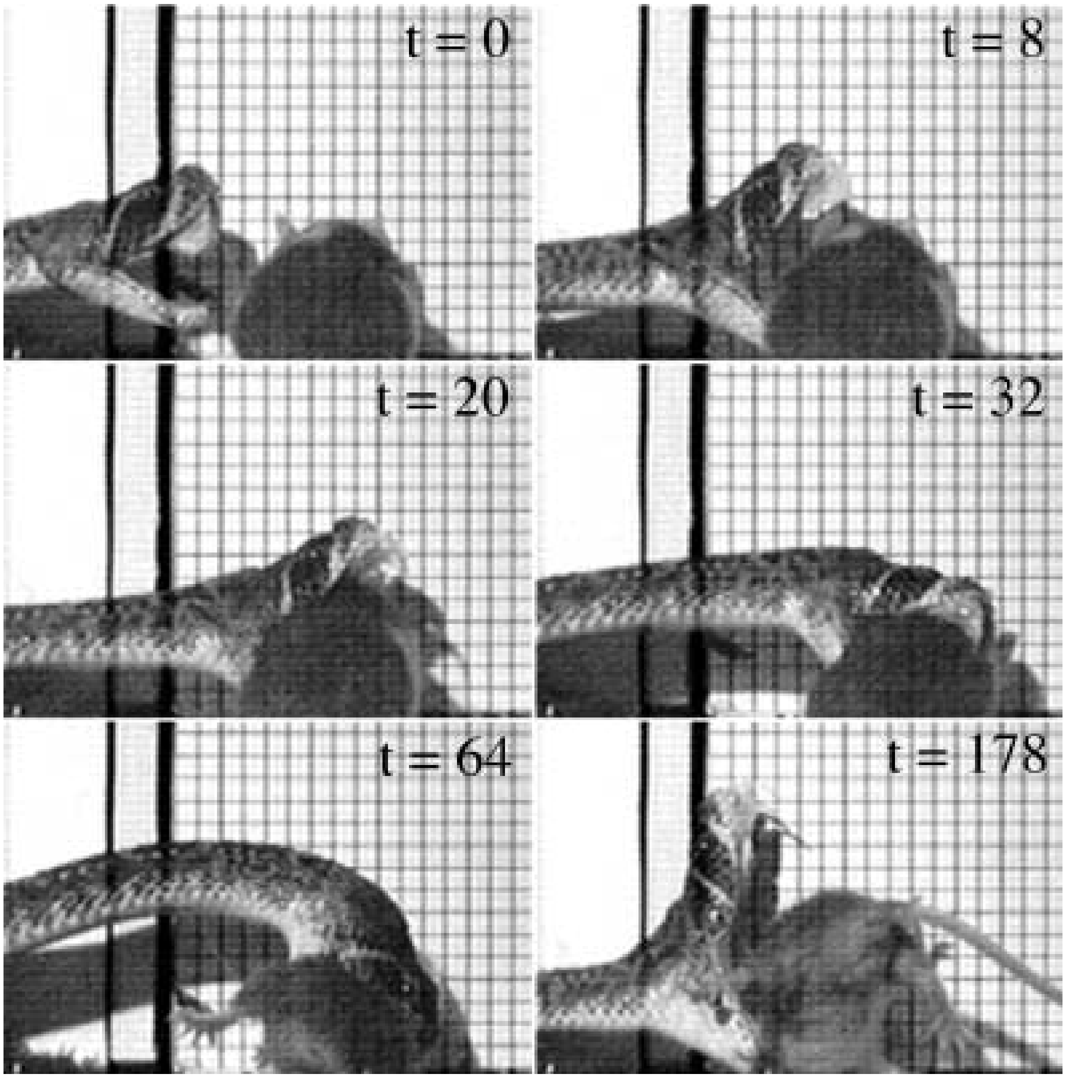

FIGURE 6: Isolated digital video frames illustrating a bilateral predatory strike. Times given are in milliseconds. Note the limited rotation of the skull over the dorsal surface of the mouse and the prominent neck arching following fang penetration.

intraspecific variation will not be explored further.

Three main comparisons were performed: 1) defensive strikes directed at the large stuffed doll against defensive strikes directed at the mouse; 2) predatory strikes directed at the small mouse against predatory strikes directed at the large mouse; and 3) defensive strikes directed at the mouse against predatory strikes directed at the large mouse. In each comparison, a single-factor between-subject Analysis of Variance was performed using strike target as the factor, and a Chi-square test was performed to compare the categorical values of the contact sites. Pearson's multiple correlation coefficients were calculated from the kinematic variables within predatory and defensive strikes. Additional comparisons were performed on portions of each data set (see below). For all statistical procedures the cutoff level for significance was Bonferroni adjusted by dividing 0.05 by the number of comparisons. Statistical procedures follow Sheskin (2000) and were performed using SYSTAT 5.12.

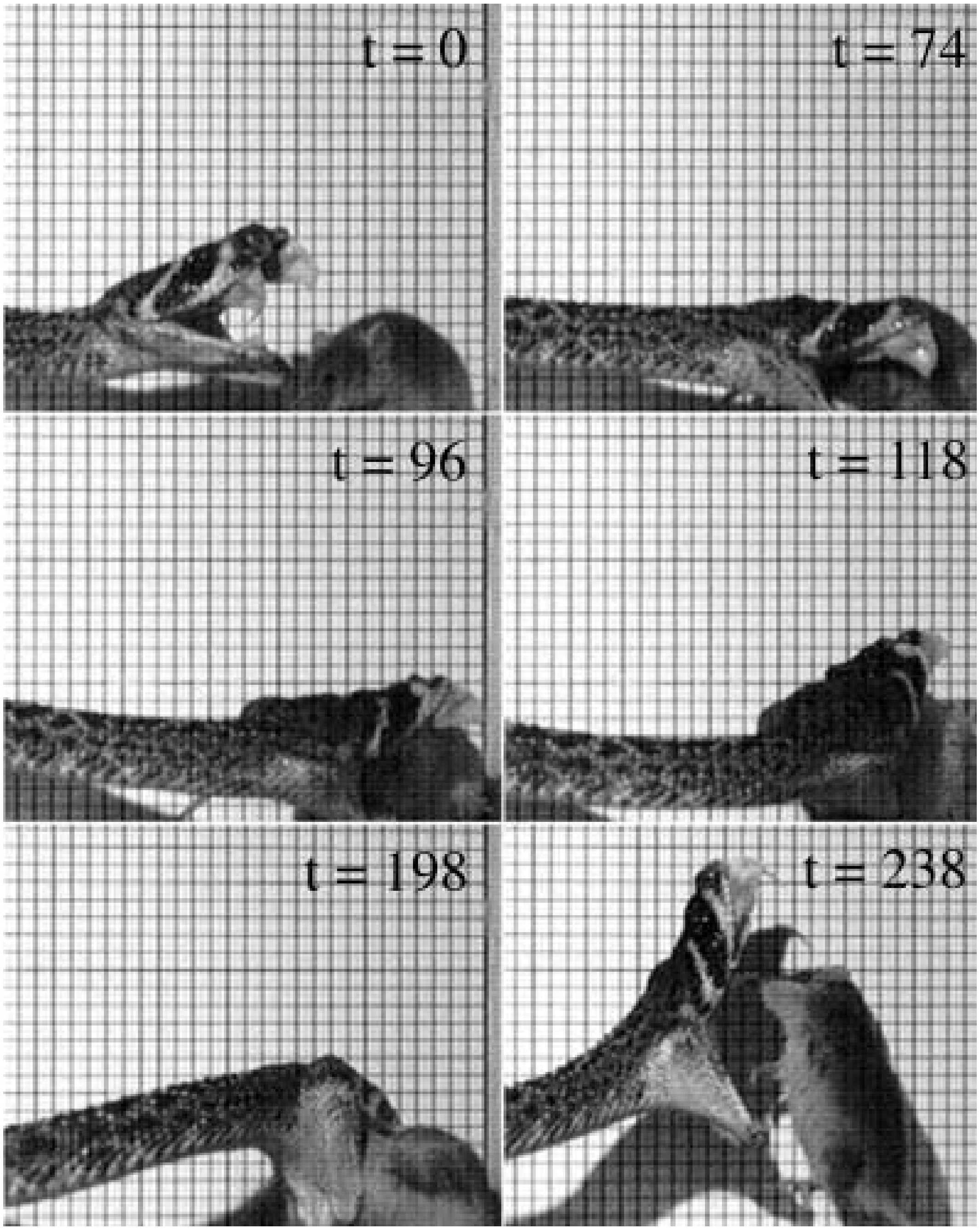

FIGURE 7: Isolated digital video frames illustrating a unilateral predatory strike. Times given are in milliseconds. Note the prominent free fang in the second frame, and the subsequent rotations of the head which resulted in penetration of this fang.

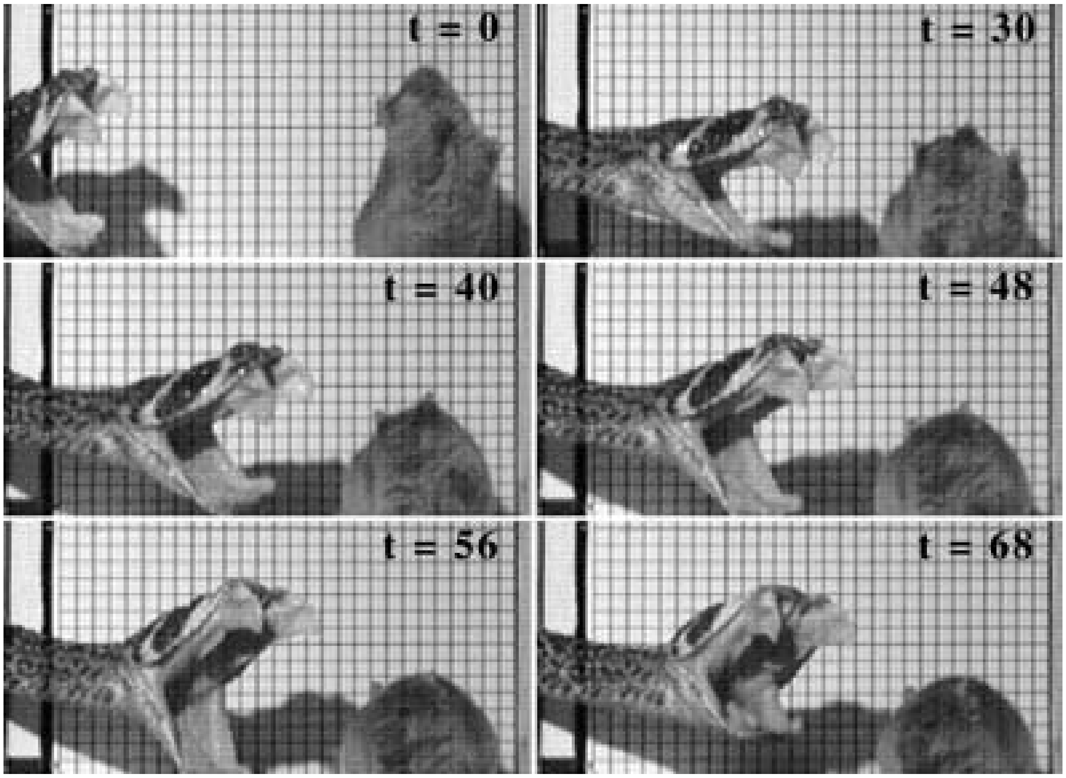

FIGURE 8: Isolated digital video frames illustrating a mid-strike correction. Times given are in milliseconds. During the first 30 milliseconds the head and anterior body follow the same trajectory, but as the strike progress the head is rotated laterally as the body continues to advance. Note that the fangs are maintained in an erect position, and the mouth is not closing until the final frame, indicating this is a correction of a strike not two sequential strikes.

RESULTS

Predatory strikes.- General behaviour. The rattlesnake responded rapidly to the presence of the mouse in every trial. The head was always oriented towards the mouse, and rapid tongue flicks were always observed. Every introduced mouse was struck. Although we could not observe venom injection, the mice all exhibited signs of envenomation (partial paralysis, loss of locomotor function, seizure) and died within a few minutes of being struck. In every case the rattlesnake ingested the presented mouse. This combined suite of behaviours, particularly in rattlesnakes which were habituated to the cage and isolated from the researchers, combined with the absence of defensive behaviours, were used to classify these strikes as predatory.

The rattlesnakes would frequently remain coiled in the narrow end of the filming cage immediately adjacent to the Plexiglas plate (Fig. 1). Our observations suggest that the snakes began to associate the light with the introduction of the mouse. When the light was turned on (a few minutes before the introduction of the mouse) the snake would frequently press its head against the Plexiglas plate and increase the frequency of tongue flicks. In 40% of the strikes the rattlesnake was in a more remote part of the filming cage, rather than being coiled beside the Plexiglas plate. These snakes all rapidly oriented to the presence of the introduced mouse, and began advancing (normally using rectilinear locomotion) toward the Plexiglas plate. In almost every case these snakes struck the mouse without first condensing their body into distinct coils; these are the snakes which were classified as having an "extended" body posture.

Qualitative description of the strikes.- For the present study, a strike is defined as directed motion of the snake leading to fang penetration of

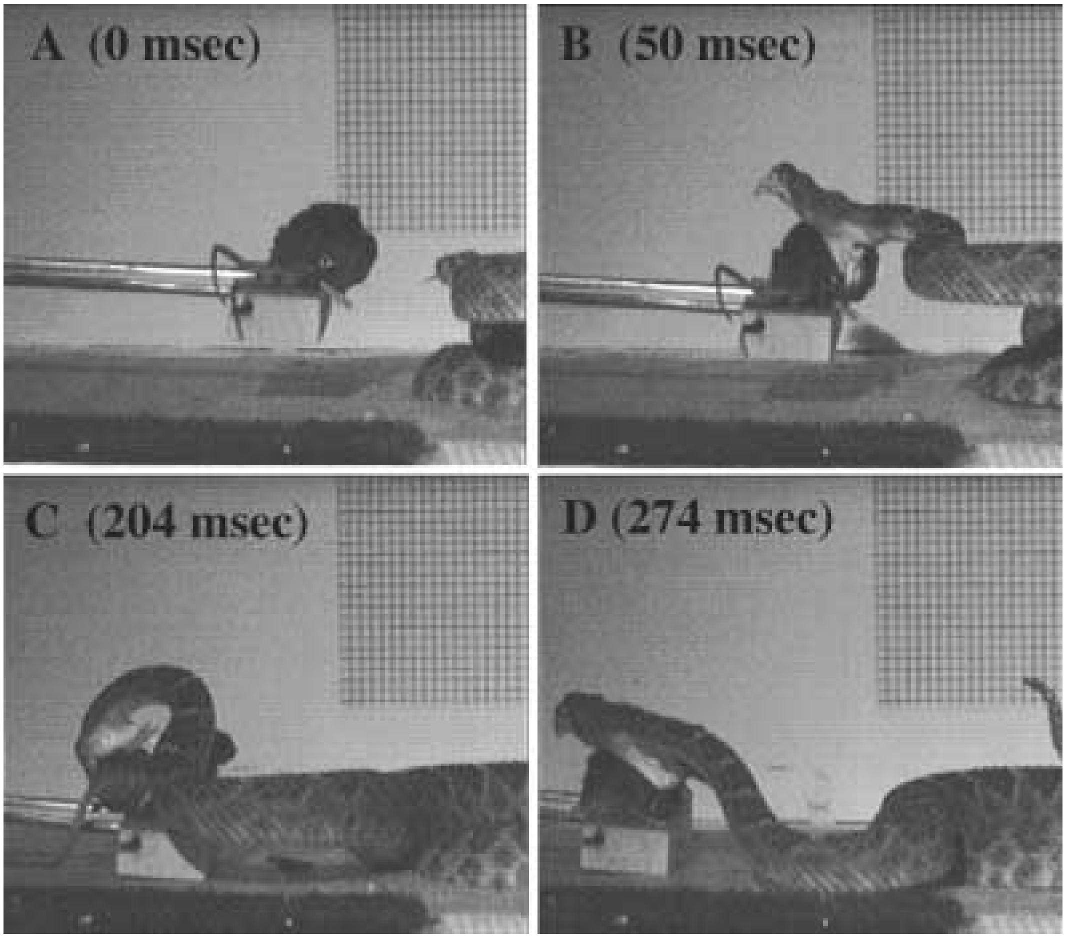

FIGURE 9: Representative sequence of a defensive strike directed at a mouse. (A) Onset, or launch of the strike, note the orientation and proximity of the mouse relative to the snake. (B) Early contact with the mouse, note that the contact is with the lower jaws, while the braincase arches over the mouse. (C) Fang penetration, note how the braincase has rolled to the far side of the mouse and the marked decrease in gape. (D) Withdrawal of the fangs and release.

the prey. The predatory strikes were initiated by an acceleration of the head toward the prey item. Almost immediately the lower jaws were abducted and the head rotated dorsally about the vertebral column (Fig. 4). The fangs were erected during this initial gape increase. In most of the strikes the snake's lower jaws made the first contact with the mouse, generally on the ventral surface of the mouse. The lower jaws remained stationary after first contact, although in some mice they pushed ventrally under the mouse's body (Fig. 4). The head and fangs normally just cleared the dorsal surface of the mouse, often with the fang sheath pushing through the mouse's fur. Depression of the braincase around the vertebral column led to fang penetration, which was normally observed on the dorsal or middle portions of the far side (that is, opposite the side contacted by the lower jaws) of the mouse's body. A combination of momentum, and particularly muscle contraction pushed the head and fangs against the mouse's body and led to a characteristic arching of the snake's neck. The period of fang penetration was characterized by little displacement of the head, particularly vertical displacement (Fig. 4). Withdrawal was achieved by rotating the head dorsally away from the body of the mouse, concurrent with abduction of the lower jaws (Fig. 4).

TABLE 1: Analysis of the influence of target size on the predatory strike. Kinematic data are in the form of mean (s.e.) for strikes on small (N = 20) and large (N = 20) mice. Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. F values given for the ANOVA results all have 1 df, as do the χ^2 values.

Variable	Small Prey	Large Prey	
Distance from target at launch	7.28 (0.79)	6.98 (0.84)	F = 0.07, p = 0.79
Horizontal distance to contact	8.85 (0.76)	8.30 (0.84)	F = 0.24, p = 0.63
Vertical distance to contact	1.72 (0.23)	1.83 (0.24)	F = 0.11, p = 0.74
Horizontal distance after contact	2.98 (0.27)	2.99 (0.37)	F = 0.01, p = 0.98
Vertical distance after contact	1.03 (0.33)	1.72 (0.43)	F = 1.65, p = 0.21
Total horizontal distance	11.83 (0.74)	11.19 (0.79)	F = 0.35, p = 0.56
Total vertical distance	2.64 (0.41)	3.44 (0.48)	F = 1.57, p = 0.22
Duration of fang penetration	186.2 (31.1)	176.7 (29.4)	F = 0.05. p = 0.83
Duration from contact to fang penetration	23.6 (4.90)	44.0 (18.15)	F = 1.18, p = 0.29
Duration from fang erection to contact	50.3 (6.8)	58.3 (9.5)	F = 0.47, p = 0.50
Incidence of prey "holding"	35%	30%	2 = 0.11, p>0.05
Gape angle at contact	76.5 (3.2)	65.3 (6.2)	F = 2.56, p = 0.12
Gape angle at fang withdrawl	97.3 (5.4)	84.5 (5.2)	F = 1.95, p = 0.18
Maximum gape angle	90.3 (4.5)	93.3 (3.9)	F = 0.26, p = 0.61
Fang angle at penetration	83.4 (4.0)	90.1 (3.9)	F = 1.45, p = 0.24
Maximum fang angle	90.9 (2.9)	92.4 (3.1)	F = 0.12, p = 0.73
Incidence of unilateral strikes	50%	20%	2 = 3.96, p = 0.04
Incidence of fang repositioning	30%	55%	2 = 2.56, p>0.05
Maximum velocity of strike	348.9 (29.2)	331.0 (18.7)	F = 0.27, p = 0.61
Maximum rotational velocity of fang	9.4 (0.5)	9.4 (0.83)	F = 0.01, p = 0.99

The combination of these movements produced a rather characteristic gape profile (Fig. 5) for predatory strikes. There was little change in gape between initial contact and fang penetration, reflecting the tendency of the snake to scrape the dorsal surface of the mouse during predatory strikes (Fig. 5). Fang penetration was marked by a decrease in gape- presumably due to a combination of jaw adduction and rotation of the head-followed by a period of fairly stable gape (Fig. 5). The withdrawal was always characterized by a marked increase in gape necessary to pull the elongate fangs free of the prey.

Two different classes of strikes were observed in *Crotalus atrox*, bilateral and unilateral strikes. In a bilateral strike the head was accelerated toward the mouse while the mouth was opened and the fangs erected (Fig. 6). The lower jaws of the snake normally made first contact with the mouse, and subsequently served as a pivot around which the snake's head rotated to the contralateral side of the mouse. As the head rotated over the body of the mouse, the maximum gape and maximum fang erection were achieved (Fig. 6). Following fang penetration, the gape decreased and the snake normally developed a prominent arch in its neck (Fig. 6). During this interval we occasionally observed fang repositioning, which we define as a rapid withdrawal and penetration of a fang which had already successfully penetrated the prey. The prey item was then either released (the kinematics of withdrawal were not analyzed) or held until ingestion.

A unilateral strike began similar to the bilateral, with acceleration of the head toward the prey, an increase in gape, and erection of the fangs (Fig. 7). In most unilateral strikes the fang made first contact with the prey, or made contact nearly synchronously with the lower jaws (Fig. 7). The snake's head typically did not rotate over the body of the mouse, so fang penetration occurred either on the dorsal surface of the mouse or on the same side as first contact (Fig. 7). The defining feature of the unilateral strike is that ini-

TABLE 2: Comparison of unilateral and bilateral predatory strikes. Kinematic data are in the form of mean (s.e.) for unilateral (N = 14) and bilateral (N = 26) strikes. Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. F values given for the ANOVA results all have 1 df, as do the χ^2 values.

Variable	Unilateral Strike	Bilateral Strike	
Distance from target at launch	8.44 (1.10)	6.42 (0.61)	F = 3.04, p = 0.09
Horizontal distance to contact	9.90 (1.09)	7.86 (0.61)	F = 3.15, p = 0.08
Vertical distance to contact	1.67 (0.33)	1.83 (0.18)	F = 0.21, p = 0.65
Horizontal distance after contact	2.64 (0.46)	3.17 (0.24)	F = 1.26, p = 0.27
Vertical distance after contact	2.10 (0.53)	0.99 (0.29)	F = 4.10, p = 0.05
Total horizontal distance	12.41 (0.87)	11.03 (0.67)	F = 1.53, p = 0.22
Total vertical distance	3.50 (0.72)	2.79 (0.31)	F = 1.14, p = 0.29
Duration of fang penetration	196.0 (31.3)	172.6 (28.2)	F = 0.28 p = 0.60
Duration from contact to fang penetration	57.4 (25.37)	21.1 (3.80)	F = 3.61, p = 0.07
Duration from fang erection to contact	72.3 (12.43)	44.6 (5.11)	F = 5.88, p = 0.02
Incidence of prey "holding"	29%	35%	2 = 0.15, p>0.05
Gape angle at contact	60.0 (6.7)	76.7 (3.8)	F = 5.57, p = 0.02
Gape angle at fang withdrawl	89.1 (6.5)	91.6 (4.8)	F = 0.06, p = 0.81
Maximum gape angle	89.3 (4.3)	93.2 (3.9)	F = 0.40, p = 0.53
Fang angle at penetration	91.8 (4.9)	83.9 (3.3)	F = 1.85, p = 0.18
Maximum fang angle	93.2 (3.8)	90.8 (2.5)	F = 0.29, p = 0.59
Incidence of fang repositioning	43%	42%	2 = 0.01, p>0.05
Maximum velocity of strike	328.4 (29.2)	346.2 (21.6)	F = 0.24, p = 0.63
Maximum rotational velocity of fang	9.5 (1.0)	9.3 (0.5)	F = 0.06, p = 0.80

tial fang penetration was achieved with only one fang (Fig. 7). At no time did we observe venom release from the “free” contralateral fang. Immediately after penetration the rattlesnake sharply flexed its neck toward the imbedded fang, rotated the head in the transverse plane such that the side with the embedded fang was depressed and the side with the free fang was elevated, and increased the gape on the side of the head with the free fang (Fig. 7). This combination of movements brought the free fang over the mouse, and a subsequent decrease in gape and opposite rotation of the head in the transverse plane resulted in fang penetration (Fig. 7). As with the bilateral strike, subsequent fang repositioning was observed in some of the unilateral strikes, and on occasion the struck mouse was held rather than released.

Quantitative Comparisons.- None of the 20 kinematic variables examined were significantly different between the small and large mice (Table 1), although three variables (incidence of prey holding, incidence of unilateral strikes, and incidence of fang repositioning) had probabilities of less than 0.05. Four variables were markedly different between unilateral and bilateral strikes (Table 2)- increased vertical distance after contact in unilateral strikes, increased durations from fang erection to contact and from contact to penetration in unilateral strikes, and the decreased angle of gape at contact in unilateral strikes- were all reflective of the movements observed when the head pivoted and the free fang (which defined the unilateral strike) was brought over, then down into, the prey item. None of these differences were significant using the more restrictive Bonferroni adjusted cut-off value of p = 0.003.

Snakes that launched a predatory strike from an extended posture (in which over 50% of the body was not formed into coils) struck over a shorter horizontal distance, with a greater vertical component, lower incidence of fang repositioning, slower rotation of the fang, and a shorter duration of fang penetration (Table 3), but these differences were not significant. Extended

TABLE 3: Analysis of the influence of snake posture on the predatory strike. Kinematic data are in the form of mean (s.e.) for extended (N = 16) and coiled (N = 24) strikes. Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. F values given for the ANOVA results all have 1 df, as do the χ^2 values.

Variable	Extended	Coiled	
Distance from target at launch	6.28 (0.81)	7.70 (0.77)	F = 1.52, p = 0.23
Horizontal distance to contact	7.56 (0.87)	9.25 (0.72)	F = 2.22, p = 0.15
Vertical distance to contact	2.10 (0.29)	1.56 (0.18)	F = 2.74, p = 0.11
Horizontal distance after contact	2.86 (0.42)	3.06 (0.26)	F = 0.18, p = 0.67
Vertical distance after contact	1.73 (0.52)	1.14 (0.29)	F = 1.17, p = 0.29
Total horizontal distance	10.31 (0.63)	12.31 (0.75)	F = 3.96, p = 0.05
Total vertical distance	3.83 (0.54)	2.51 (0.36)	F = 4.49, p = 0.04
Duration of fang penetration	205.4 (37.5)	167.1 (25.2)	F = 0.77 p = 0.39
Duration from contact to fang penetration	53.4 (22.3)	20.8 (3.96)	F = 3.03, p = 0.09
Duration from fang erection to contact	51.5 (8.3)	56.2 (8.0)	F = 1.53, p = 0.70
Incidence of prey "holding"	38%	29%	2 = 0.34, p>0.05
Gape angle at contact	57.8 (5.8)	79.6 (3.7)	F = 11.30, p = 0.002
Gape angle at fang withdrawl	90.1 (7.9)	91.0 (4.0)	F = 0.009, p = 0.92
Maximum gape angle	92.0 (6.2)	91.6 (2.8)	F = 0.004, p = 0.95
Fang angle at penetration	92.3 (4.7)	83.0 (3.3)	F = 2.76, p = 0.11
Maximum fang angle	92.8 (3.1)	90.9 (2.9)	F = 0.18, p = 0.68
Incidence of unilateral strikes	38%	50%	2 = 0.07, p>0.05
Incidence of fang repositioning	69%	25%	2 = 7.52, p = 0.01
Maximum velocity of strike	337.9 (27.8)	341.3 (22.3)	F = 0.009, p = 0.92
Maximum rotational velocity of fang	10.9 (0.81)	8.4 (0.49)	F = 7.97, p = 0.008

strikes were characterized by significantly lower gapes at contact (Table 3). The orientation of the mouse had little impact on the kinematics of the strike. When the mouse adopted an orientation which was parallel to that of the snake, it. walked directly at the head of the snake. Because of this behaviour, the resulting strike covered a shorter horizontal distance (Table 4) though this difference was not significant.

Little correlation was detected among these kinematic variables (Table 5). With the exception of the correlation between fang angle at penetration and maximum fang angle, those variables that were significantly correlated were all co-determined (i.e., horizontal distance to contact and total horizontal distance).

Variation in contact site.- In the majority of the offensive strikes examined the prey item first made contact with the lower jaws of the snake (Table 6). This pattern held regardless of how the strikes were divided into subsets (e.g., coiled versus extended or unilateral versus bilateral strikes). Unilateral strikes had the lowest (57.1) percentage of strikes involving first contact with the lower jaws, while bilateral strikes had the highest (92.3) percentage (Table 6), but this difference was not significant. Most of the strikes made first contact with the abdomen of the mouse (Table 7), but there were two significant exceptions. Strikes directed at the larger mice had a higher incidence of contact with the thorax; this may simply reflect the challenge of striking the thorax of a small mouse. The most divergent pattern was observed in strikes at mice oriented parallel to the snakes; almost half of these strikes impacted the head of the mouse (Table 7), creating a significant departure from strikes at oblique or parallel oriented mice. In most of the strikes the fangs penetrated near the dorsal surface of the mouse (Table 8). Strikes directed at small mice, and those directed at mice oriented perpendicular to the snake, were more likely to penetrate near the dorsal-ventral midline of the mouse, but this difference was not significant.

TABLE 4: Analysis of the influence of prey orientation on the predatory strike. Kinematic data are in the form of mean (s.e.) for strikes directed at prey oriented parallel (N = 15), perpendicular (N = 10), or oblique (N = 15) to the long axis of the snake's head. Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. F values given for the ANOVA results all have 2 df, as do the χ^2 values.

Variable	Parallel	Perpendicular	Oblique	
Distance from target at launch	5.62 (0.81)	7.70 (1.03)	8.26 (1.00)	F = 2.34, p = 0.11
Horizontal distance to contact	6.72 (0.87)	9.93 (0.86)	9.52 (0.94)	F = 3.77, p = 0.03
Vertical distance to contact	1.71 (0.25)	1.99 (0.45)	1.70 (0.21)	F = 2.76, p = 0.76
Horizontal distance after contact	3.18 (0.46)	2.86 (0.32)	2.86 (0.34)	F = 0.23, p = 0.80
Vertical distance after contact	1.25 (0.43)	2.14 (0.76)	0.99 (0.28)	F = 1.43, p = 0.25
Total horizontal distance	9.78 (0.74)	12.79 (0.83)	12.39 (0.97)	F = 3.60, p = 0.04
Total vertical distance	2.99 (0.57)	4.12 (0.74)	2.37 (0.33)	F = 2.44, p = 0.10
Duration of fang penetration	156.4 (38.3)	215.7 (48.9)	182.0 (26.1)	F = 0.59 p = 0.56
Duration from contact to fang penetration	50.8 (24.1)	16.6 (3.6)	28.3 (6.1)	F = 1.10, p = 0.34
Duration from fang erection to contact	50.7 (8.2)	43.8 (5.1)	64.9 (12.4)	F = 1.13, p = 0.33
Incidence of prey "holding"	33%	30%	33%	2 = 0.04, p>0.05
Gape angle at contact	68.0 (6.2)	75.3 (5.2)	70.8 (6.5)	F = 0.31, p =0.74
Gape angle at fang withdrawl	84.1 (7.6)	81.4 (8.3)	103.7 (6.9)	F = 2.65, p = 0.09
Maximum gape angle	94.0 (3.6)	90.9 (4.8)	90.2 (6.4)	F = 0.17, p = 0.85
Fang angle at penetration	85.1 (5.6)	87.2 (5.0)	88.0 (4.0)	F = 0.11, p = 0.90
Maximum fang angle	87.2 (2.9)	90.8 (3.5)	96.6 (4.0)	F = 2.00, p = 0.15
Incidence of unilateral strikes	47%	30%	27%	2 = 1.46, p>0.05
Incidence of fang repositioning	47%	30%	47%	2 = 0.85, p>0.05
Maximum velocity of strike	337.9 (27.8)	341.3 (22.3)	315.7 (22.4)	F = 1.07, p = 0.35
Maximum rotational velocity of fang	10.9 (0.81)	8.4 (0.49)	8.8 (0.8)	F = 0.79, p = 0.46

TABLE 5: Significant Pearson correlation coefficients determined for all predatory strikes. Note that few of the variables are significantly correlated.

Variable	Co-Variable	r	(p)
Distance from target at launch	Horizontal distance to contact	0.95	(<0.01)
	Total horizontal distance	0.89	(<0.01)
Horizontal distance to contact	Total horizontal distance	0.91	(<0.01)
Vertical distance after contact	Total vertical distance	0.84	(<0.01)
Fang angle at penetration	Maximum fang angle	0.67	(0.02)

Corrections.- Among the predatory strikes recorded, including some not analyzed for the present study, were multiple strikes in which the rattlesnake missed the prey item completely with both fangs. After each of these failed strikes, the snake launched one, or more, additional predatory strikes until making contact with the mouse. When examining these failed strikes, or the successful strikes described above, for evidence of mid-strike adjustment or correction, it was imperative to have a clear definition of what constitutes a correction. Of particular importance was distinguishing a correction from a second strike launched in a diverging direction. For this purpose we defined a mid-strike correction as occurring when the long axis of the rattlesnake's head, and/or anterior body, changed direction during a strike without partial or complete retraction of the fangs (which occurs at the end of failed strikes), a decrease in gape, or a cessation of movement of the snake's neck and anterior body. In short the snake was still moving forward with

TABLE 6: Site on the snake's body to make first contact with the prey. Note the prevalence of first contact with the lower jaws.

	Fang	Lower Jaw	Roof of Mouth	Closed Mouth
Large Prey (n=20)	5	70	15	10
Small Prey (n=20)	10	90	0	0
2 = 6.5, 3 df, p = >0.05				
Extended Posture (n=16)	6.3	75	6.3	12.5
Coiled Posture (n=24)	8.3	83.3	8.3	0
2 = 3.2, 3 df, p = >0.25				
Prey Released (n=27)	3.7	81.5	11.1	3.7
Prey Held (n=13)	14.3	71.4	7.1	7.1
2 = 2.1, 3 df, p = >0.50				
Unilateral Strike (n=14)	14.3	57.1	14.3	14.3
Bilateral Strike (n=26)	3.8	92.3	3.8	0
2 = 7.8, 3 df, p = >0.05				
Prey Parallel (n=15)	13.3	73.3	0	13.3
Prey Perpendicular (n=10)	10	80	10	0
Prey Oblique (n=15)	0	86.7	13.3	0
2 = 7.3, 6 df, p = >0.25				

TABLE 7: Site of fang penetration on the prey's body. Note the general prevalence of fang penetration in the abdomen, and the significant influence of prey size and orientation.

	Head	Thorax	Abdomen	Pelvis and Legs
Large Prey (n=20)	25	40	30	5
Small Prey (n=20)	5	10	75	10
2 = 10.4, 3 df, p = <0.02				
Extended Posture (n=16)	18.8	31.3	43.8	6.3
Coiled Posture (n=24)	12.5	20.8	58.3	8.3
2 = 1.1, 3 df, p = >0.75				
Prey Released (n=27)	11.1	29.6	51.9	7.4
Prey Held (n=13)	23	15.4	53.8	7.7
2 = 1.0, 3 df, p = >0.75				
Unilateral Strike (n=14)	21.4	35.7	35.7	7
Bilateral Strike (n=26)	11.5	19.2	61.5	7.7
2 = 3.6, 3 df, p = >0.25				
Prey Parallel (n=15)	40	26.7	26.7	6.7
Prey Perpendicular (n=10)	0	10	80	10

mouth open and fangs erect, but it actively turned its head in an effort to make contact with the prey. Using this definition, we found only two examples of mid-strike correction in *Crotalus atrox*.

Both corrections had similar kinematics (Fig. 8). The initial strike appeared to be slightly short of, and lateral to, the prey item. While most of the strike was linear, as the head approached the prey item there was a clear deflection of the head such that the fangs approached the prey item closer than they would have without a correction (Fig. 8). Both corrections were brief (the redirection occurring in under 20 msec) and neither resulted in the fangs penetrating the prey. In both cases

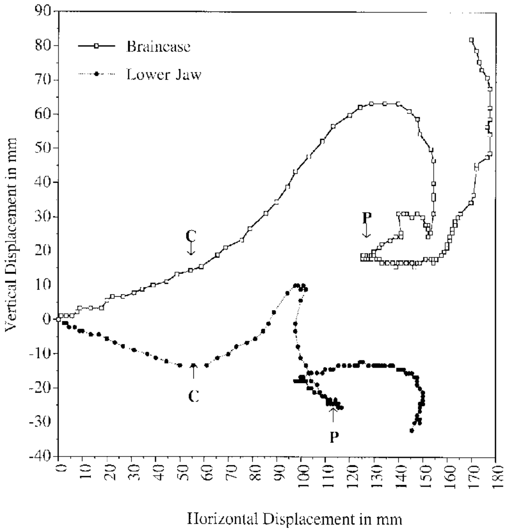

FIGURE 10: Representative displacement of the braincase and lower jaw during a defensive strike directed at a mouse. Note the characteristic motions of the lower jaw relative to the mouse between contact and fang penetration and the distinctive arching of the braincase over the mouse during this same period. Since each point represents a successive frame, with a constant 2 msec time interval between them, the relative velocity and acceleration can be seen from the spacing between successive points. C- frame of first contact; P- frame of fang penetration.

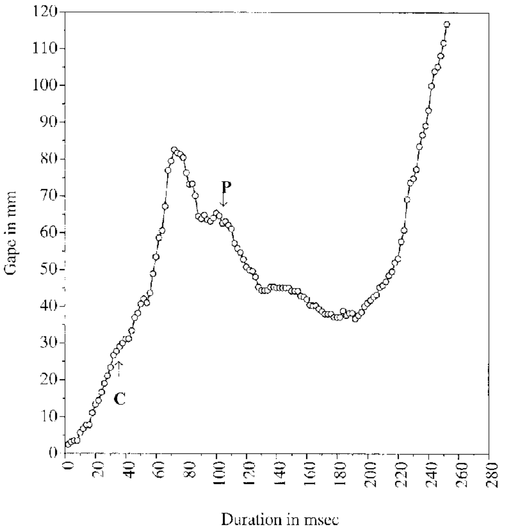

FIGURE 11: Representative pattern in changes of gape during a defensive strike directed at a mouse. Note how the gape increases after contact and decreases during fang penetration. The marked increase in gape associated with fang withdrawal is always preceded by a period characterized by relatively static, or constant gape. C- frame of first contact; P- frame of fang penetration.

the snake was able to immediately launch a second strike which proved successful.

Defensive strikes.- Kinematics of defensive strikes at mice. While variations were observed, the kinematics of defensive strikes directed at the mice were rather consistent. From the onset of the strike (Fig. 9A) the head was accelerated horizontally with only modest vertical trajectory. The strike was directed such that the lower jaws made the first contact with the mouse (Fig. 9B). The lower jaws remained fairly stationary and served as a fulcrum over which the momentum of the strike rotated the snake's braincase up and over the mouse. Fang penetration typically occurred on the far side of the mouse and was associated with a distinct decrease in gape (Fig. 9C). Fang withdrawal was associated with an increase in gape and a marked rotation of the braincase relative to the mouse (Fig. 9D).

The average defensive strike directed at a mouse was launched from 3.8 cm away (Table 9). In most cases the strike was launched while the target was moving away from the snake, thus the mean horizontal distance to contact of 4.7 cm exceeded the distance at which the strike was launched (Table 9). Prior to contact with the mouse, the braincase and lower jaws follow similar, though inverted, trajectories (Fig. 10) which produced a mean gape angle at contact of 87.7° (Table 9). First contact was made by the lower jaws in 19/35 (54%) of the strikes analyzed. In 10/35 of the strikes (29%) the first contact was with the roof of the mouth; in these strikes the braincase continued over the mouse until the mouse made contact with the lower jaws. Following contact, the lower jaws were elevated, then there was an abrupt reversal and the lower jaws were depressed (Fig. 10). During these movements the surface of the mouse visibly deformed as the teeth of the lower jaws penetrated and stretched the skin of the mouse.

Following contact the braincase continued to move vertically, thus increasing the gape angle. As the gape angle increased towards the maximum of 128° (Table 9) the braincase traced an arching trajectory over the mouse (Fig. 10). As

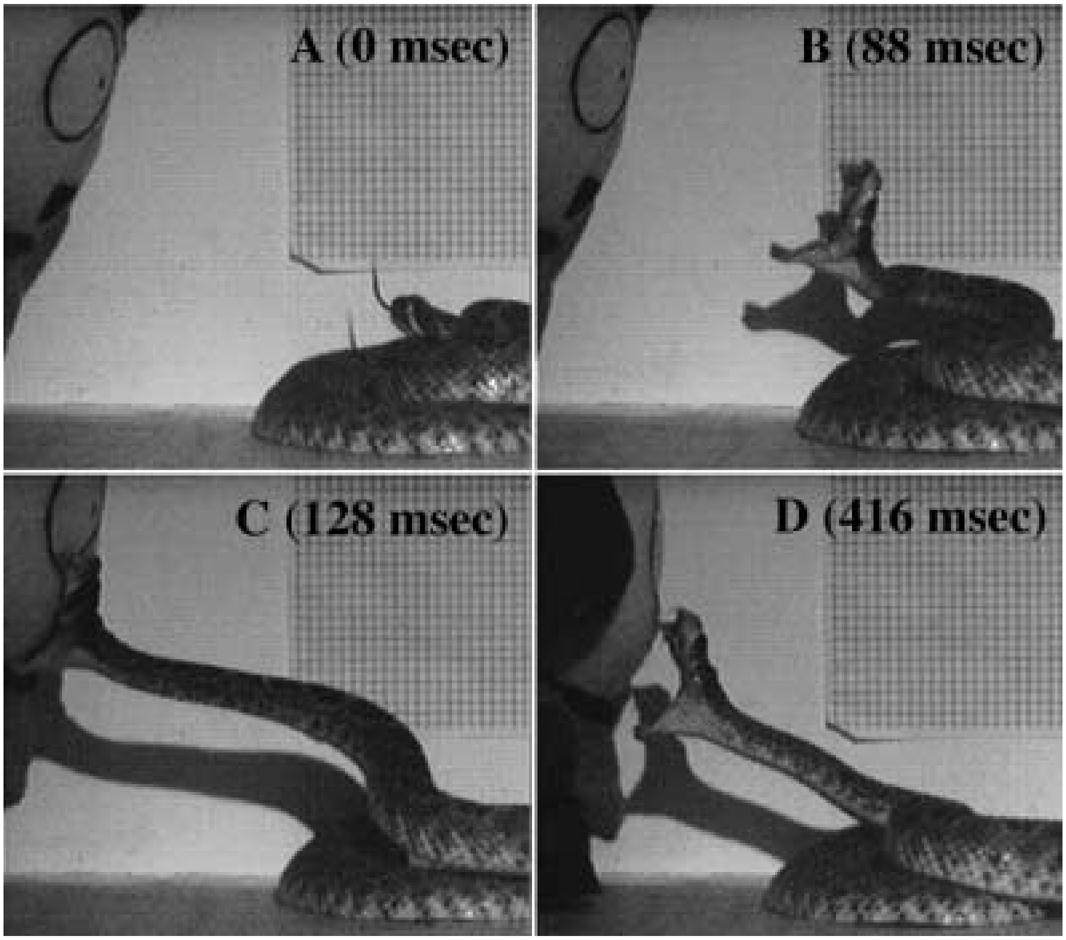

FIGURE 12: Representative sequence of a defensive strike directed at a large doll. (A) Onset, or launch of the strike, note the orientation and distance of the doll relative to the snake. (B) Mid-strike, note the large gape and the vertical orientation of the braincase. (C) Contact and fang penetration, note the sustained large gape and the vertical distance covered during the strike. (D) Withdrawal of the fang and release.

the braincase reached the far side of the mouse the gape angle decreased, thus bringing the fangs toward the now stationary lower jaws and the intervening mouse. The fangs were erected well before the snake contacted the mouse (mean = 48 msec, Table 9). During the nearly 30msec which elapsed between contact and fang penetration the fang angle reached its maximum (97.1°, Table 9). Following fang penetration the gape angle was reduced slightly by opposing vertical movements of the braincase and lower jaws (Fig. 10). These vertical movements stopped and there was a period of nearly pure horizontal displacement in both the braincase and lower jaws (Fig. 10). Fang withdrawal was achieved by opposing vertical motions of the lower jaws, and, more extensively, the braincase (Fig. 10). The defensive strikes directed at mice had a mean duration of fang penetration of 211.8 msec.

Using stationary scalation points near the distal tip of the lower jaw and braincase, the distance between the points could be calculated as gape distance (Fig. 11). The defensive strikes directed at mice produced a characteristic pattern of temporal variation in gape. Gape increased from the launch of the strike to contact. After contact the gape continued to increase as the braincase rotated over the mouse; the greatest accelerations and velocities occurred as the braincase reached the apex of its trajectory over the mouse (Fig. 11).

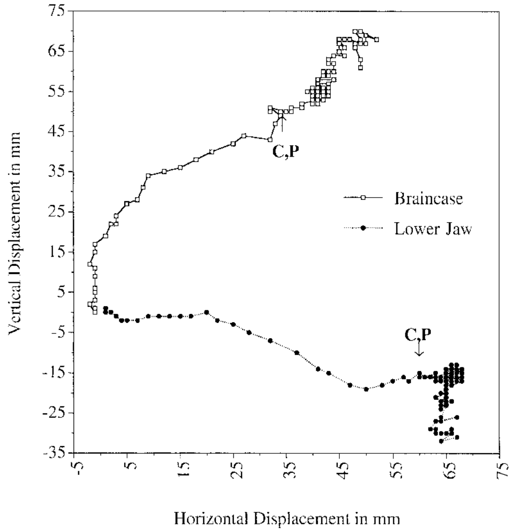

FIGURE 13: Representative displacement of the braincase and lower jaw during a defensive strike directed at a large doll. Note the greater vertical displacement of the braincase, the simultaneous contact and fang penetration, and the limited displacement after contact. C- frame of first contact; P- frame of fang penetration.

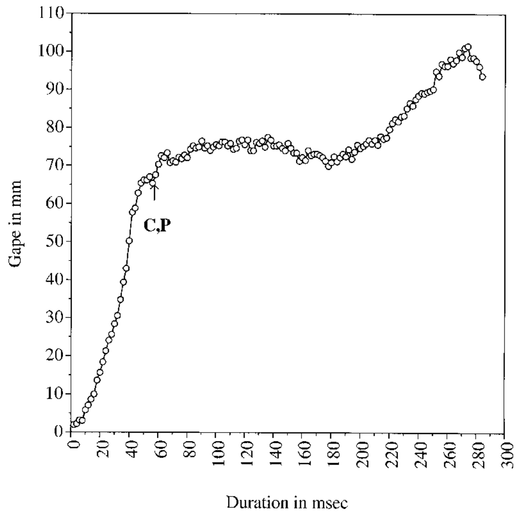

FIGURE 14: Representative pattern in changes of gape during a defensive strike directed at a large doll. Note how the gape shows rapid increase prior to contact and stays relatively constant after contact until the increase in gape associated with withdrawal of the fang and release. C- frame of first contact; P- frame of fang penetration.

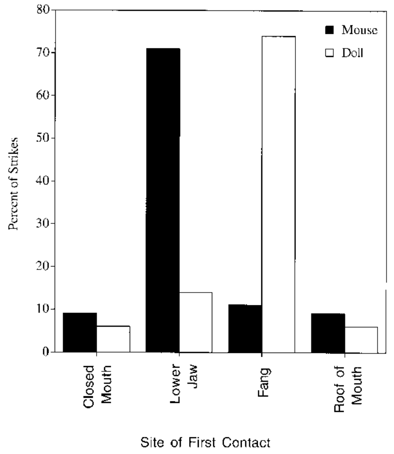

FIGURE 15: Distribution of strikes by first contact point on the snake. Note the prevalence of fang first contact strikes at the large doll, and lower jaw first contact strikes at the mouse. Closed mouth contact is defined as contact with the nasal or mental surface; roof of mouth is defined as that area on the upper jaw caudal to the fangs.

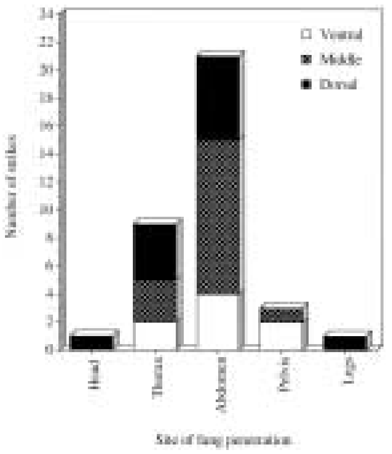

FIGURE 16: Distribution of strikes by first contact point on the mouse. The mouse was divided into five cranial- caudal zones (head, thorax, abdomen, pelvis, legs) and three dorsal- ventral levels (dorsal, middle, ventral). Note the prevalence of strikes at the abdominal zone, and at the middle level of the mouse.

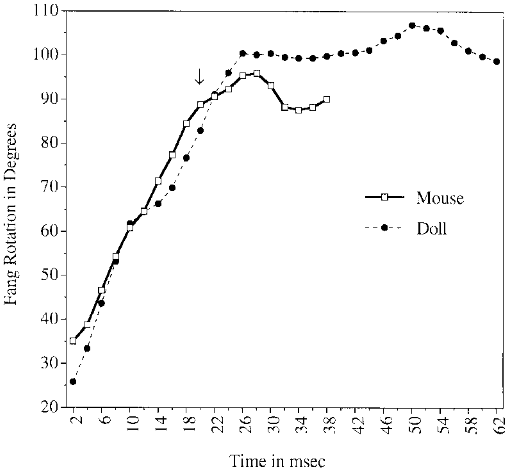

FIGURE 17: Rotary displacement of the fangs relative to the supralabial scales in two representative strikes. Note the similar rates of rotary displacement, the slight plateau in fang rotation that occurs near sixty degrees, and the final variation in fang angle that precedes penetration. For the mouse strike, initial contact is indicated by the arrow, for both strikes, the final point represents fang penetration.

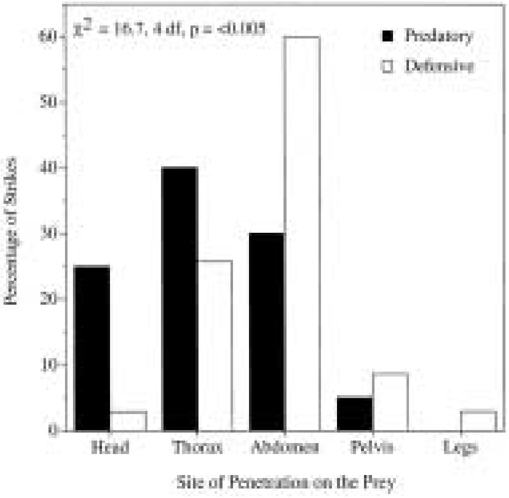

FIGURE 19: Site of fang penetration from 55 strikes launched by *Crotalus atrox* at mice. Significant differences in the relative distribution of target penetration sites between predatory (dark bars) and defensive (open bars) strikes arose in part due to the prevalence of fang penetration in the abdomen during defensive strikes.

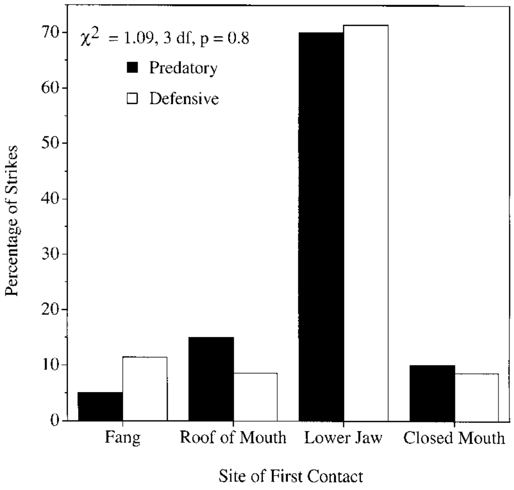

FIGURE 18: Site of first contact from 55 strikes launched by *Crotalus atrox* at mice. Predatory (dark bars) and defensive (open bars) strikes have similar distributions of contact sites, with lower jaw contact occurring in the majority of the strikes.

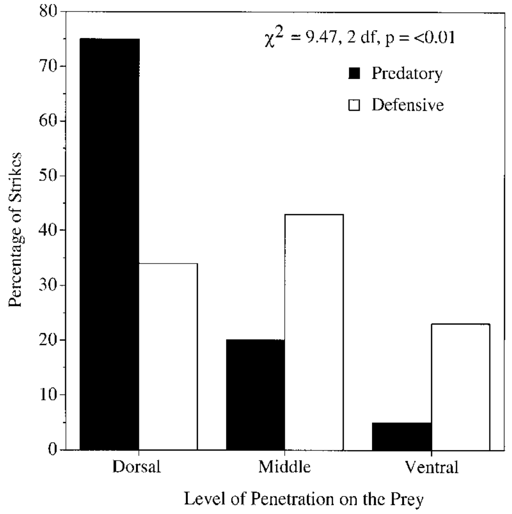

FIGURE 20: Level of penetration from 55 strikes launched by *Crotalus atrox* at mice. Significant differences in the relative distribution of penetration levels between predatory (dark bars) and defensive (open bars) strikes arose due to the prevalence of dorsal penetration in predatory strikes.

TABLE 8: Level of fang penetration on the prey's body. Note the prevalence of fang penetration on the dorsal surface of the mice.

	Dorsal	Middle	Ventral
Large Prey (n=20)	75	20	5
Small Prey (n=20)	40	55	5
2 = 5.4, 2 df, p = >0.05			
Extended Posture (n=16)	62.5	31.3	6.3
Coiled Posture (n=24)	54.2	41.7	4.2
2 = 0.5, 2 df, p = >0.97			
Prey Released (n=27)	63	37	0
Prey Held (n=13)	46	38.5	15.4
2 = 4.3, 2 df, p = >0.10			
Unilateral Strike (n=14)	57.1	28.6	14.3
Bilateral Strike (n=26)	57.7	42.3	0
2 = 3.7, 2 df, p = >0.10			
Prey Parallel (n=15)	73.3	20	6.7
Prey Perpendicular (n=10)	40	50	10
Prey Oblique (n=15)	53.3	46.7	0
2 = 4.5, 4 df, p = >0.25			

TABLE 9: Analysis of the influence of target size on the defensive strike. Kinematic data are in the form of mean (s.e.) for strikes on mice (N = 35) and the large doll (N = 35). Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. F values given for the ANOVA results all have 1 df, as do the χ^2 values.

Variable	Mouse	Doll	
Distance from target at launch	3.80 (0.52)	12.66 (1.24)	F = 60.59, p = <0.003
Horizontal distance to contact	4.66 (0.47)	10.10 (1.05)	F = 27.62, p = <0.003
Vertical distance to contact	3.06 (0.28)	6.79 (0.52)	F = 52.99, p = <0.003
Horizontal distance after contact	8.61 (0.79)	2.93 (0.48)	F = 50.78, p = <0.003
Vertical distance after contact	2.01 (0.42)	1.15 (0.23)	F = 3.71, p = 0.06
Total horizontal distance	13.22 (0.88)	12.39 (1.03)	F = 0.58, p = 0.45
Total vertical distance	4.98 (0.57)	7.88 (0.52)	F = 16.45, p = <0.003
Duration of fang penetration	211.8 (25.0)	189.5 (16.1)	F = 2.92, p = 0.03
Duration from contact to fang penetration	29.9 (3.3)	11.6 (4.3)	F = 3.65, p = 0.01
Duration from fang erection to contact	48.2 (2.6)	48.8 (3.5)	F = 0.32, p = 0.86
Gape angle at contact	87.7 (5.8)	110.4 (6.6)	F = 3.35, p = 0.02
Gape angle at fang withdrawl	99.1 (5.3)	137.9 (3.7)	F = 3.20, p = 0.02
Maximum gape angle	128.2 (2.9)	145.7 (2.9)	F = 0.94, p = 0.45
Fang angle at penetration	86.2 (2.6)	94.1 (2.5)	F = 2.60, p = 0.05
Maximum fang angle	97.1 (3.1)	98.1 (2.5)	F = 2.17, p = 0.08
Maximum velocity of strike	245.3 (13.8)	349.3 (18.6)	F = 2.59, p = 0.05
Maximum rotational velocity of fang	9.5 (0.5)	10.2 (0.6)	F = 0.97, p = 0.43

The gape decreased both before and after fang penetration (Fig. 11). After the decrease in gape associated with fang penetration there was a period (from 130-200 msec in Fig. 11) of relative gape constancy. Subsequently the gape increased rapidly as the braincase and lower jaws were withdrawn from the mouse (Fig. 11).

Kinematics of defensive strikes at large doll.- The strikes directed at the large doll were fairly consistent. Rather than striking horizontally for

TABLE 10: Significant Pearson correlation coefficients determined for the defensive strikes directed at mice and the large stuffed doll. Note that most of the variables are significantly correlated.

Variable	Co-Variable	r (p)
Distance from target at launch	Horizontal distance to contact	0.91 (<0.01)
	Vertical distance to contact	0.71 (<0.01)
	Horizontal distance after contact	0.51 (<0.01)
	Total horizontal distance	0.49 (<0.01)
	Total vertical distance	0.47 (<0.01)
	Duration from contact to fang penetration	0.53 (<0.01)
	Gape angle at contact	0.48 (<0.01)
	Gape angle at fang withdrawl	0.44 (0.02)
	Maximum gape angle	0.52 (<0.01)
	Maximum velocity	0.64 (<0.01)
Horizontal distance to contact	Vertical distance to contact	0.55 (<0.01)
	Horizontal distance after contact	0.43 (0.03)
	Total horizontal distance	0.58 (<0.01)
	Duration from contact to fang penetration	0.48 (<0.01)
	Gape angle at contact	0.43 (0.03)
	Gape angle at withdrawl	0.42 (0.04)
	Maximum velocity	0.59 (<0.01)
Vertical distance to contact	Horizontal distance after contact	0.47 (<0.01)
	Total vertical distance	0.82 (<0.01)
	Duration from contact to fang penetration	0.49 (<0.01)
	Gape angle at contact	0.47 (<0.01)
Horizontal distance after contact	Duration from contact to fang penetration	0.51 (<0.01)
	Gape angle at fang withdrawl	0.42 (0.03)
Vertical distance after contact	Total vertical distance	0.47 (<0.01)
	Gape angle at contact	0.43 (0.02)
Duration from contact to fang penetration	Duration from fang erection to contact	0.52 (<0.01)
	Gape angle at contact	0.74 (<0.01)
Fang angle at penetration	Maximum fang angle	0.72 (<0.01)

the legs of the large doll, almost every strike was directed at the face of the large doll which necessitated a prominent vertical component to the strike (Fig. 12). Prior to contact there was extensive displacement of the braincase about the vertebral column, and of the lower jaw about the braincase. In some cases these displacements resulted in the oral cavity being directed purely vertically during the strike; in every case a large gape angle was achieved before contact was made with the large doll. First contact was made with the fang in 26/35 (74%) of the strikes (Fig. 12). Following first contact the momentum of the snake drove the braincase and jaws apart on the surface of the large doll, resulting in a slight increase in gape angle. Little movement was observed following the initial impact until the snake thrashed laterally and managed to increase its gape slightly thus withdrawing the fangs (Fig. 12).

The defensive strikes were initiated while the large doll was relatively removed from the snake (mean = 12.7 cm); and most were launched while the doll was moving toward the snake, resulting in a horizontal distance to contact which was lower than the distance at launch (Table 9). The strikes always included a prominent vertical component before contact (mean = 6.8 cm); but the large inertia of the large doll resulted in little horizontal or vertical movement after contact

TABLE 11: Analysis of defensive strikes directed at the mouse-sized doll. Kinematic data given in the column "mouse-sized doll" are in the form mean (s.e.) for strikes (N = 10) directed at the mouse-sized doll. Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. Values given in the other two columns are the results of ANOVA with the respective data sets, reported in the form F-value, p; for this analysis the F-values have df = 2.

Variable	Mouse	Mouse-Size Doll	Doll
Distance from target at launch	2.41, 0.13	5.52 (1.00)	8.90, <0.003
Horizontal distance to contact	2.54, 0.12	6.34 (1.11)	3.30, 0.08
Vertical distance to contact	6.61, 0.01	1.58 (0.42)	27.16, <0.003
Horizontal distance after contact	0.12, 0.73	7.99 (1.99)	13.70, <0.003
Vertical distance after contact	0.37, 0.55	1.48 (0.73)	0.34, 0.57
Total horizontal distance	0.28, 0.60	14.33 (2.54)	0.69, 0.41
Total vertical distance	2.89, 0.10	3.00 (0.83)	20.95, <0.003
Duration of fang penetration	1.00, 0.32	164.0 (14.5)	0.66, 0.42
Duration from contact to fang penetration	0.43, 0.52	35.8 (12.3)	5.43, 0.03
Duration from fang erection to contact	0.28, 0.60	52.0 (10.3)	0.14, 0.71
Gape angle at contact	0.10, 0.75	83.9 (9.7)	4.21, 0.05
Gape angle at fang withdrawl	0.38, 0.54	105.9 (6.5)	15.92, <0.003
Maximum gape angle	1.73, 0.20	120.9 (2.7)	19.30, <0.003
Fang angle at penetration	0.02, 0.88	87.2 (11.4)	0.84, 0.37
Maximum fang angle	2.88, 0.10	108.6 (6.0)	3.21, 0.08
Maximum velocity of strike	0.57, 0.45	225.2 (10.8)	12.20, <0.003
Maximum rotational velocity of fang	1.67, 0.20	10.8 (0.6)	0.30, 0.59

TABLE 12: Analysis of the influence of Behavioural context on the strike. Kinematic data are in the form of mean (s.e.) for defensive (N = 35) and predatory (N = 20) strikes at similar sized mice. Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. F values given for the ANOVA results all have 1 df, as do the χ^2 values.

Variable	Predatory	Defensive	
Distance from target at launch	6.98 (0.84)	3.8 (0.52)	F = 11.6, p = <0.003
Horizontal distance to contact	8.30 (0.84)	4.66 (0.47)	F = 16.8, p = <0.003
Vertical distance to contact	1.83 (0.24)	3.06 (0.28)	F = 8.8, p = <0.003
Horizontal distance after contact	2.99 (0.37)	8.61 (0.79)	F = 26.6, p = <0.003
Vertical distance after contact	1.72 (1.90)	2.01 (2.46)	F = 0.21, p = 0.65
Total horizontal distance	11.19 (0.79)	13.22 (0.88)	F = 2.43, p = 0.13
Total vertical distance	3.44 (0.48)	4.98 (0.57)	F = 3.34, p = 0.07
Duration of fang penetration	176.7 (29.4)	211.8 (25.0)	F = 0.64, p = 0.43
Duration from contact to fang penetration	44.0 (18.2)	29.9 (3.3)	F = 0.96, p = 0.33
Duration from fang erection to contact	58.3 (9.5)	48.2 (2.6)	F = 1.65, p = 0.21
Gape angle at contact	65.3 (6.2)	87.7 (5.8)	F = 6.15, p = 0.02
Gape angle at fang withdrawal	84.5 (5.2)	99.1 (5.3)	F = 2.47, p = 0.12
Maximum gape angle	93.3 (3.9)	128.2 (2.9)	F = 53.0, p = <0.003
Fang angle at penetration	90.1 (3.9)	86.2 (2.6)	F = 0.74, p = 0.39
Maximum fang angle	92.4 (18.7)	97.1 (3.1)	F = 0.98, p = 0.33
Maximum velocity of strike	331.0 (18.7)	245.3 (13.8)	F = 13.8, p = <0.003
Maximum rotational velocity of fang	9.4 (0.8)	9.5 (0.5)	F = 0.04, p = 0.84

TABLE 13: Comparison of two compound categories of predatory strike. Kinematic data are in the form of mean (s.e.) for the two categories: small prey/coiled posture/ bilateral fang penetration (N = 9), and large prey/extended posture/unilateral fang penetration (N = 5). Distances are in cm, durations are in msec, angles are in degrees, velocity of the strike is in cm/sec, and rotational velocity of the fang is in degrees/msec. F values given for the ANOVA results all have 1 df, as do the χ^2 values.

Variable	Small Prey Coiled Posture Bilateral Strike	Large Prey Extended Posture Unilateral Strike	
Distance from target at launch	7.30 (1.28)	7.46 (2.18)	F = 0.01, p = 0.95
Horizontal distance to contact	8.77 (1.25)	8.94 (2.23)	F = 0.01, p = 0.95
Vertical distance to contact	1.52 (0.19)	1.59 (0.56)	F = 0.02, p = 0.90
Horizontal distance after contact	3.49 (0.45)	2.67 (1.31)	F = 0.52, p = 0.48
Vertical distance after contact	0.93 (0.63)	3.54 (1.20)	F = 4.62, p = 0.05
Total horizontal distance	12.26 (1.24)	11.24 (1.29)	F = 0.28, p = 0.61
Total vertical distance	2.37 (0.70)	5.13 (1.56)	F = 3.49, p = 0.09
Duration of fang penetration	203.5 (48.5)	255.5 (67.8)	F = 0.39, p = 0.55
Duration from contact to fang penetration	27.1 (9.6)	127.2 (62.5)	F = 4.55, p = 0.05
Duration from fang erection to contact	56.0 (11.6)	82.4 (15.7)	F = 1.84, p = 0.20
Incidence of prey "holding"	11%	20%	c2 = 0.09, p>0.75
Gape angle at contact	81.9 (4.4)	34.4 (9.2)	F = 28.29, p <0.003
Gape angle at fang withdrawl	90.6 (8.3)	90.8 (18.2)	F = 0.00, p = 0.99
Maximum gape angle	91.9 (4.9)	93.9 (9.0)	F = 0.05, p = 0.83
Fang angle at penetration	75.7 (6.5)	101.7 (11.0)	F = 4.76, p = 0.05
Maximum fang angle	90.5 (4.0)	94.4 (2.8)	F = 0.43, p = 0.52
Incidence of fang repositioning	22%	80%	c2 = 4.40, p = 0.04
Maximum velocity of strike	335.5 (52.3)	291.5 (59.2)	F = 0.28, p = 0.61
Maximum rotational velocity of fang	9.2 (0.6)	11.7 (2.0)	F = 2.50, p = 0.14

(Table 9). Plotting a typical trajectory (Fig. 13) shows that relative to the lower jaw, the braincase goes through more vertical motion but less horizontal displacement. The end result is that the head was arched backwards with the lower jaws leading the strike (Fig. 12). Nevertheless, due to the curvature of the face of the large doll, the fangs made first contact in most strikes. The greatest velocity and acceleration were observed shortly before impact with the large doll; relative velocity and acceleration are given by the spacing between successive points in Figure 13. The diverging braincase and lower jaws produced a mean gape angle at contact of 110° (Table 9). The motions of the braincase and lower jaws after contact were largely vertical (Fig. 13) resulting in an increase in gape angle by approximately 30°. The mean duration from contact to fang penetration was low (11.6 msec) due to the prevalence of fang first contact; fang erection began nearly 49 msec prior to contact which gave the snake ample time to achieve fang angles of over 90° (Table 9). The mean total duration of fang penetration was 189.5 msecs (Table 9).

Gape distance was calculated using stationary scalation points near the distal tip of the lower jaws and braincase (Fig. 14). The defensive strikes directed at the large doll produced a fairly simple temporal pattern of gape change. There was an initial rapid increase in gape associated with the launch portion of the strike (Fig. 14). After contact with the large doll there was an extended phase (from roughly 60- 190 msecs in Figure 14) in which the gape was relatively constant. Beyond this the gape increased again, though more slowly than during the launch, as the snake expanded its mouth to withdraw the fangs (Fig. 14).

Quantitative comparison.- Of the 17 variables examined, six were significantly different between the two targets (Table 9), while another nine variables had probabilities below 0.09. Strikes directed at the large doll were faster, covered a greater distance before contact and a greater total vertical distance, had higher gapes, and involved greater fang rotation prior to penetration. Of the variables which were significantly different between mouse and large doll strikes, only the horizontal distance after contact was higher in defensive strikes directed at mice (Table 9).

The Pearson correlation coefficient analysis revealed significant correlations (defined as a probability of < 0.05) involving every variable except the duration of fang penetration and the maximal rotary velocity of fang erection (Table 10). The distance from target at launch had the highest number of significant correlations with other variables (10), but four other variables (horizontal distance to contact, vertical distance to contact, duration from contact to fang penetration, and gape at contact) were each significantly correlated with at least five other variables (Table 10).

Variation due to contact site.- The location of first contact site on the snake showed a clear pattern (Fig. 15). The majority (74%) of the strikes directed at the large doll involved first contact with the fangs, while most (71%) of the strikes directed at the mouse involved first contact with the lower jaws (Fig. 15). This difference in contact sites was significant (c^2= 31.45, df = 1, p < 0.01). In the majority (21/35 or 60%) of the defensive strikes directed at the mice the fangs penetrated the abdomen of the mouse; the thorax had the second highest incidence of fang penetration (9/35 or 26%). In the abdomen the fangs were more likely to penetrate near the dorsal-ventral midline, whereas fang penetration occurred most commonly in the dorsal portion of the thorax (Fig. 16).

Fang rotation.- The rotational erection of the fang exhibited a rather consistent pattern in the defensive strikes. There is an initial rapid rotation of the fang from retracted to approximately 60° (Fig. 17). This 60° plateau was more pronounced in large doll strikes, and within doll strikes was more pronounced in strikes that covered a greater distance before contact. After the 60° plateau fang erection continued until a fully erect level was reached; the final periods of the strike before fang penetration were always characterized by slight variation in the angle of the fang (Fig. 17). Maximal rotary velocity of the fang always occurred as the fang elevated to the 60° plateau. There was no significant difference in the velocity of fang rotation; however, the strikes directed at the large doll did have a significantly higher fang angle at penetration (Table 9).

Defensive strikes at a mouse-sized doll.- Strikes directed at the mouse-shaped doll covered a greater vertical distance than those directed at the mice, but this difference was not significant. None of the other 17 variables approached the Bonferroni adjusted cut-off probability of 0.05/17 or 0.003. A comparison of the mouse-shaped doll with the large doll reveals 7 of the 17 kinematic variables to be significantly different, with four other variables markedly different (Table 11). These same variables were found to be different between strikes directed at the large doll and the mice during the defensive trials.

Behavioural context.- After visual and tactile stimulation every snake exhibited typical crotaline defensive behaviours (e.g., Hayes and Duvall, 1991); an elevated coil, pronounced rattling and slow tongue flicks. Venom deposition was observed on the mouse after many of the strikes, but no quantitative measurements were taken. Post-strike, the snakes remained in a tight coil and continued rattling, showing no behavioural orientation toward the just-struck mouse.

Introduction of the mouse during predatory bouts elicited a suite of behaviours from the snake including; rapid tongue flicks, orientation of the head toward the mouse, and movement toward the mouse. Defensive behaviours were not observed during the predatory bouts. During many of the predatory trials the snakes were preferentially coiled against the Plexiglas partition; from this position strikes were launched immediately after introduction of the mouse so that many predatory bouts were completed within 2 seconds of the introduction of the mouse. Post-strike, all mice showed signs of envenomation (including partial paralysis and seizures), and died within a few minutes of being struck. All struck mice were subsequently ingested by the snake.

Comparison.- Predatory strikes were launched over a significantly greater horizontal distance (Table 12), but the defensive strikes incorporated significantly greater horizontal movement after prey contact (Table 12). While the total horizontal distance was greater for defensive strikes, this difference was not significant (Table 12). The vertical distance to contact was significantly greater in defensive strikes (Table 12); although vertical distance after contact and total vertical distance were greater in defensive strikes, these differences were not significant (Table 12). Defensive strikes included larger gapes, but only the maximum gape angle was significantly different (Table 12). No significant differences in durations were observed between the two classes of strikes; the mean duration between fang erection and contact and the mean duration between contact and fang penetration were longer in predatory strikes, but the mean duration of fang penetration was longer in defensive strikes (Table 12). Defensive strikes had a greater mean maximum fang angle, while predatory strikes had a greater mean fang angle at penetration; neither difference was significant (Table 12). Maximum rotational velocities of the fang were almost identical in the two classes of strikes (Table 12). Predatory strikes achieved a significantly greater maximum velocity than the defensive strikes (Table 12).

Out of the 20 kinematic variables examined, eight were significantly different between defensive and predatory strikes. Of the eight significantly different variables, two relate to contact sites between the snake and the mouse (level of fang penetration, site of fang penetration), the other six were angular or linear displacements quantified from the video records. Of these six displacements, three (distance from target at launch, horizontal distance to contact, maximum velocity) were significantly greater in predatory strikes, and three (vertical distance to contact, horizontal distance after contact, and maximum gape) were significantly greater in defensive strikes. Nine of the kinematic variables were measured prior to contact with the mouse, of these nine, five were significantly different between the two classes of strikes. Seven of the kinematic variables were measured between first contact with the mouse and fang penetration and, of these, one was significantly different. Four of the kinematic variables were directly related to fang penetration, and two of these were significantly different.

Contact sites.- In both defensive and predatory strikes, the lower jaw normally made first contact with the mouse (Fig. 18). In the majority of predatory strikes, the fangs penetrated on the dorsal portion of the mouse (Fig. 19). More diversity in level of fang penetration was observed in defensive strikes; the higher incidence of fang penetration at the middle level of the mouse was significantly different than in the predatory strikes (Fig. 19). Approximately 25% of predatory strikes made contact with the head of the mouse, a contact site that was very rare in defensive strikes (Fig. 20). Defensive strikes had a higher incidence of contact with the abdomen than did predatory strikes (Fig. 20); overall the site of first contact with the mouse was significantly different between the two classes of strikes.

DISCUSSIONS

In tests on venom regeneration following maximal manual venom expulsion, Kochva (1987) found that peak rates of venom synthesis occurred 4-9 days after expenditure, and returned to baseline after 2-3 weeks post-milking. The schedule for filming bouts was set up to allow each snake two weeks between strikes, thereby avoiding any behavioural influence of depleted venom reserves. This two-week interval also ensured that the snakes' hunger levels were appropriate for inducing predatory encounters (Murphy and Armstrong, 1978). Previous studies have not shown any kinematic differences associated with hunger levels in rattlesnakes (Dullemeijer, 1961; Hayes, 1993). Alving and Kardong (1994) suggested that rattlesnake behaviour may be altered by prolonged captivity, but Chiszar et al., (1993) found no significant differences in the predatory behaviour of zoo-bred and wild-caught specimens. Nevertheless, as a precaution, snakes used in this study were in captivity less than six months to combat any potential performance decay.

Qualitative and quantitative analyses of the high speed digital video of *Crotalus atrox* suggests that the strike can be divided into four kinematic phases; targeting, launch, contact, and fang penetration. These phases differ from those described by Kardong and Bels (1998) reflecting the narrower focus of the present study; while Kardong and Bels (1998) were interested in the entire body of the snake, and included a "retract" stage, the current study was restricted to the head and excluded fang withdrawal. As the term is used here, targeting refers to the behavioural triggering of the strike. Several studies have explored the sensory cues involved in rattlesnake predation (e.g., Chiszar and Scudder, 1980; Dickman et al., 1987; Hennessy and Owings, 1988; Hayes and Duvall, 1991; Kardong, 1992; Alving and Kardong, 1996; Haverly and Kardong, 1996). For this study we attempted to standardize the olfactory cues (by using targets with mammalian hair and hair oils) and the thermal cues (by using targets with temperatures above ambient before presentation) in an attempt to isolate physical size as a sensory cue. The launch phase refers to the kinematics of the rattlesnake head from the first motion directed at the target until the period of first contact. Two key kinematic events occur during the launch phase, the mouth is opened and the fangs are erected. The contact phase is that portion of the defensive strike between first contact with the target and fang penetration. Herein the term fang penetration is applied to that phase of the strike between first contact with the fangs and fang withdrawal.

The results of the present study also suggest that the strike of *Crotalus atrox* can be envisioned as having two distinct components; a behavioural response and a physical response. The behavioural response comprises the targeting and launch phases of the strike where there is clear qualitative and quantitative evidence that the snake is not only actively responding to the targets, but differentially responding due to perceptual information. The physical response represents the contact and fang penetration phases of the strike in which the kinematic displacements appear to be greatly influenced by the inertia of the snake's head and body. The structural flexibility of the rattlesnake skull is such that this inertia produces quantitatively different displacements between targets. The emphasis on the role of inertia in the physical response component of the strike should not be misinterpreted as a claim that forces resulting from coordinated cephalic and axial muscle contraction do not influence the kinematics.

Predatory strikes.- Our experimental design incorporated low size range (maximum of 2 gm) within each prey class, a size difference (10 gm) between the two prey classes which resulted in a clearly visible difference in overall size (Fig. 3), and a balanced design in which each snake struck equal numbers of small and large prey. This design was intended to provide two discrete classes of prey items, both of which fell within the normal prey range of every snake, and neither of which were large enough to induce defensive behaviours in the snakes. The procedures used to isolate the snakes and present the mice appeared to be successful in that all presented mice were struck, exhibited signs of envenomation and died within 5 minutes, and were ingested by the snakes while still in the filming cage. Furthermore, there were few incidences of snakes exhibiting defensive behaviours during the feeding bouts, and none of these episodes were analyzed.

Significant differences between strikes directed at small and large prey were only observed in one variable; strikes directed at small mice were more likely to penetrate the mouse's abdomen (Table 7). This difference may reflect that these mice were small targets relative to the width of the snake's head, resulting in differences in the physical response more than the behavioural response. Our results are in good agreement with those of Kardong and Bels (1998) who found little difference in the predatory strikes of *Crotalus viridis oreganus* directed at small and large mice. Kardong (1986a) reported that 17% of mice were held following predatory strikes of *C. v. oreganus*, the incidence of prey holding increased with smaller mice as well as with larger snakes. The overall incidence of prey holding we observed was higher than that reported by Kardong (1986a), and did not significantly differ by prey or snake size; however, most of the snakes used by Kardong were smaller (in many cases less than half the SVL) than those used in the present study. Prey holding by venomous snakes is often interpreted as occurring when the prey has little chance of effective retaliation (e.g., Klauber, 1956; Radcliffe et al., 1980), but the source of this behaviour is not always clear (e.g., Barr et al., 1988).

Small mice are the dominant prey item for *Crotalus atrox* (Beavers, 1976; Reynolds and Scott, 1982). Stomach contents indicate that *C. atrox* also preys upon amphibians, lizards, snakes, birds, larger mammals, and carrion (e.g., Klauber, 1956; Ernst, 1992); it remains to be seen if similar strikes are used when foraging for these other prey items. Hayes (1992b) found that during predatory strikes *C. v. viridis* was significantly more likely to "hold" a sparrow than it was a mouse, but no other details of the kinematics were provided.

Kardong (1986b) described unilateral strikes as one category of "flawed" strikes. We observed unilateral strikes in 35% of the predatory strikes by *Crotalus atrox*. In every case the snake used the penetrated fang as a pivot and rotated the contralateral side of the skull in both the frontal and transverse planes. The combination of these rotations elevated the free fang over the body of the mouse; rapid depression of the head then drove the fang into the mouse. These motions accounted for most of the kinematic differences in the contact phase of the strike- greater vertical distance after contact and greater duration from fang erection to contact in unilateral strikes- between unilateral and bilateral strikes (Table 2). Unilateral strikes were characterized by a lower gape at contact, which supports Kardong's (1986b) assessment that these strikes are kinematically flawed. Although unilateral strikes were significantly more common with small prey, there were no significant differences between bilateral and unilateral strikes in the contact sites or levels on either the snake or the prey.

Most previous studies of the rattlesnake strike, as well as almost all popular accounts, emphasize the coiled ambush aspect of prey capture (e.g., Van Riper, 1954; Kardong, 1986a; Kardong and Bels, 1998). The extended body posture and active pursuit we observed in this study has been described in both field and laboratory studies, particularly during rodent trailing (e.g., Klauber, 1956; Dullemeijer, 1962; Gillingham and Clark, 1981). Despite the importance of body coiling in accelerating the snake's head forward (Kardong and Bels, 1998; Cundall and Greene, 2000), little kinematic difference was observed between the coiled and extended strike (Table 3). The relatively close range over which the predatory strikes were launched may minimize the biomechanic advantage of the coiled posture. When the snake struck from the coiled posture its head moved further horizontally, whereas strikes launched from the extended posture had a greater vertical component (Table 3). In the extended strikes the snakes had a tendency to "drop down" onto the prey rather than to drive over it as in the coiled strike. This resulted in a higher, but not significantly so, incidence of fang penetration on the dorsal surface of the mouse in extended strikes (Table 8), occasional closed mouth contact (Table 6), and a significantly higher incidence of fang repositioning (Table 3).

General descriptions of the rattlesnake strike portray the prey being oriented perpendicular to the snake's head, yet prey orientation is seldom detailed in feeding studies. In Minton's (1969) study of the predatory strike of *Crotalus h. horridus*, he noted that most of the mice in his study were perpendicular to the snake and that mice moving parallel to the snake evoked defensive behaviours or unusual strikes. In this study, strikes delivered at parallel oriented prey differed in several respects which suggest a difference in behavioural response; these strikes covered shorter horizontal distance (Table 4), and had a higher incidence of fang penetration in the mouse's head (Table 8). It has long been recognized that the displacement of the palato-maxillary arch which erects the fangs also induces some rotation in the transverse plane so that the fang tips diverge from one another (e.g., Mitchell, 1861; Zamudio et al., 2000). This spread of the fang tips is often described as an advantage that increases the striking zone of the snake. While this may be true for strikes directed at perpendicularly oriented mice, mice, particularly small mice, oriented parallel to the snake's head appear to be more difficult to hit, at least with both fangs.

Kardong (1986a) reported that the predatory strike of *Crotalus v. viridis* most commonly landed on the thorax of mice. This was interpreted as a targeting behaviour which increased the effectiveness of the snake's venom by preferentially injecting it into the thoracic cavity and the sensitive tissue contained therein. Kardong supported this hypothesis in a subsequent paper (Kardong, 1996) which showed that mechanical damage from fang penetration alone was unlikely to disable or kill a mouse, a claim made indirectly by Minton (1969). In the current study, most of the mice were struck in the abdomen, not the thorax (Table 7). Hayes (1992a) examined the predatory strikes of *C. v. viridis* and found no preferential contact with the thorax, a result which may have been influenced by evasive movements of the prey.

Taken collectively, the results of the present study suggest that *Crotalus atrox* exhibits little modulation or fine tuning of its predatory strike, at least when directed at mouse-sized prey. To emphasize this we performed a three-way ANOVA examining the combined effects of prey size, snake posture, and unilateral versus bilateral strikes on each kinematic variable. No significant effects were found. To explore this further, we isolated two subsets of data, one consisting of strikes directed at large prey, launched from an extended posture, and resulting in unilateral fang penetration (N = 5), the other consisting of strikes directed at small prey, launched from a coiled posture, and resulting in bilateral fang penetration (N = 9). Four of the five specimens were represented in both data sets, the fifth only contributed a single strike to the small prey/coiled posture / bilateral fang penetration data set. Comparing these two data sets reveals only one kinematic variable- the gape angle at contact- to be significantly different (Table 13).

Our conclusion that the predatory strike of *Crotalus atrox* is characterized by little modulation or fine tuning is further supported by our finding of few corrections within these strikes. Given our definition of a mid-strike correction, only two examples were observed in over 100 recorded strikes. In both cases only relatively modest correction of the head was observed (Fig. 8). Kardong (1986b) found no corrections in the head's path of travel during strikes by *C. v. oreganus*. A subsequent study of *Vipera ammodytes* by Janoo and Gasc (1992) described multiple strikes, as were observed in the present study, but no correction. Although we did observe mid-strike correction in *C. atrox*, the relative scarcity of this behaviour and the low magnitude of the corrective displacement, is similar to the patterns described by Kardong (1986b) and Janoo and Gasc (1992).

Defensive strikes.- Comparison of the defensive strikes revealed differences in three of the strike phases. Differences in the targeting phase are reflected in the finding that defensive strikes directed at the large doll were launched from a significantly greater distance (by a factor of almost four) than were those directed at the mouse or mouse-sized doll (Table 9). Furthermore, the motion of the two targets at the onset of the strike was different; strikes at the large doll were launched mainly while the doll was advancing toward the rattlesnake, whereas those directed at the mouse were launched while the mouse was being retracted from the snake.

There was little apparent qualitative difference in the motion of the fangs during the launch portion of strikes directed at the different targets. The mean fang angle at penetration was approximately 8° higher in strikes directed at the large doll, though maximum fang angle was not significantly different in the two strikes (Table 9). The two kinematic variables associated with fang angle were not significantly correlated with any other variable; as such, the greater fang rotations recorded from large doll strikes can not be explained by the greater duration or distances associated with these strikes. The rotary kinematics of the fangs were similar in the launch phase of the mouse and large doll strikes (Fig. 17), but the fangs remain erect for a longer duration in strikes directed at the doll (Fig. 17, Table 9). Beyond the (relatively earlier) point of contact in mouse strikes the fang rotation in mouse strikes is lower in magnitude and higher in variation (Fig. 17). This suggests that some of the motions of the braincase relative to the mouse during the contact phase may be influencing the position of the fangs.

The opening of the mouth during the launch phase of defensive strikes directed at the mouse involved fairly symmetric motions of the braincase and lower jaws (Fig. 10). The kinematics of the lower jaws during large doll strikes is similar to that observed during mouse strikes; however, during doll strikes the braincase moves over a greater vertical distance (Fig. 13). This differential displacement of the braincase, coupled with the significantly greater vertical trajectory of the strikes directed at the doll (Table 9) result in distinctly different positions of the head at contact. The small, relatively cylindrical shape of the mouse's body combined with the symmetrical gape and roughly horizontal posture of the snake's head during mouse strikes (Fig. 9) maximized the chance that the lower jaws or roof of the snake's mouth will make first contact with the mouth (Fig. 16). The asymmetric gape observed during the large doll strikes, combined with the vertical component of the strike and the rounded contour of the target, accounted for the high incidence of fang first contact (Fig. 15). The gape angle at contact was almost 30° higher in large doll strikes, and the maximum gape angle was also greater, though not significantly so (Table 9). We could not determine if the greater vertical component of the strikes directed at the large stuffed doll were a result of the snake's targeting the artificial eyes (e.g., Herzog and Bern, 1992) located on the expanded face.

The contact portion of the defensive strike was the most variable. In *Crotalus atrox*, the contact phase is rarely present in strikes directed at large targets, due to the prevalence of fang first contact (Fig. 15). The defensive strikes directed at the mouse were kinematically more complex due to the initial contact with the lower jaw (Fig. 9). The motion of the braincase over the mouse (Figs. 9,10) may be produced exclusively by inertial forces producing first rotation of the skull about the lower jaw contact point, then flexion of the jaw joints. Alternatively, activation of some of the jaw adductors may function to decrease the gape, thereby bringing the fangs into contact with the far side of the mouse. Kardong et al (1986) documented electrical activity in the jaw adductors of *C. durissus* during the later portion of the strike, but their results can not be interpreted relative to the kinematics presented herein. The sharp change in direction of the braincase immediately prior to fang penetration (Fig. 10) is suggestive of muscle, not inertial, forces.

The different motions of the braincase during the contact phase of the strike resulted in several significant differences between the quantitative features of the mouse and large doll strikes. Mouse strikes had a greater horizontal and vertical distance after contact, and a greater total horizontal distance (Table 9). The duration from contact to fang penetration was higher in strikes directed at the mouse (Table 9), but not significantly so. In *Crotalus atrox*, the fang penetration phase of the strike was kinematically similar in defensive strikes at large dolls and mice. In both, the early portions of fang penetration were associated with changes in gape: a slight increase during large doll strikes (Fig. 14) and a larger decrease in gape during mouse strikes (Fig. 11). The fang penetration phases of both defensive strikes were characterized by a period of relatively static gape (Figs. 11,14). In the mouse strikes, this relatively static gape was lower than observed in the large doll strikes, leading to a more pronounced displacement during fang withdrawal in the former. There was no significant difference in the duration of fang penetration between the two targets, nor was this variable correlated with any other feature (Tables 9,10).

In this study of defensive strikes, the majority of the strikes at the mouse involved fang penetration in the abdomen (Fig. 16). The lack of significant differences among the different contact sites on the mouse indicate that the differential mechanical properties of the mouse's body (e.g., relative abundance of bone, thickness of muscle layer, etc.) do not alter the kinematics of the defensive strike.

This study represents the first quantitative analysis of the defensive strike of the rattlesnake. Our results support early descriptions of the influence of target size on the strike (Mitchell, 1861), as well as more recent depictions of the strike (e.g., Kardong, 1986a). The use of a dead mouse as the target of a defensive strike did not appear to influence the kinematics of the strike. Only one variable, the vertical distance to contact (Table 11) was markedly different (though not significant) between strikes directed at a dead mouse and a mouse-sized doll. Presumably this difference reflects slight variation in the presentation of the two targets. The marked similarity in the kinematics of defensive strikes directed at dead mice and a mouse-shaped doll, and the common differences between these strikes and those directed at the large doll, indicate that the rattlesnake's defensive strike was not corrupted by the use of a potential prey item as a target.

Behavioural context.- This analysis of *Crotalus atrox* revealed significant differences in the kinematics of strikes performed under different behavioural contexts. Six of the 17 measured kinematic variables examined were significantly different (Table 12) and two of the three categorical kinematic variables examined were significantly different, although the strikes were directed at similar targets. While kinematic variation was evident in both the defensive and predatory strikes, the differences between these two kinematic classes were great enough to create two distinct strike models.

Typically the snake was close (mean 3.8 cm) to the target when launching a defensive strike; initial acceleration included a horizontal (mean 4.66 cm) and substantial vertical (mean 3.06 cm) component prior to contact with the mouse (Table 12). During defensive strikes the snake generally contacted the mouse with its lower jaws first (Fig. 18) and with a large gape angle (mean 87.7 degrees, Table 12); this gape angle continued to expand to its maximum (mean 128.2 degrees, Table 12) as the braincase moved both horizontally and vertically in a pronounced rotation over the mouse, resulting in fang penetration on the far side of the mouse (Fig. 19). The snake's forward momentum, in part influenced by the velocity of the defensive strike (mean 245.3 cm/s) carried the snake horizontally (mean 8.61 cm) after contact with the mouse (Table 12).

Predatory strikes, in contrast, were launched from further away from the mouse (mean 6.98 cm), and were dominated by horizontal (mean 8.3 cm) rather than vertical (mean 1.83 cm) displacements (Table 12). Although in the majority of predatory strikes the lower jaws were the first contact point (Fig. 18), the gape upon initial contact was smaller (mean 65.3 cm), and the rotation of the braincase was more modest, resulting in a smaller maximum gape (mean 93.3 degrees) and fang penetration on the dorsal surface of the mouse (Table 12, Fig. 20). Although predatory strikes attained a higher maximum velocity (mean 331.0 cm/s), the snake did not travel as far horizontally after contact (mean 2.99 cm) (Table 12).

This comparison represents the first documentation of quantitative differences between defensive and predatory strikes that can be attributed to behavioural context. LaDuc (2000) also used high speed video analysis to compare defensive and predatory strikes in *C. atrox*; however, LaDuc used a large stuffed doll as the target for the defensive strikes and an anesthetized mouse for the target in predatory strikes (the manual manipulation of which he reports as inducing rattling). Without controlling for differences between the targets (including size, texture and motion), differences in strike kinematics cannot be attributed to behavioural context.

LaDuc (2000) followed common practice in defining predatory strikes by target, under the assumption that any strike directed at a potential prey item must be predatory. The results of this study clearly show that *C. atrox* uses different strikes (defensive and predatory) when a mouse is presented under different behavioural contexts. Eight statistically significant differences, in addition to qualitative differences between the classes of strikes, were observed between strikes launched at similar-sized mice during predatory and defensive encounters.

LaDuc (2000) questioned whether predatory or defensive strikes were likely to be faster. Due to the technological challenges involved, few studies have provided reliable values for the velocity of the rattlesnake strike. Van Riper (1954) reported values of 247 cm/sec, while LaDuc (2000) gave values of 261 cm/sec and 371 cm/sec for predatory and defensive strikes, respectively. These values are in general agreement to those obtained in the current study (mean 331.0 cm/s for predatory strikes and 245.3 cm/sec for defensive strikes, Table 12). The combined results of these studies suggest that rattlesnakes strike with a fairly constant acceleration, and that the differences reported in velocity are due primarily to differences in distance to the target, rather than different speeds for different behavioural contexts. Velocities deduced from the displacement graph published by Kardong and Bels (1998) for predatory strikes in *Crotalus. v. oreganus* are much slower (approx. 100 cm/sec) which may reflect the smaller size of their specimens or interspecific variation among rattlesnakes- Lester (1955) suggested that *C. atrox* strikes faster than other rattlesnakes.

Kardong and Bels (1998) argued that during the predatory strike *C. v. oreganus* slowed down slightly immediately prior to contact, and that peak velocities were obtained as the braincase moved over the prey. No such pre-contact deceleration was observed in either the predatory or defensive strikes recorded from *C. atrox* (Fig. 3), nor is this deceleration evident in the velocity graphs presented by Kardong and Bels (1998). Post-contact acceleration of the braincase is possible, but reflects a force-couple between the snake's lower jaws and the target, and thus would be highly variable.

In this study a suite of behaviours, taken largely from Hayes and Duvall (1991) and including body posture, sound production and tongue flick rate, were used to define the behavioural context of the strike. Several researchers have used post-contact neck arching as a key feature of a predatory strike; lack thereof is thought to be indicative of a defensive strike (e.g., Kardong, 1986a; Janoo and Gasc, 1992). In the present study post-contact neck arching was observed in every strike, although it was more pronounced in defensive strikes (Figs. 6,9). The disparity between our results and the previous studies may arise from the use of large, relatively-flat targets in the earlier studies (e.g., Kardong, 1986a; Janoo and Gasc, 1992; LaDuc, 2000). These large targets may physically preclude the braincase from rotating over the target (Mitchell, 1861); neck arching without rotating the braincase could result in hyperflexion of the braincase about the vertebral column, particularly with the large gapes associated with defensive strikes. A smaller defensive target does not impose the same constraints. In this study, the greater rotation of the braincase observed during defensive strikes was always accompanied by prominent neck arching (Fig. 9). Neck arching was present in the predatory strikes (in agreement with previous claims), but the reduced rotation of the braincase led to concomitant reduction in neck arching.

The use of a live unrestrained mouse in the predatory trials prevented rigorous control of its position relative to the snake during the strike, which presumably added some kinematic variation. As part of the analysis of the predatory strikes, the effect of the mouse's orientation relative to the snake (defined as parallel, perpendicular, or oblique) as well as the body posture of the snake (defined as extended or coiled) were examined and found to have minimal influence. Thus the more controlled presentation of a perpendicularly orientated mouse target to a coiled rattlesnake during the defensive strike could not account for the significant differences observed between the predatory and defensive strikes (Table 12). The mice used in defensive strikes were elevated approximately 2 cm off the floor of the cage due to their attachment to a small wooden platform; this elevation may account for the difference between defensive and predatory strikes in the snake's vertical displacement prior to contact (Table 12). The average fang penetration duration in predatory (0.18 s) and defensive (0.21 s) strikes were not significantly different (Table 12), but did fall within the previously reported range from 0.03 to 0.71 s (e.g., Rowe and Owings, 1990; Kardong and Bels, 1998; Hayes et al., 2000).

Rattlesnakes are ambush predators which rely on the element of surprise provided by their quick strikes. Envenomation, the rattlesnake's prey capture technique, depends on fang penetration. Our observations suggest that predatory strikes are more accurate than defensive strikes in terms of the percent of strikes which impact the target. This study suggests that one of the key kinematic differences between the strike classes is the relatively larger gape in defensive strikes. The large gape of a defensive strike may serve to make the snake appear larger and more intimidating; an open-mouth posture is a common defensive behaviour in snakes (e.g., Carpenter and Ferguson, 1977; Greene, 1988), though not in rattlesnakes. The wide gape in defensive strikes may maximize the chance that the snake's mouth will contact the target; fang contact may not be critical, since any contact may be enough to terminate an encounter. Two important consequences of the wide gape are increased torque of the braincase about the lower jaw (leading to greater horizontal and vertical displacement) and minimal friction between the braincase and target prior to fang penetration.

The smaller gape characteristic of predatory strikes may both facilitate accurate fang positioning and increase the snake's ability to quickly launch a second strike if necessary. A smaller gape at prey contact means a greater chance that the braincase, and even the fang sheath, will drag across the mouse (slowing the snake) and results in a reduced torque of the braincase about the lower jaw.

This interpretation of strike kinematics suggests that predatory strikes will show little variation among prey items (since accurate fang positioning is the goal of all predatory strikes), whereas the variation in size, body shape and relative aggression among the different predators and harassers of rattlesnakes would result in substantial kinematic diversity in defensive strikes. This analysis also suggests that the distinct differences in targeting and kinematics could result in differences in the impulse experienced by both the fangs and target during the strike.

This study focused on *Crotalus atrox*, which is one of the larger rattlesnakes and an ecological generalist. It would be interesting to see if this same pattern held in smaller, more ecologically specialized crotalines such as *Crotalus pricei*, which only reaches a maximum length of 66 cm and feeds on sceloporine lizards (Ernst, 1992). Additional comparisons with other major lineages, such as elapids, may reveal aspects of the ecological and evolutionary diversity of snakes. This study of *C. atrox* only examined strikes against mice. Western diamondbacks feed on a range of prey items, from rabbits to lizards, and a number of different animals can antagonize, or prey upon, western diamondbacks (Ernst, 1992). As such, our results do not reflect the full range of predatory and defensive behaviours, and, accordingly, probably underestimate the variation in strike behaviours.

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FIRST REPORT ON THE HERPETOFAUNA OF PULAU AUR, JOHOR, WEST MALAYSIA

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ABSTRACT.– With the exception of Tweedie's (1983) account of *Calamaria lovii,* published accounts on the herpetofauna of Pulau Aur, located 63 km off the south-east coast of peninsular Malaysia in the South China Sea did not exist prior to this report. The only species known from the island were based on the museum records of *Limnonectes blythii, Mabuya multifasciata, Bronchocela cristatella, Gehyra mutilata, Varanus nebulosus* and *Ahaetulla prasina* deposited in the Raffles Museum of Biodiversity Research. A short expedition to the island on 15-16 July 2001 yielded an additional 12 species, comprising 10 lizards and two snakes: *Limnonectes blythii*; *Bronchocela cristatella; Cnemaspis* cf. *nigridia;Cosymbotus platyurus; Cyrtodactylus consobrinus*; *Gehyra mutilata; Gekko monarchus; Hemidactylus frenatus; Dasia olivacea; Emoia atrocostata; Lygosoma bowringii; Mabuya multifasciata; Sphenomorphus scotophilus; Varanus nebulosus; Varanus salvator; Ramphotyphlops* cf. *braminus; Calamaria lovii* and *Macropisthodon flaviceps*).

KEY WORDS.– Pulau Aur, Seribuat Archipelago, Malaysia, herpetofauna,

INTRODUCTION

Pulau Aur is a small island (5.5 x 3 km) lying 63 km off the south-eastern coast of peninsular Malaysia. It is the most easterly island of the Malay Peninsula and the most isolated within the Seribuat Archipelago and lies within the State of Johor. The interior of Pulau Aur has limited permanent running water and is characterized by large granitic outcrops that make the terrain steep, rugged and difficult to negotiate. Two peaks form the dominant topographical features at each end of the island with the southernmost, Bukit Makum, reaching 522 m. Much of the original forest cover along the low-lying coastal periphery of Pulau Aur has been cut and replanted with coconut palms. Dense primary forest with closed canopy, however, remains on some of the steeper slopes and at higher elevations.

Other than a notation by Tweedie (1983) of *Calamaria lovii,* nothing has been published on the herpetofauna of Pulau Aur. To our knowledge the only herpetofaunal records from the island are museum specimens of *Limnonectes* *blythii* (ZRC.1.719), *Mabuya multifasciata* (ZRC.2.1672-77), *Bronchocela cristatella* (ZRC.2.341-42), *Gehyra mutilata* (ZRC.2.1104), *Varanus nebulosus* (ZRC.2.1880), *Calamaria lovii* (ZRC.2.2684), and *Ahaetulla prasina* (ZRC.2.4130, 4135) deposited in the Zoological Reference Collection (at present, the Raffles Museum of Biodiversity Research) at the National University of Singapore. Between 15-16 July 2001, we visited Pulau Aur specifically to make preliminary observations on the herpetofauna and document the existence of additional species.

MATERIALS AND METHODS

During the afternoon and evening on 15 July 2001, collections were made at the village of Kampong (Kg.) Berhala, 02º 27' 53"N; 104º 30' 15" E, around its outskirts and within the disturbed forest on the slopes, up to an altitude of 74.5 m, immediately surrounding the village. At Telok (Tk.) Teluran, 02º 27' 52"N; 104º 30' 25"E, collections were made during the morning on 16 July along the rocky coast, edged with secondary forest and along a small stream in primary forest. Kampong Meriam was only briefly visited on the morning of 16 July. Species collected are listed below. Museum acronyms are ZRC = Zoological Reference Collection, at present the Raffles Museum of Biodiversity Research, National University of Singapore; LSUPC = La Sierra University Photographic Collection at the Department of Biology, La Sierra University, Riverside, CA 92515-8247.

RESULTS

Anura

Limnonectes blythii (Boulenger, 1920) (ZRC 1.8242-46; ZRC.1.719).- Adults and juveniles were collected during the afternoon and evening in small pools along an intermittently flowing stream behind Kg. Berhala in heavily disturbed secondary forest. Juveniles were observed in small pools along a stream in primary forest at Tk. Teluran. This species was previously known from the island based on a specimen (ZRC.1.719) collected in June 1938.

Squamata (Lizards)

Bronchocela cristatella (Kuhl, 1820) (ZRC 2.5117; ZRC.2.341-42).- One individual was collected from primary forest at Tk. Teluran. It was initially observed 5 m above the ground on a branch. Another individual was observed on a large leaf approximately 3 m above the ground during the morning of 16 July at Kg. Meriam. This species was previously known from two specimens (ZRC.2.341-42) collected in May 1927.

Cnemaspis cf. *nigridia* (Smith, 1925) (ZRC 2.5093-96; LSUHC 3938-46).- Several size-classes of this species were seen on rocks during the day and night at all three localities. During the day, these lizards remained on the steep, shaded sides of large rocks and within the cave-like microhabitats formed from the overhangs of large boulder piles within secondary forest. During the evening hours, they were common on all rock surfaces. Egg scars were found in a single secluded portion, accessible to human observers only through crawling. An estimated 200-250 egg shells were found within a patch measuring 20 x 20 cm, suggesting both communal nesting and site fidelity. Since none of the eggs were developing at the time of our visit, the emergence time is presumably earlier in the year. Specimens were collected from Kg. Berhala. The systematic status of these lizards from Pulau Aur and Pulau Tioman is under study by I. Das and L. Grismer.

Cosymbotus platyurus (Schneider, 1792) (ZRC 2.5114).- Several individuals were observed on structures within Kg. Berhala. One was collected.

Cyrtodactylus consobrinus (Peters, 1871) (ZRC 2.5109).- One individual was collected during the evening behind Kg. Berhala as it walked across a clearing on the forest floor toward some boulders in disturbed secondary forest.

Gehyra mutilata (Wiegmann, 1834) (ZRC 2.5107; ZRC.2.1104).- Several individuals were observed on structures within Kg. Berhala. One was collected (ZRC 2.5197). This species was previously known from a specimen (ZRC.2.1104) collected in May 1927.

Gekko monarchus (Duméril & Bibron, 1836) (ZRC 2.5097-5102). During the day, approximately seven individuals were observed in a cave formed from large boulders piled on top of one another behind Kg. Berhala. Several places within this cave served as communal nesting areas with as many as 100 egg remains at one site. *Gekko monarchus* was common at night on all rock surfaces. Two eggs were opened and near-term embryos were extracted.

Hemidactylus frenatus (Duméril & Bibron, 1836) (ZRC 2.511-13).- Several individuals were observed on structures within Kg. Berhala. Three were collected.

Dasia olivacea Gray, 1839 (ZRC 2.5110).- One individual was observed during the afternoon behind Kg. Berhala approximately 4 m above the ground on a tree with a trunk diameter of approximately 0.75 m. It escaped capture by crawling up into the foliage. Two individuals were observed on the trunks of coconut palms during the morning at Tk. Teluran. One was approximately 12 m above the ground and escaped by crawling up into the fronds. The other was approximately 7 m above the ground and was knocked down with a blow pipe.

Emoia atrocostata (Lesson, 1830).- One individual was observed by LLG and ID foraging through rocks along the shore at Tk. Teluran. It was not collected.

Lygosoma bowringii (Günther, 1864) (ZRC 2.5115-16).- One specimen was collected under surface debris in Kg. Berhala and another under surface debris near an abandon house at Tk. Teluran.

Mabuya multifasciata (Kuhl, 1820) (ZRC 2.5103-06; ZRC.2.1672-77).- Adults and juveniles were observed and collected during the day at both main collecting sites. This species was previously known from six specimens (ZRC.2.1672-77) collected in May 1927. One specimen was gravid, containing three ova. This species is known to be viviparous.

Sphenomorphus scotophilus (Boulenger, 1900).- Several individuals were observed on large rocks along the stream courses at both collecting sites by LLG, JLG, NSY and KMC. None were captured.

Varanus nebulosus (Gray, 1831) (ZRC.2.1880).- Individuals were seen in the coconut groves behind Kg. Berhala. This species was previously known from a specimen (ZRC.2.1180) collected in 1929.

Varanus salvator (Laurenti, 1768) (ZRC uncatalogued).- Individuals were seen along the coast at Kg Berhala. One juvenile was collected.

Squamata (Snakes)

Ramphotyphlops cf. *braminus* (Daudin, 1803) (ZRC 2.5108).- One individual was collected during the afternoon beneath the trunk of a fallen coconut palm in a coconut palm grove behind Kg. Berhala. Superficially it resembles *R. braminus* but its colour pattern is different in that it has a blue-grey body with a white chin. Further investigations are being conducted to determine if this specimen represents undescribed species.

Calamaria lovii (Boulenger, 1887) (ZRC.2.2684).- Tweedie (1983) reports this species as present from Pulau Aur based on a specimen collected in 1938.

Macropisthodon flaviceps (Duméril, Bibron & Duméril, 1854).- One individual was observed by LBL and NSY at the edge of a small stream in Kg. Berhala during the evening as it was presumably foraging for *Limnonectes blythii.* It was not collected.

DISCUSSION

Substantial collections from other islands of the Seribuat Archipelago have been made from Pulau Tioman (Day, 1990; Grismer et al., 2001; 2002; Hendrickson, 1966a,b; Lim and Lim, 1999) and its neighbouring Pulau Tulai (Hendrickson, 1966a; Grismer et al. in prep.). All species reported from Pulau Aur also occur on Pulau Tioman with the exception of *Cyrtodactylus consobrinus, Calamaria lovii* and perhaps *Macropisthodon rhodomelas.* On Pulau Tioman, however, additional species of these genera include *Cyrtodactylus tiomanensis* and two species of *Calamaria* (Grismer et al., in prep.).

Villagers from Pulau Aur report the presence of "cicak kubing" (either *Draco* or *Ptychozoon*) in the forest and we suspect that probably both genera are present. Many villagers also speak of large pythons (presumably *Python reticulatus*) and a terrestrial turtle. More extensive field work is currently being planned for this island.

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First record of *Amphiesma venningi* (Wall, 1910) (Serpentes, Colubridae, Natricinae) from India, with remarks on its subspecies

(with four text-figures)

While conducting a survey of the snakes of Changlang District, Arunachal Pradesh, India, the first author encountered five live examples of *Amphiesma venningi* (Wall, 1910), a little known natricine. All were found within half a day's walk from Gandhigram (also called Shidi) village, ca. 27°26'N; 96° 55'E, and represent the first record of this species in India. It has previously been reported only from Upper Myanmar (from near Bhamo and Putao) and from Yunnan Province, southern China (Mengla, Jinhong, in the extreme south of the province, close to the borders of Myanmar and Laos) (Smith, 1943; Dowling and Jenner, 1988; Kou, 1985; Zhao and Adler, 1993; Zhao et al., 1998). Morphological characters, such as measurements, standard scalation characters, and pattern of all five snakes were recorded after which they were photographed and released. We were unable to sex the snakes. Additionally, colour photographs (Figs. 1-4) of one of the individuals have been provided to help facilitate identification and substantiate some of our comments. We believe these to be the first ever colour photographs of this species in life (deposited at the Center for Herpetology, Madras Crocodile Bank, Vadanemmeli, India).

Dates of collection.- Specimen #1: 16. iii. 1999. Found at 1550 h. - Specimen #2: 31. iii. 1999. Found at 1400 h. - Specimen #3: 18. v. 1999. Found at 1400 h. - Specimen #4: 20. v. 1999. Time of collection not recorded. - Specimen #5: 24. v. 1999. Time of collection not recorded.

Measurements and scale counts appear in Table 1. All specimens are slender bodied (Fig. 1) and characterized by a constant number of 17 dorsal scales throughout the body. Upper scale rows feebly but distinctly keeled, outer rows smooth. Dorsum olive-brown, indistinctly checkered with black. Anterior body with dorso-lateral ochre spots (Fig. 3). Several scales flecked with black, some entirely black (Figs. 1-3). Head with lighter vermicular marks on most shields; internasals truncate but distinctly narrowed anteriorly, almost as long as prefrontals (Fig. 3). Supralabials pale ochre with black posterior margins. Ochre colouration continued posterio-dorsally onto the nape to form an interrupted thin pale ochre elliptical backward-pointing mark (Fig. 2). A thin line of the same colour continues forward from the middle of this mark to the posterior edge of the inter-parietal suture, which has a pair of pale ochre dashes on either side (Fig. 3). Infralabials, first few ventrals white, other ventrals coral red with outer edges fawn smudged with black. Most subcaudals olive-brown with black smudges near their outer edges; the posterior subcaudals more black than brown (Fig. 4). Tongue base black, tongue tip light.

All specimens were found near hill streams, ca. 1,400 m, close to what could be described as disturbed evergreen montane forest. There were several clumps of wild bamboo nearby. Inoffensive in nature, when handled, these snakes coiled their hind body and tail around the fingers and did not attempt to bite.

Smith (1943) recognized two subspecies based on subcaudal counts (*Natrix v. venningi*- 117-140 subcaudals and *Natrix v. taronensis* - 84-106 subcaudals). It must be noted that Smith (1940: 483) in his original description of the subspecies *taronensis* states that it "Differs from the typical form in having fewer caudal shields, 92-106; ventrals 166-176". It remains unclear whether the discrepancy (in the lower range of subcaudals for *taronensis*) is a typographical error or more specimens were found between 1940 and 1943. One Indian individual (No. 2) conforms to *Amphiesma v. venningi*, while another (No. 1) conforms to *A. v. taronense*. *Amphiesma* is neutral, and therefore *Natrix v. taronensis* becomes *Amphiesma v. taronense* (David et al., 1998).

One example (No. 5) had a subcaudal count just below Smith's range for *Amphiesma v.*

TABLE 1: Scalation characters of *Amphiesma venningi* from near Shidi (Gandhigram) Village, Changlang District, Arunachal Pradesh, India. Measurements in mm. Asymmetric values in left/right order. Supralabials touching eye in brackets. SVL.- Snout-vent length; tL - tail; TL - total body length; Ratio tL/TL - ratio of tail/ total body length.

	#1	#2	#3	#4	#5
Ventrals	160	159	160	167	161
Anal	2	2	2	2	2
Subcaudals	104	118	87+?	103+?	115
Supralabials	9(4-6)	9(4-6)	9(4-6)	9(4-6)	9(4-6)
Infralabials	?	10	10	10	?
Preoculars	L1, R2	2	2	2	2
Postoculars	L3, R2	3	2	2	3
Temporals	1+1	1+1	1+1	1+1	1+1
SVL	550	425	400	405	415
tL	230	220	170+?	180+?	195
Ratio tL /TL	0.295	0.341	0.298 +	0.308+	0.320

venningi and might arguably be placed there. Two more had incomplete tails. As all the snakes were found in the same area and were visibly 'the same kind of animal', we provisionally assign all of them to *Amphiesma v. venningi*. The same mixture of supposedly subspecific differences in subcaudal counts appeared in Kou (1985) and Zhao et al. (1998: 89) for Yunnan specimens: 3 males from Mengla have 105, 114 and 136 scales, whereas one male and one female from Jinhong have 120 and 106 subcaudals, respectively. The validity of the subspecies *A. v. taronense* seems doubtful and should be re-evaluated based on subcaudal counts of more specimens of *A. venningi* from throughout its known range.

Our five Indian specimens agree well in scalation with the data of Smith (1943) and do not modify the ranges given by this author for the counts of ventrals and subcaudals. However, our largest specimen, with a total length of 780 mm, is 100 mm longer than the maximum size cited by Smith (1943).

Edmond V. Malnate confirmed our identification and mentioned that *A. venningi* has body scales in 17:17:17 rows (Malnate, pers. comm.), as does *A. sauteri* from China (David, pers. com). Venning (1911: 774) however recorded an aberrant specimen - No. 43/10 that had its posterior body scale rows reduced to 15/16. Judging from his notes, it is certain that Venning (1910, 1911) saw at least three of these snakes alive. Despite this, he does not mention their striking coral red ventral colouration. Wall (1910, 1925a, 1925b, 1926) and Smith (1943) both of whom probably never saw this species alive, do not record it either. More recently, Kou (1985) who discovered the Chinese specimens, also did not mention this unusual colouration, but it is unclear whether he collected the specimens himself and so saw them alive. While it is possible that this is a regional colour variation, variation in the genus *Amphiesma* is often very subtle (P. David, pers. comm.) and the possibility that the Indian specimens represent another undescribed taxon cannot as yet be ruled out. Observations on live material from various ranges of their distribution are needed to conclusively prove either possibility. However the bright coral red colour of the ventrals in life is not unique to this species. It has been described by David et al. (1998) in *Amphiesma optatum* (Hu & Djao, 1966), a species occurring in southern China and northern Vietnam. The red ventral colour of David et al.'s (1998) specimen vanished in preservative in only a few weeks and turned to a pale yellowish cream, a colour under which the belly of this species was largely described in literature. Additionally both *venningi* and *optatum* have a V-shaped nuchal streak directed backwards. Despite these similarities, *A. venningi* differs appreciably from *A. optatum* in several respects:

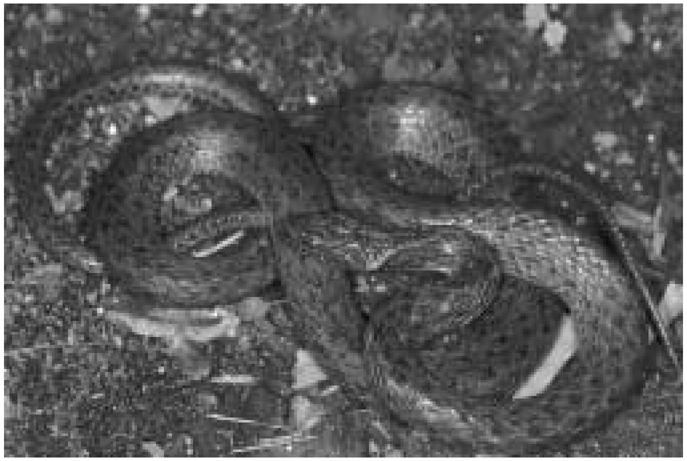

FIGURE 1: Dorso-lateral view of entire body of *Amphiesma venningi* in life.

FIGURE 2: Dorso-lateral view of head and anterior body of *Amphiesma venningi* in life. Note supralabials and temporals.

FIGURE 3: Dorsal view of head and fore-body of *Amphiesma venningi* in life. Note internasals, head markings and thin pale crescentic mark on the nape.

FIGURE 4: Ventrum of *Amphiesma venningi* in life. Ventrals coral red ventrals; subcaudals brown-black.

greater number of maxillary teeth (*venningi* – 27-32 fide-Smith 1943; *optatum*– 18-23+2 fide-David et al, 1998), dorsal scale rows (*venningi* – 17:17:17 pers. obs.; *optatum*– 19:19:17; fide David et al., 1998), as well as in showing a different dorsal colour and pattern (*venningi* see above; *optatum* – 'deep bluish-black, marked on each side with bright yellowish vertical bars'; fide David et al,. 1998). *Amphiesma* currently represents a genus with 38 species (David, pers. comm.) in which the relationships of *venningi* and *optatum* are still poorly understood.

The herpetology of north-eastern India is still very poorly known. We recently discovered another snake species previously known only from China and Myanmar, the pitviper *Trimeresurus medoensis* Djao in: Djao & Jiang, 1977 (David et al., in prep.). The importance of this region of the Eastern Himalayas as a center of herpetological biodiversity must be stressed, and it is fortunate that the State government has afforded protection to several localities. Further observations on live specimens of *Amphiesma venningi* throughout its range are necessary to determine whether the coral red ventral colouration is merely a regional variation, and also whether the validity of the subspecies *A. v. taronense* should be upheld.

Field work in Arunachal Pradesh would have been impossible without the assistance of: Itanagar- S. R. Mehta (Principal Chief Conservator of Forests), S. N. Kalita (Chief Conservator of Forests - Wildlife), Mr. Deori (Director- State Forest Research Institute) and P. Ringu (Deputy Conservator of Forests.- Wildlife); Miao- D. N. Singh (Field Director- Namdapha Tiger Reserve), A. Gupta Choudhury (Assistant Field Director - N.T.R.), S. S. Chandiramani (Research Officer- N.T.R.), P. Thongon (Block Development Officer/Extra Assistant Commissioner), Phupla Singpho, Murthy, Bom Bahadur and Teg Bahadur; Mohonbari- the Indian Airforce and the Department of Supply and Transport (Arunachal Pradesh); and in the forest- The Lisus of Gandhigram, Vijoynagar, Shiddi Co and Hazolo- Thank You all. We thank Edmond V. Malnate for confirming our identification; Van Wallach and P. David for their lucid comments on our note. We thank P. David and Xiaohua Tu for making available to us translations of literature in Chinese which were otherwise impossible for us to access. In Pune, the first author would like to thank J., R. and S. Kadapatti for the unlimited use of their computer.

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Range extension of *Ansonia ornata* (Günther, 1875) and *Indirana brachytarsus* (Günther, 1875)

Ansonia ornata, the black torrent toad, is an endemic of the Coorg and Neria region of Dakshina Kannada District of Karnataka, south-western India, with a localized distribution, at around 12º-13º N; 400 to 800 m msl (Daniel, 1963; Inger and Dutta, 1986; Daniels, 1991; 1992; 1997; Dutta, 1992). One specimen (BNHS Re 4061) was recorded from a stream within the evergreen forests of Kuppalli Bioreserve (75º 15'-75º 20' E; 13º 35'-13º 40' N), which although belongs to described altitude range for the species, located 110 km north and 175 km north-west of the earlier report from Neria (Daniels, 1992) and Brahmagiri Hills (Daniel, 1967), respectively. This indicates its range extension from 13° N to 14° N.

Description.- A small aquatic toad (SVL 35 mm), without cranial ridges and parotid glands. Dorsally brownish black, underparts with black and yellow spots, limbs cross-barred. Webbing absent on forelimbs. First finger smaller than second, hindlimb 2.3 times longer than forelimb; length of femur nearly 3 times its width and 4/5th length of tibia. Two prominent metatarsal tubercles, webbing full, reaching terminal dilation of all toes, except toe IV.

Indirana brachytarsus, the short-legged frog, is an endemic of the Western Ghats of Kerala and Tamil Nadu, south-western India, between coordinates 8-11º N, and at altitudes ranging between 0-1000 m msl (Daniels, 1992, 1997; Dutta, 1992). It has been reported earlier that the species is having broad ecological range in Kerala, distributed evergreen forests, moist deciduous forests, secondary growth, open grasses and also along streams and litter mat of forest floors (Inger et al., 1984). However, in the present study, one specimen of *I. brachytarsus* (BNHS Re 4062) have been recorded along the litter mat near the stream in the Bhagavathi forest of Kudremukh National Park (13° 10'-13° 26' N; 75° 05'-75° 10' E), nearly 410 km north-west from earlier report of Annamalai Hills.

Description.- Small litter frog (SVL 34 mm). Colouration is similar to *Indirana beddomii,* with prominent black horizontal streak on interorbital space, cross-bars on limbs and lower jaw. Black streak from tympanum to nostril passing through eye and canthus rostralis. Longitudinal warts prominent posterior to eye. Tongue without papilla. Interorbital space smaller than internasal and diameter of eye, however the internasal distance and distance between eye and nostril are equal (Table 1). The specimen agrees the description of this species given by Inger et al. (1984) and can be differentiated from *I. beddomii* by absence of lingual papilla, presence of a greater number of longitudinal warts posterior to eye and on mid-dorsum. Small tympanum (ca. 85% that of *I. beddomii*) and greater ratio between forelimb and hindlimb (*I. beddomii*, 1:0.32 vs *I. brachytarsus*, 1:0.39) with tibiotarsal articulation reaching the nostril. Discs on finger and toe tips smaller and inner metatarsal tubercles less prominent compared to *I. beddomii*.

The forests of Western Ghats of India is an abode for various amphibian species. This region harbours as many as 123 species (Molur, 1997; Krishnamurthy, 1999). However, repeated and in-depth surveys were resulted either addition of new species or extension of range of distribution. It has been felt that the intensive observation certainly results in the discovery of new species and improvement in understanding the distribution of amphibian fauna (Inger and Dutta, 1986).

SVK is thankful to Department of Science & Technology for awarding the research project (Number SP/SO/C-39/97) to study the diversity and habitat ecology of amphibians in Malnad region. Facilities provided by Zoological Survey of India, Chennai for the identification of these two species are acknowledged. A. H. Manjunatha Reddy and K. V. Gururaja are thankful to DST for the fellowship awarded to work on amphibian diversity and habitat ecology.

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Notes on the distribution of *Lygosoma lineata* (Gray, 1839) and comments on the systematic status of *L. vosmaerii* (Gray, 1839)

Chiamela lineata Gray, 1839 was described from India, without a specific locality, and allocated to *Lygosoma* by Boulenger (1887). The species is know from a few specimens collected from Maharashtra (Pune, Belgaum, and Matheran) and Karnataka (North Kanara) (Smith, 1935). Further records of the species are Annamalai Nagar, Chidambaram District, Tamil Nadu and Salsette Island, Maharashtra (Chari, 1960). The distribution of the species indicates that the species is endemic to the Western Ghats and Eastern Ghats. More recently, the species was reported from Gujarat State (Naik and Vinod, 1994) from the right banks of Narmada River, Kevadia (21°

TABLE 1: Morphometric data on *Lygosoma lineata* (Gray, 1839), from Bhavnagar District, Gujarat, deposited in the collection of the Bombay Natural History Society (BNHM). Specimen with five digits on right fore limb marked with an asterisk.

Measurements (in mm)		BNHM 1453*	BNHM 1454
From tip of snout to vent	SVL	52.50	48.50
From cloaca to tail tip	TL	68.50 (tail tip missed)	68.00
Total body length	TBL	121.00	116.50
Distance from forelimb to snout tip	DFL-ST	9.68	9.40
Distance between angle of jaw and snout tip	HL	3.40	3.30
Head width at angle of jaw	HW	3.20	3.10
Axilla to groin distance	A-G	40.00	37.80
Greatest eye diameter	ED	1.10	0.84
Eye – nostril distance	E-N	1.50	1.10
Eye – snout-tip distance	E-S	1.86	1.50
Ear opening – eye distance	E-E	2.92	3.44
Greatest length of ear opening	EL(S)	0.50	0.70
Least distance between upper eyelids	IO	0.50	0.70
Distance between nostrils	IN	0.82	0.88
Upper labials (touching eye) no. Right/Left	UL R/L	7 : 7 (4, 5, 6 touch to eye)	7 :7 (4, 5, 6 touch to eye)
Lower labials Right/Left	LL R/L	7 : 7	7 : 7
Dorsal body scale rows	DO-SR	22	22
Scales on back from nuchal to hind limb		110	110
Belly scale rows (between fore and hind limbs)	BE-SR	92	92
Digit lamellae (inner to outer) 1:2:3:4	DL	L= 3:4:4:5; R= 3:4:4:5:2	3:4:4:5
Toe lamellae (inner to outer) 1: 2:3:4	TL	3:4:6:6	3:4:6:6

16’ N; 72° 56’ E), Narmada District) and from Naomibohai village, Dharampur (20° 32’ N; 73° 13’ E), Valsad District (Gayen, 1999) and Gira Falls of Gira River (part of Purna Wildlife Sanctuary: 20° 51’-21° 21’N; 73° 32’- 73° 48’ E), Dangs District (Anon., 1999), both localities situated further north.

I collected two further specimens of the species at Velavader National Park (21° 56’ N; 71° 10’ E), Bhavnagar District, in the first week of October 2000. Both specimens were deposited in the museum of Bombay Natural History Society, Mumbai (BNHM 1453-54). Measurements are in Table 1. Other characters and colouration match the description in Smith (1935), except that one (BNHM 1453) has five fingers on the right front limb, four on the left. This character raises the question of the species identification and the status of *L. vosmaerii* (originally described as *Hagria vosmaerii* Gray, 1839). The two species differ on this character (Gray, 1839; Smith, 1935), *L. lineata* having four digits on each foot and *L. vosmaerii* having four.

Boulenger (1890) considered the holotype (MNHN 777; ex-MNHN 3007; fide Brygoo, 1985) of *L. vosmaerii* to be an apparently anomalous specimen of *L. lineata*, although Smith (1935) treated both as distinct, remarking, *“*I seen no reasons to regards this specimen as an ‘apparently anomalous’ example of *lineata*, as Boulenger has done. The loss of a digit is not uncommon among degenerate skinks, and as a specific character it appears to count among them*”*.

One of the specimens thus shows the characters of both *lineata* and *vosmaerii* and supports Boulenger (1890). Additionally, *L. vosmaerii* was described on the basis of single specimen from “Bengal” (either the modern West Bengal State of eastern India or Bangladesh. Bengal also included parts of eastern Bihar state and north-eastern India in the past) in 1839; no further specimens have come to light.

The present record of *Lygosoma lineata* from the dry arid area of VNP, Bhavnagar district further extends the range of the species. These records and the earlier ones by Naik and Vinod (1994) from Kevadia, indicate that the species is distributed outside the Western Ghats and Eastern Ghats. Chari (1960) noted that the Zoological Survey of India had specimens from Madhya Pradesh, which, if confirmed, would close the gap between the records from western India discussed, and the "Bengal" type locality of *L. vosmaerii*.

I therefore suggest the synonymy of *L. vosmaerii* (Gray, 1839) under *L. lineata* (Gray, 1839).

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Recent distribution records and a significant range extension for *Manouria impressa* in Myanmar

The impressed tortoise, *Manouria impressa* (Günther, 1882) is a rare inhabitant of hill forests from eastern Myanmar (Burma), east to Thailand, Laos, Vietnam, Cambodia, and southern China, and south through Peninsular Malaysia (Smith, 1931; Ernst and Barbour, 1989; Iverson, 1992; Das, 1997). In Myanmar, *M. impressa* has been previously reported only from the Karenni Hills in Kayah and Kayin States, and Bago (formerly Pegu) in Bago Division (Fig. 1; Smith, 1931; Iverson, 1992). However, there are no recent records of *M. impressa* in Myanmar, and its occurrence elsewhere in the country remains speculative (Dijk, 1993; Das, 1997). Herein we provide recent distributional records of *M. impressa* from Myanmar, including heretofore unreported localities in western regions of the country.

These records were gathered opportunistically during fieldwork conducted from 1999 to 2001. We measured carapace and plastron length (CL and PL, respectively), counted carapace annuli if discernible (Zug, 1991), and photographed each specimen. Voucher photographs were deposited in the Campbell Museum (CUSC), Clemson University, Clemson, South Carolina, USA. Place names are in accordance with Nelles® 1:1,500,000 map of Myanmar, al-

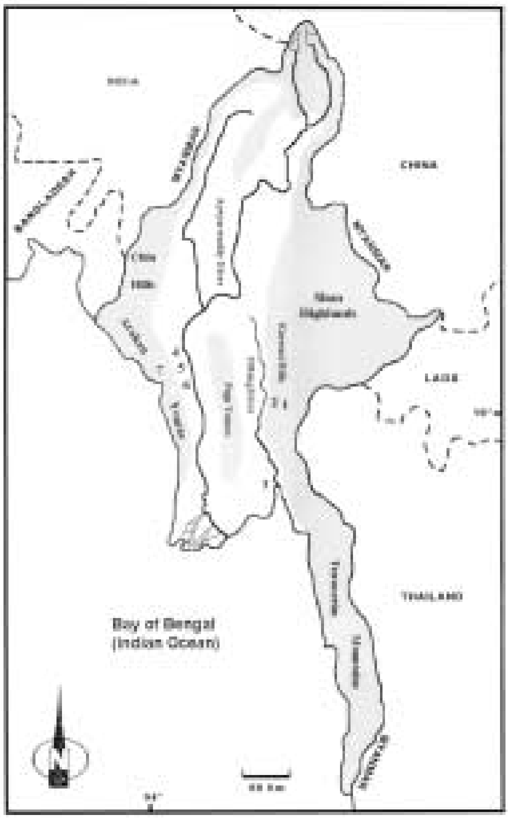

FIGURE 1: Map of Myanmar illustrating major rivers, mountain ranges, and collection localities for *Manouria impressa* specimens mentioned in the text. 1 = Loikaw; 2 = Pyingye Reserved Forest; 3 = Bago; 4 = Sedouttaya Village; 5 = Padein Village; 6 = Mindon Village; 7 = Bogyi Mauk Taung Mountain.

though local names were used for sites not labeled.

We examined five specimens (one living tortoise and four carapaces without plastrons) of *Manouria impressa* in Myanmar. One carapace (CL = 24.3 cm; annuli not discernible; CUSC 2029) was obtained on 30 November 1999 from a wildlife trader in Loikaw (19° 36' N; 97° 20'E), Kayah State (Fig. 1). According to the trader, the tortoise was captured locally, but a specific provenance could not be ascertained.

A living female (CL = 20.3 cm; PL = 18.4 cm; 24 annuli; CUSC 2030) was examined on 4 July 2000 in the Pyingye Reserved Forest of south-western Shan State (Fig. 1). This tortoise was captured by villagers in evergreen forest along the Paunglaung River (19° 37' N; 96° 47'E) in the piedmont of the Shan Highlands (Terra, 1944). The vegetation of this region is described as evergreen or monsoon forest dominated by *Dipterocarpus*, *Ficus*, *Hopea*, *Vatica,* and *Paynea* with a dense understory of palms and bamboo (Stamp, 1924; Terra, 1944). *Manouria impressa* has been reported from similar evergreen hill forests in north-eastern Thailand (Chan-ard et al., 1996).

Three *Manouria impressa* were obtained from villages in Magway Division along the eastern base of the Arakan Yoma Mountains (Fig. 1). A carapace (CL = 23.7 cm; 19 annuli; CUSC 2031) was obtained in Sedouttaya Village (20° 18' N; 96° 47' E) on 2 April 2000, and another (CL = 21.3 cm; 24 annuli; CUSC 2033) from a wildlife trader in Padein Village (19° 58' N; 94° 32' E) on 25 May 2000. Both tortoises were reportedly captured in the nearby Arakan Yoma Mountains. A third carapace (CL = 27.9 cm; 19 annuli; CUSC 2032) was obtained on 14 February 2000 from a hunter in Mindon Village (19° 20' N; 94° 44' E). This specimen was collected during May 1999 from evergreen forest on the upper slopes of Bogyi Mauk Taung Mountain (19° 10' N; 94° 20' E) in the Arakan Yomas. The hunter considers *M. impressa* uncommon, although he collects several each year. These specimens constitute the first records of *M. impressa* from the Arakan Yoma Mountains (maximum elevation = 1,150 m), a southern extension of the Himalayas extending for 500 km along the western border of Myanmar (Henderson et al., 1971; Salter, 1983). These mountains are characterized by evergreen forest (Stamp, 1924, 1930; Terra, 1944) of poorly known floristic composition (Salter, 1983). Extensive tracts of bamboo (*Melocanna bambusoides*) occur throughout the Arakan Yomas, developing in response to human disturbances such as shifting cultivation, fire, or both (Stamp, 1924, 1930; Terra, 1944).

Collectively the Arakan Yoma specimens extend the known distribution of *Manouria impressa* approximately 350 km west of earlier records from eastern Myanmar. Moreover, these specimens represent the western-most records in the global distribution of *M. impressa*. The northern range limit of *M. impressa* in the mountains of western Myanmar remains to be determined. However, it is likely the distribution extends northwards into the Chin Hills, a mountain range contiguous with the Arakan Yomas (Fig. 1). The Chin Hills provide seemingly suitable evergreen forest habitat preferred by *M. impressa* (Chan-ard et al., 1996), but remain poorly known biologically (Sayer, 1983; Robson et al., 1998).

The current conservation status and prospects for the continued survival of *Manouria impressa* in Myanmar are uncertain. Given the widespread and intensive harvest of chelonians for local consumption and export to food markets in southern China (Platt et al., 2000), it is likely that *M. impressa* populations are being depleted throughout the country. Significantly, *M. impressa* has not been reported from any protected area in Myanmar, although this is probably due to the lack of surveys rather than actual rarity. *Manouria impressa* is likely to occur within suitable habitat in Gwa Elephant Sanctuary (Arakan Yomas) and possibly Natma Taung National Park (Chin Hills). Future surveys of these areas are therefore warranted.

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The first female topotype of the montane agamid *Pseudocalotes flavigula* (Smith, 1924) from Peninsular Malaysia, with description of colouration in life

(with three text-figures)

In Peninsular Malaysia, three species of the agamid genus *Pseudocalotes* Fitzinger, 1843 are currently known, namely *P. flavigula* (Smith, 1924), *P. dringi* Hallermann and Böhme, 2000 and *P. larutensis* Hallermann and McGuire, 2001. All three species are confined to montane forests in the peninsula. *Pseudocalotes flavigula* was first described based on a single male type, which was collected from the Cameron Highlands (Pahang) at an elevation of 'between 5,000 and 6,000 feet' with no specific locality given, in October, 1923 by the staff of the Federated Malay States Museums. In his succinct description of this new species (then regarded as *Calotes*), Smith outlined, in a few paragraphs, sufficient diagnostic characters that are unique to the named species. Although no specific etymology was indicated, it is obvious that the species was named after the bright yellow gular pouch observed by Smith in his male specimen (*flavus* - Latin for yellow, *gula* - Latin for throat). In a subsequent herpetological survey to the Cameron Highlands (Smedley, 1931), there were no records of any specimens of *P. flavigula* from the type locality. This species has not been reported from any other montane localities in the peninsula. Apart from the holotype (BMNH 1946.8.11.14), only two other specimens are known from the type locality (ZFMK 16501 - Tanah Rata, and FMNH 14903 - Gunong Brinchang), both of which are also males.

In July of 2001, a small agamid (subsequently identified as *Pseudocalotes flavigula*) was obtained from a local resident at Brinchang, Cameron Highlands (Figs. 1-2). He had captured the individual from the adjacent montane forests and was maintaining it in captivity, together with another highland agamid, *Gonocephalus robinsonii* Boulenger, 1908. Diagnostic features of the genus *Pseudocalotes* include its relatively small size, lack of a pronounced dorsal crest, weak limbs, and the third and fourth toes being subequal in length (Cox et al., 1998; Hallermann and Böhme, 2000). Diagnostic features of the species *P. flavigula* include: six upper and eight lower labials, less than 40 scales around midbody, and a distinct yellow gular pouch in the male (this yellow colouration is also present in the gular region of the female). The female was maintained in captivity for two weeks, after which it was preserved and deposited at the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, NUS (ZRC.2.5162).

While in captivity, its live colouration was noted. The basal colour of its body was a light olive green on the dorsum and flanks. This colour was also present on its head, limbs and tail. The head was speckled with brown on the top; its tympanum dark brown; the labial and throat region white and continues behind and below the tympanum towards the axillary region. A distinct patch (15 x 4 mm) of mustard yellow was present in the gular region. At the thoracic region, just posterior to the yellow patch, was an area of light iridescent blue. The abdominal region was ivory white. Along the dorsum, a series of evenly spaced brown saddle patches were obvious. The first brown saddle was situated just posterior to the pectoral region. The second and third saddles were at the thoracic and abdominal regions, respectively. The fourth patch was at the pelvic region. Subsequent brown patches were uniformly distributed along the length of the tail. Upon preservation, the uniform green background of the body faded to a dirty brown-grey. The yellow throat, blue thorax and brown saddles all faded significantly. The white on the labial, gular and abdominal regions were retained.

During captivity, endoparasites were recorded from this individual. A total of 11 individual nematodes (ca. 10-15 mm in length) were found crawling away from a freshly extruded faecal sample. All worms were preserved in 75% alcohol. In addition, the female (noticeably gravid) laid a clutch of three chalky white eggs, each measuring about 15 x 8 mm (Fig. 3). The eggs were also preserved in 75% alcohol. After fixation, body measurements and scale counts were obtained from the female *P. flavigula*. Using a slide vernier, measurements of its snout-vent length was 80.2 mm; tail length 132.8 mm; total length 213.0 mm; head length 23.5 mm; head width 13.0 mm; tympanum diameter 2.5 mm; fore-limb length 29.3 mm; hind-limb length 41.5 mm; hind-foot length 18.2 mm. It had 7 scales which comprised the nuchal crest; 6 upper labials; 8 lower labials; 36 scales around mid-body; 26 scales under fourth finger; 31 scales under fourth toe. The subdigital scales of the third toe are bicarinate.

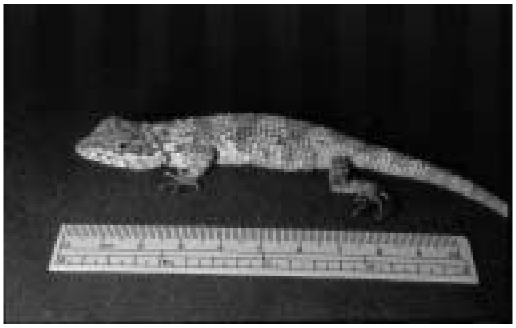

FIGURE 1: Gravid *Pseudocalotes flavigula* female (ZRC.2.5162).

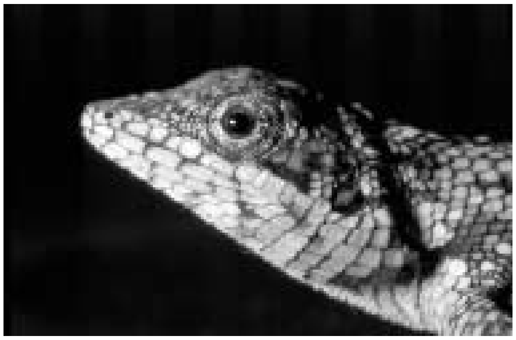

FIGURE 2: Head close-up of female *Pseudocalotes flavigula* (ZRC.2.5162), illustrating supra- and infralabials.

FIGURE 3: The three eggs (ca. 15 x 8mm each) laid by female *Pseudocalotes flavigula* (ZRC.2.5162).

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Defensive behaviour in the montane horned frog *Megophrys longipes* (Boulenger)

(with two text-figures)

The megophryid *Megophrys longipes* (Boulenger, 1885) is known to inhabit montane forests of Thailand, Cambodia, south Vietnam and Peninsular Malaysia (Leong and Chou, 1998). Within Peninsular Malaysia, this species has been recorded from most highland localities, such as Maxwell's Hill (Bukit Larut) in Perak, Gunong Angsi in Negri Sembilan, Gunong Bunga Buah in Selangor, Fraser's Hill and Cameron Highlands in Pahang (Berry, 1975).

The first record of a behavioural response from this species towards handling by humans was made by Butler (1904) during his stay at Bukit Larut. He exclaimed that when the frogs were "… seized in the hand, they frequently opened their mouths widely for some seconds - a very unfroglike proceeding!" However, Butler provided no additional information with regards to this intriguing form of self-defence. Subsequently, Butler's exact observation of this mouth-opening phenomenon was faithfully cited by Boulenger (1908, 1912) and Taylor (1962). Although this species was also encountered during other montane explorations in the peninsula (Smith, 1922, 1930; Smedley, 1931), there was no mention of any behavioural response.

In my previous encounters with the adults of this species, I had not observed any 'mouth-opening' responses from them. However, during a night walk in the Cameron Highlands, an adult female was encountered on the side of a forest trail near the Robinson Falls (2130 hours, 31 July 2001). It was removed for subsequent ex-situ photography. After a few frames were taken (using flash), the frog leapt away but was recaptured and replaced in its previous spot. When the camera was brought near, the subject inflated its lungs and body, while elevating itself by extending all four limbs (Fig. 1). This action exposed the reddish colours, otherwise con-

FIGURE 1: Lateral view of *Megophrys longipes* (ZRC 1.8377) showing elevated body, inflated lungs and open mouth.

FIGURE 2: Frontal view of *Megophrys longipes* (ZRC 1.8377) revealing the yellow tongue of the gaping mouth. Notice also the distinct black patch above the knee, which may also serve as a deterrent ‘eyespot’.

cealed within the inguinal area. In addition, symmetrical black patches at the knee may serve as 'eyespots' when the hind limbs are extended. When the frog was approached with a finger from the front, it opened its mouth, revealing a bright yellow tongue (Fig. 2). No vocalisation accompanied this action. If a finger were extended towards it from the left side, the frog would tilt its body in that direction, and vice versa.

The defensive behaviours of lung inflation, body elevation and mouth gaping have apparently been observed in *Megophrys montana* as well (Duellman and Trueb, 1986). Robert F. Inger and Robert B. Stuebing (pers. comm.) have witnessed *Megophrys nasuta* vomit its stomach contents following capture, which naturally involved a gaping behaviour. However, there have been no previous records of aposematic colouration or body-tilting in other members of this genus. This behaviour of tilting the body in the direction of threat is also used by some species of *Bufo*, such as *B. alvarius* (Hanson and Vial, 1956). The yellow tongue revealed by *Megophrys longipes* is also comparable to the bright orange tongue of *Hemiphractus fasciatus* when exhibiting its mouth gaping strategy (Duellman and Trueb, 1986). This may be an example of evolutionary convergence of anti-predator behaviours between anuran species from different continents. The above frog was preserved as a voucher specimen and deposited at the Zoological Reference Collection of the Raffles Museum of Biodiversity Research (ZRC.1.8377, SVL 50.2 mm).

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Report on the herpetofauna of Pulau Tulai, west Malaysia

Pulau Tulai is a small islet (1.6 km^2) lying 40 km off the south-eastern coast of peninsular Malaysia and 5 km off the north-west coast of Pulau Tioman. It is a T-shaped island 1.6 km in length along an east-west axis and 1 km in width along a north-south axis. Its interior is steep sided and rocky but lacks permanent fresh water. Most of the island had been cleared for coconut plantations prior to 1960 but some large dipterocarps were left and secondary growth is now extensive (Bullock and Medway, 1966).

The herpetofauna of the much larger Pulau Tioman has been extensively studied (Day, 1990; Grismer et al., 2002 and in prep.; Hendrickson, 1966a,b; Lim and Lim, 1999) whereas that of the nearby Pulau Tulai has been less well documented. In fact, the only published account of the herpetofauna comes from Hendrickson (1966a) who reported the presence of *Cnemaspis kendallii, C.* cf. *nigridia, Mabuya multifasciata* and *Sphenomorphus scotophilus.* A museum specimen of *Varanus salvator* (ZRC.2.5063) exists at the Raffles Museum of Biodiversity Research at the National University of Singapore. The museum acronym ZRC is for the Zoological Reference Collection (at present, the Raffles Museum of Biodiversity Research).

We visited the island on three separate occasions on 13-15 July 2001 with the specific goal to observe and sample its herpetofauna. To the list of Hendrickson (1966a) we add seven species: six lizards and one snake.

During the mornings and afternoons of 13-15 July 2001, collections were made in the vicinity of Telok Bakau on the north-western side of the island. Specimens were observed by walking along the forest trail to Bukit Candang at approximately 100 m, and by searching through the leaf-litter by hand at the base of boulders and large trees.

Species observed on Pulau Tulai not reported by Hendrickson (1966a) are as follows:

Bronchocela cristatella (ZRC 2.5081). - One individual was collected from a tree along the trail to Bukit Candang on 14 July.

Gekko monarchus (ZRC 2.5086). On 13 July three individuals were uncovered beneath an exfoliating piece of granite on a large boulder. One was collected.

Gekko smithii (ZRC 2.5082; LSUHC 3891). Seven individuals were observed head-down 3-6 m above the ground on large trees. Two were collected. One individual was observed resting on three eggs stuck to the side of the tree approximately 4.5 m above the ground.

Ptychozoon kuhli. - On 13 July one individual was observed head up on a large tree approximately 3 m above the ground. It escaped by running up the tree. On 14 July, two individuals were observed on different trees head up 3-5 m above the ground which escaped by running up the trees.

Emoia atrocostata (ZRC 2.5092).- On 13 July one individual was collected off large boulders at the water's edge.

Larutia sp. nov. (ZRC 2.5088-90). On 14 July one individual was found beneath a cement bag in bamboo leaf-litter approximately 20 m in elevation. The next day, two additional individuals were found in the same general vicinity. One was beneath bamboo leaf-litter at the base of a large boulder and the other was approximately 1 cm below the surface of the ground beneath leaf-litter between two large boulders. Another specimen was uncovered beneath bamboo leaf-litter but escaped. These individuals represent a new species which is currently being described (Grismer et al. in prep.).

Dibamus cf. *alfredi* (ZRC 2.5092).- On 15 July one individual was found beneath leaf-litter in the vicinity of the *Larutia* (see above). Along with two other specimens from Pulau Tioman, it probably represents a new species of *Dibamus* and is currently being studied.

Ahaetulla prasina (ZRC 2.5083). - On 13 July one juvenile was collected crawling across the forest floor beneath a fallen tree.

With the exception of *Larutia,* the herpetofauna of Pulau Tulai is a subset of that of Pulau Tioman although it is expected that *Larutia* will also be found on Pulau Tioman. The same is true for *Emoia atrocostata* which was collected from Pulau Tulai but remains and unconfirmed sighting on Pulau Tioman (Grismer et al. in prep.; Hendrickson, 1966a). The absence of conspicuous diurnal arboreal agamids such as *Draco* is puzzling. There is sufficient comparable habitat to that in which they are found on Pulau Tioman which supports at least four and possibly five species (Grismer et al. in prep.) yet they appear to be absent on Pulau Tulai. The absence of amphibians on Pulau Tulai (see also Hendrickson, 1966b) is probably related to the lack of permanent fresh water. More field work is planned for this island.

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Recent record of *Cantoria violacea* (Girard, 1857) from North and Middle Andaman Islands, India with a note on its bite

(with one text-figure)

Cantoria violacea is a little known homalopsine, known from coastal regions of Myanmar, south to the Malay Peninsula, from the Gulf of Martaban to Singapore, the Andaman Islands and Indo-Australian Archipelago (Smith, 1943; Gyi, 1970). Wall (1914) recorded the species from Ross Island 13°19'N; 93°03'E, North Andaman Islands, and Rao et al. (1992) reported it from North Reef Island 13°04'-05'N; 92°41-43'E (Middle Andaman), the latter report remarkably from a freshwater ecosystem, this species typically being associated with mangroves. The basis of the report, especially if this was based on collected specimens remain unknown and no scalation data were presented. We report here 16 sightings of this little known homalopsine with scalation data of six specimens, two of which have been deposited with the Zoological Survey of India, Kolkata.

While surveying snakes in the Andaman Islands in July 2000, two specimens of *Cantoria violacea* were found on mudflats in mangrove swamps, at low tide, close to Burma Dera 12°55'N; 92°54'E, south of Mayabunder in Middle Andaman Island. They were caught late at night, their scales were counted, photographed and released close to the capture site. In June 2001, during surveys around the Chepoo settlement in Casuarina Bay 13°32'N; 92°55'E (on the western side of North Andaman Islands), 14 additional specimens were encountered at night, in the shallow run-off streams in mangrove swamps. Two examples were collected and are deposited with the Zoological Survey of India, ZSI 25353-54. Scalation data were recorded for six of the above mentioned specimens (Table 1). Characters diagnostic include: body cylindrical, elongate; head barely distinct from neck; tail moderate, slightly compressed; subcaudals paired, tail-tip blunt, eye with vertical pupils, loreals not in contact with internasal, frontal much broader than supraocular; parietals elongate; loreal separated from single internasal; one preocular, two postocular and one subocular, one long anterior temporal, five supralabials, third and forth below the eye, but not in contact, and the fourth and fifth were the largest, inframaxillaries 2 + 2, scales smooth in 19 : 19 : 17 rows; the ventrals well developed; anal divided. Other data are in Table 1.

Colouration of juveniles Andaman specimens (in life) resembles Form 1 (sensu Smith, 1943); however, Smith's description of the head with white spots does not match with the six examples dealt with in this note. The head markings include two pale yellow bands, the first one passing through most of the prefrontals, the second through the hind portion of the frontal, both bands end at the supralabials and the rostral is yellow. These markings are relatively more faint in adults. There are 57-66 lemon yellow bands on the body and 13-19 on the tail. Adults show paler bands. A single juvenile specimen from North Andaman (ZSI 25354) has bands encircling the body; the others have uniform, unbanded blackish-gray ventrals All specimens were found on mudflats in mangrove marshes, and observations indicate that *Cantoria violacea* is nocturnal, feeding during low tide and on open mud flats when it is easy to catch crabs and small fish stranded in small pools and in shallow run-off streams. The Middle Andaman examples were found with their tails inside crab holes and within 6 m apart from each other. In the North Andamans *C. violacea* is fairly common in the mangroves and several specimens were observed with their posterior half inside crab holes. Four larger specimens (ca.1.5 m total length) were observed in waist deep mangrove mud along a drainage stream and all specimens observed were in pairs, about 0.5-1 m apart.

Several old Karens (immigrants from Myanmar) separately informed us that they knew two people who had been bitten by this snake-one had died and the other remained unconscious for 2-3 days. Symptoms mentioned by them included acute abdominal pain, vomiting blood

TABLE 1: Morphometry and scalation of *Cantoria violacea* from the Middle and North Andaman Islands, Bay of Bengal, India. Measurements in mm; specimens 1 and 2 from Middle Andaman, others from North Andaman.

	Spm #1	Spm #2	ZSI 25353	ZSI 25354	Spm # 5	Spm # 6
Ventrals	246	250	260	262	252	253
Subcaudals	65	66	59	58	53	66
Infralabials	10	10	8	8	8	8
SVL	510	490	730	640	930	930
Tail length	100	100	100	80	160	180

FIGURE 1: Cantoria violacea from the Andaman Islands, India.

and swelling at the site of the bite. Roots of a local cactus-like plant that grows in mangrove swamps were crushed and applied at the site of the bite, the juice of the roots was also taken orally. They claim that this is the only known remedy for the bite of this species and one of the victims was our Karen guide's father. Since *Cantoria violacea* is generally considered to be harmless to humans, it may be possible that the cases referred to are bites from the Andaman krait (*Bungarus andamanensis*) which somewhat resembles *C. violacea*. Contrary to this supposition, Karen natural history observations are extremely accurate and it is odd that they would mix up two species. More research is needed to determine whether the saliva of *C. violacea* is harmful to humans, or this is indeed a case of folklore.

We would like to thank Alok Saxena and Ghramduhari of Andaman and Nicobar Forest Department for their assistance and encouragement during the survey. Special thanks are due to Ravi Sankaran for his help and company in the field. Our sincere thanks are due to the ANET (Andaman & Nicobar Environmental Team) especially Saw Agu, Saw John, the late Saw Shwetey, Monto, Saw Uncle Paw, Saw Thapaw, Saw Poloaye, Saw Alex and Saw Uncle Pamway for support and assistance in field work; Manish Chandi for support and logistics; Ashok Captain for help and guidance in writing this manuscript; Romulus Whitaker and H. V. Ghate for their suggestions that have greatly contributed to this manuscript. We are also grateful to Harold K. Voris and Alan Resetar for providing information on distribution, and finally, to the Madras Crocodile Bank Trust for support and coordination.

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Enhydris plumbea (Boie, 1827) (Serpents: Colubridae; Homalopsinae), a new record for India

(with two text-figures)

In March 2001, while surveying the snakes of Great Nicobar Island, Bay of Bengal, India, we came across a dead juvenile *Enhydris plumbea* (Boie, 1827). Subsequently in June 2001, at 41 km road point on the Galathea River bank, Great Nicobar, we found another dead specimen. Both were preserved and deposited in the collection of the Zoological Survey of India, Kolkata (ZSI 25349-50, respectively). Though the head was damaged, the juvenile specimen was assigned to *E. plumbea* by matching other scalation data (midbody scale rows, ventral and subcaudal counts) as well comparing its colour pattern with the undamaged specimen.

Neither Smith (1943), Gyi (1970), Murphy and Voris (1994), nor Das (1997) record this species from India. However, Sclater (1891) gave the following distribution for *E. plumbea*: "S. India, Ceylon, Bengal, Assam, Burma, Southern China, Indo-China, Malay Peninsula and Islands." As this species has subsequently never been reported from India, there exists a strong possibility that its range was confused with that of *E. enhydris* (H. K. Voris, pers. comm). The nearest records of this species to the Nicobarese ones being reported here are from Sumatra (Indonesia), ca. 90 km from the southern tip of Great Nicobar. The present record extends its geographic range into India.

TABLE 1: Morphometry (in mm) and scalation of *Enhydris plumbea* from Galathea, Great Nicobar Island, India.

Specimen	ZSI 25349	ZSI 25350
Scales	19:19:17	19:19:17
Ventrals	123	126
Subcaudals	44	32
Infralabials	?	10
Genials	?	2 + 2
Anal	2	2
Snout-vent length	110	370
Tail length	20	100

FIGURE 1: *Enhydris plumbea* (Boie, 1827, ZSI 25350) from the Galathea River bank, Great Nicobar, India. Lateral view of head.

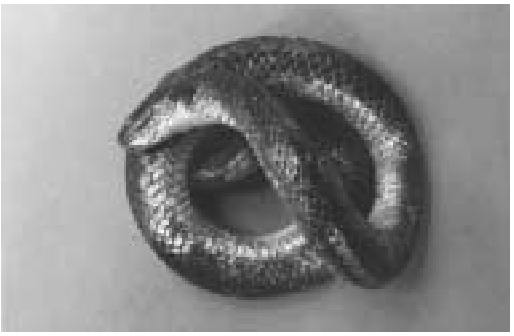

FIGURE 2: *Enhydris plumbea* (Boie, 1827, ZSI 25350) from the Galathea River bank, Great Nicobar, India. View of entire body.

Description and scalation of ZSI 25350: body cylindrical, scales smooth, head not very distinct from neck; snout broadly rounded; a single internasal not in contact with the loreal; loreal as long as high; frontal broader than supraocular; supralabials eight (4th touching the eye), 6th and 7th largest; eye small, pupil vertically elliptical. Additional scalation data are in Table 1.

We would like to thank Alok Saxena and Yashoratnam of Andaman and Nicobar Forest Department for their assistance and encouragement during the survey. Our thanks go to ANET (Andaman & Nicobar Environmental Team) especially Saw Agu, Saw Glain for assistance in field work; Captain Sitaram for his cooperation in Galathea, Manish Chandi and Rauf Ali for support and logistics; Rom Whitaker for his encouragement and support; Ashok Captain for help in writing this manuscript; H. V. Ghate for his suggestions that have greatly contributed to this manuscript. We are also grateful to H. K. Voris for providing recent records and the Madras Crocodile Bank Trust for support and coordination.

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A record of *Amphiesma venningi* (Wall, 1910) (Serpentes: Coludridae) from Meghalaya state, India.

Amphiesma venningi (Wall, 1910) was originally described from the Chin Hills, Burma (Myanmar). According to Smith (1943), it has not been recorded from India. This note reports the occurrence of *Amphiesma venningi* for the first time from the Jayantia Hills, Meghalaya State, north-eastern India (see Mathew, 1983, for a list of reptiles known from this state). Captain and Bhatt (2001) recently recorded the species from Arunachal Pradesh, based on a series of specimens taken from Gandhigram.

The Zoological Survey of India received a specimen (ZSI 25337) collected from Sonapur in the Narphu Reserve Forest, Jaintia Hills, Meghalaya State, north-eastern India on 13 September 1998. It was collected by N. Sen. The specimen has a total body length of 740 mm and tail length of 185 mm. Head moderate; eyes large; pupil rounded; a single loreal, squarish, slightly narrow in upper portion; supralabials 9, 4th, 5th and 6th touching eye; one preocular, 3 postoculars; temporal 1 + 2. Dorsal scales keeled, arranged in 17 rows. Ventrals 155; subcaudals 81; anal divided. Colour in alcohol, dark grey above with indistinct black squarish spots along the dorsal length; a dorso-lateral chain of yellowish white spots; each ventral scale yellowish with a dark-brown spot on each side.

I am grateful to J. R. B. Alfred, Director, Zoological Survey of India for providing facilities and S. J. S. Hatter, Officer-in-Charge, Eastern Regional Station, ZSI, Shillong for sending the material for study, and to S. K. Chanda for comments on the manuscript.

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AMPHIBIANS AND REPTILES OF MADAGASCAR AND THE MASCARENE, SEYCHELLES, AND COMORO ISLANDS by Friedrich-Wilhelm Henkel and Wolfgang Schmidt. 2000. English edition. Krieger Publishing Company, Malabar, Florida. viii + 316 pp. Hardcover. ISBN 1-57524-014-9. Available from Krieger Publishing Company, P. O. Box 9542, Melbourne, FL 32902-9542, USA. Fax: ++ 321 951 3671; Email: marketing@krieger-pub.com. Price (excluding postage): US$ 64.50

Originally published in German in 1995, the English language edition of the work originally entitled 'Amphibien und Reptilien Madagaskars der Maskarenen, Seychellen, und Komoren' is now available as yet another title in the growing series of volumes on herpetology issued by Krieger Publishing Company.

Although the cover page identifies only Henkel and Schmidt as the authors of the volume, the preliminaries show that the taxa covered by the volume was the work of three additional authors- Michael Knöthig (geckos and skinks), Klaus Liebel (frogs and snakes) and Roland Zobel (plated lizards). The final translation and technical edit was done by Hinrich Kaiser.

The organisation of the book includes: a preface by the first two authors, an account of the geological history, climate, vegetation and fauna of Madagascar, Comoro, Seychelles and the Mascarene Islands, followed by the species accounts. Finally, there is a three and a half page section on references and an index to scientific names, locality names, and various English names of species, herpetological and otherwise.

Species accounts for 240 species of amphibians and reptiles native to the region (plus introduced species such as *Calotes versicolor* and *Lycodon aulicus*) comprise the current scientific name and authority (updating the taxonomy from the original German edition), type locality, distribution (within the region, as well as extralimital), a general description of habitat, size, distinguishing features, biology and vivarium care. A colour photo is printed on the same page, when available. While the text will allow field identification, it is also geared for use by the terrarium-crowd, and contains tips on housing, feeding and breeding many of the rarely seen species from this archipelago.

Admitted the volume is expensive, the placement of photos of individual species within the species account (rather than bundled together and placed in one section of the book) may be one of the factors. The photos themselves are uniformly good, and many are apparently "shot in the field".

Overall, this is yet another fine production from Krieger, and deserves place in every library concerned with the herpetology of Africa and of island herpetofaunas.

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AMPHIBIANS AND REPTILES OF THE HASHEMITE KINGDOM OF JORDAN. AN ATLAS AND FIELD GUIDE by Ahmad M. Disi, David Modrý, Petr Necas and Lina Rifai. 2001. Edition Chimaira, Frankfurt am Main. 408 pp. Hardcover. ISBN 3-930612-12-7. Available from Chimaira Buchhandelsgesellschaft mbh, Friedberger Anlage 14, D-60316 Frankfurt am Main, Germany; Tel: + 49 69497223; Fax: + 49 69497826; Email: frogbook@aol.com. Price (excluding postage): DM 78.00 (Euro 40).

The herpetofauna of the Hashemite Kingdom of Jordan, unlike some of neighbouring countries, suffered from a lack of an accessible field guide to its herpetofauna. Written by a well-known team of Jordanians and Moravians have rectified the situation with this excellent field guide.

The contents of the work include: a preface (by Wolfgang Böhme), acknowledgements, an introduction with notes on format of the work, abbreviations used, an account of the geography and climate of Jordan, biogeography, an account of the history of herpetological research, hints on field observations and herpetological collecting in Jordan, threats and conservation of the herpetofauna, a list of protected areas, herpetofauna in the cultural heritage (including a recipe for cooking the Dabb, *Uromastyx aegyptia*), venomous snakes, snake-bite, snake venom, and treatment of snake-bite, identification keys to amphibians (including the larval stages) and reptiles, species accounts, a list of additional species likely to occur in Jordan, or questionably recorded from the country (e.g., *Triturus vittatus*), the appendices (including mention of amphibians and reptiles in the Quran and the Bible), a gazetteer of localities, list of antivenom serum for Jordanian snakes and their suppliers, common Arabic names of Jordanian amphibians and reptiles (using Arabic script, as well as their English transcriptions, and finally, 20 pages of references.

Species accounts comprise the current scientific name and authority, the original citation, a list of common names in English, German and French, systematic notes, general distribution, local (i.e., within Jordan) distribution, habitat, description, notes on biology, additional remarks (including miscellaneous remarks on systematics, folklore, etc.) and finally, the pertinent references. A dot-map shows the Jordanian distribution of each of the five species of amphibians and 85 species of reptiles.

Overall, this is an excellent production from Chimaira, a relatively newcomer in herpetological publishing, with several new titles as well as reprints of important works. The binding is solid and the work is entirely printed on art paper. Colour photos of species, which, by the way, are excellent, are placed directly opposite the description. What this work does lack is an index of scientific names, and perhaps also names of author and of localities.

Arguably, this is the best herpetological field guide published this year, for content, format and affordability.

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LIFE, LOVE AND REPTILES by Sherman A. Minton, Jr., M.D. 2001. Krieger Publishing Company, Malabar, Florida. 236 pp. ISBN 1-57524-172-2. Available from Krieger Publishing Company, P. O. Box 9542, Melbourne, FL 32902-9542, USA. Fax: ++ 321 951 3671; Email: marketing@krieger-pub.com. Price (excluding postage): US$ 24.50.

Between the Ditmars era and "us" (baby boomers and such) exists another generation of herpetological mentors and luminaries and Dr. Sherman Minton is one of them. I'm kind of intimidated by the lab herpetologists - they communicate just fine among each other but somehow, it's usually the field person who has the time and patience to listen and answer the ravings of a noviciate.

From what people tell me, Sherman was just that. I do know he answered my inane letters (usually snakebite and venom queries) with thoughtful responses. I regret never having been in the field with Sherman but I did get to meet him at the First World Congress of Herpetology in Canterbury in 1989 and a few other herp get-togethers. Naturally we talked about India, Pakistan and snakebite - trying to spew out all my pent-up questions before the rest of the gang surrounding Sherman whisked him off to their subject.

It was a pleasure to read Sherman's autobiography. For one thing, names of folks I know or idolise keep popping up and his descriptions of herp hunting in remotest Pakistan and tropical México were reminiscent of the nostalgic favourite, Kauffeld's 'Snakes and Snake Hunting'. I didn't realise both Sherman and wife Madge were scuba divers. The sea snake work he carried out in the Pacific with William Dunson and Hal Heatwole is seminal. It's a real shame we still know almost nothing about sea snakes in the vast waters surrounding India.

And Sherman just kept jumping into things that have a deep fascination for the herpeto-naturalist. Which made him a pre-emptor who hit upon or at least proposed what later became common knowledge. For example, his supposition that some populations of the whiptail lizard (*Cnemidophorus*) of the American West may be all female (and parthenogenetic) which indeed some are! Being a venom man (besides all his other interests and accomplishments), Sherman was also fascinated with so-called non-venomous snakes actually being very dangerous. He reminds us of German colleague Robert Merten's death by the bite of an African bird snake, then considered harmless. Mertens kept a detailed record of the symptoms as did another friend, Karl Schmidt who was fatally nailed by an African boomslang. Mertens ended his record with the sentence "for a herpetologist, a singularly appropriate end."

Zipping through the list of 200 publications that Sherman had, the range of subjects befits his accomplishments. An amazing array that includes a paper on gas gangrene for "War Medicine" (1942), many on snake venoms and bites, all the way to a forty-five year overview of amphibian populations in his home state of Indiana (1998).

Sherman's adventure-loving wife, Madge didn't "put up with" a herpetologist's strange ways, she was part of it all and this comes through very strongly. The book is interspersed with personal statements by herpetologists who know and worked with Sherman as well as numerous black and white photos. I wasn't too impressed with the pictures - a better selection, including creatures talked about would have enhanced this book. An index of all the people, places and critters in the text would have been really helpful too.

Having been in México a lot in the 1960's I was amused by Sherman's reference to trying a small slice of the hallucinogenic peyote cactus and not feeling anything. Hell, we used to chomp down a whole cactus and it was so bitter we'd mix the awful stuff in a milk shake or even a peanut butter and jelly sandwich. Man, was it worth it though - but that's another story.

Sherman comes through as a very modest man (his pal, Dr. Bernard Bechtel sets the record straight in the concluding "Retrospective" chapter). Maybe this is why I was disappointed with the writing style. His exciting life is told to us in straight-faced diary form. 'Life, Love and Reptiles' is a good read for those of us in the herp fraternity but might not hold the interest of all those underprivileged normal folks out there.

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LAWRENCE WESLEY SWAN

(1922-1999)

Raja of the Autonomous Native State of Cooch Nahai

Educator and explorer of the high Himalayas and herpetologist, Lawrence Wesley Swan (born 1922), passed away on 5 May 1999. Swan described himself as an "ecologist-zoogeographer, anatomist, evolutionary philosopher with entomological, avicultural, botanical, behavioral and molecular biases and an obdurate dreamer".

The son of Methodist missionaries, Swan was born and raised near Darjeeling, in what is now the east Indian State of West Bengal. Swan attended the University of Wisconsin and Stanford University, receiving both masters and doctoral degrees (1952) in biology from the latter institution. In 1954, he returned to India and Nepal as a member of the first American Himalayan Expedition, researching the zoology of the high Himalayas, coming again for a second expediton, with Sir Edmund Hillary, in 1960, as part of a team to conduct high-altitude research. Throughout his career he led numerous additional educational expeditions to other parts of the world, including Africa, South America, Australia, New Zealand and Asia.

Swan was an outstanding educator and one of the pioneers of television education in the western United States; he was a brilliant lecturer and on his last trip to India (1984), he addressed the Bombay Natural History Society on the roof of the Society building in Bombay (now Mumbai). In 1967, Swan received the Distinguished Teacher Award from the California State University.

Among Swan's most important contributions to science was the discovery and definition of the Aeolian Zone at the upper border of the alpine region. This zone is devoid of autotrophic vascular plants and supplied with air-borne nutrients, such as pollen and oceanic albuminoids. Autotrophic algae, lichens and moss, as well as a variety of heterotrophic animals and plants occur here. Swan further classified the aeolian zone into terrestrial, nival and aquatic divisions. An abiding interest of Swan's was the so-called 'Abominable Snowman' or yeti, the subject of some of his writings, such as a 1958 note in the prestigious journal, *Science*. Swan concluded that the footprints hitherto attributed to the yeti, were, in fact, those of the mountain fox, known for its curious hopping gait. Swan concluded the elongated "footprint" and the toe-like impression were caused by sublimation of one of the exposed sides to a greater degree than the other. With Alan E. Leviton, in 1962, Swan prepared a review of the herpetofauna of Nepal, an essential biogeographic synthesis of the fauna; this was the subject of his (Swan's) masters thesis.

Swan was a born collector. One of his early notes from 1956 in *Turtox News*, was on the utility of insect nets for field personnel (uses include picking up hot dishes, catching chickens for dinner, obtaining frogs and lizard specimens, paddle

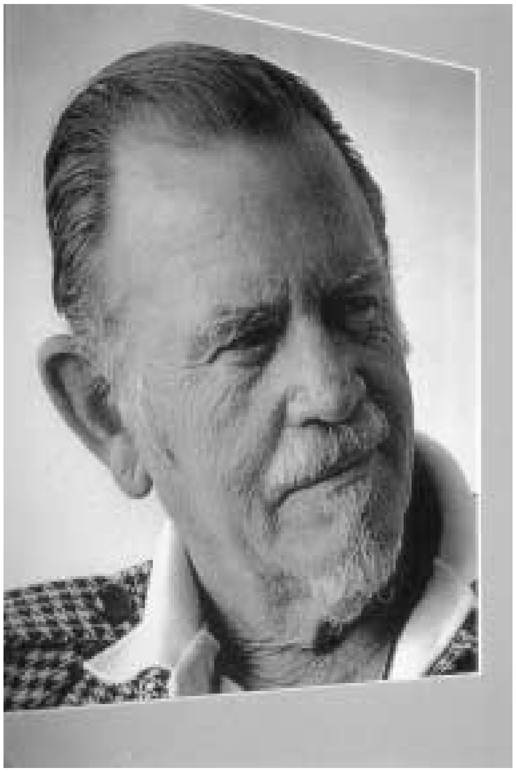

FIGURE 1: Portrait of Lawrence W. Swan (1922-1999).

FIGURE 3: Robert C. Drewes at the Tomb of the Unknown Frog, Autonomous Native State of Cooch Nahai.

for an air-mattress boat, keeping snow out of the eyes, while permitting vision during a blizzard, scaring buffalos and dogs, decoy for leeches, use as sieve, mosquito net, tent pole, seat, fan, pillow and even for catching insects).

Eccentricity often accompanies genius. Larry Swan "seceded" his 40,000 feet property in Redwood City, California, from the USA, appointing himself Raja of the Autonomous Native State of Cooch Nahai (literally, 'nothing' in Hindi) ; his wife Ruth became the Rani. Cooch Nahai printed its own stamps (Fig. 3), had a national holiday (21 June, coinciding with the summer solstice), a national symbol (the extinct dodo, also the currency of the State), and its memorials include the Tomb of the Unknown Frog (Fig. 4) and the Great Wall of Cooch Nahai, upon which he cemented oddities collected around the world by his graduate students. In a tongue-in-cheek letter to S. H. Cantwell, Jr., then Minister of the Department of Public Works, County of San Mateo, CA, dated 3 April 1979, Swan drew the attention to the existence of this Autonomous State and its secession on 21 June 1978 from the USA, witnessed by "one hundred and fify loyal subjects" (most of whom were fellow faculty members and students, current and past, of Swan's at San Francisco State University). Cooch Nahai was the repository for obscure collections by his students as well as his own of stamps, ethnic masks, books and biological oddities including a two-headed cat. Cooch Nahai was famous for its network of walk-in aviaries which were interconnected by wire tubes, some of which were even vertical. To visit this independent Native State was to be surrounded by flocks of birds, from finches and weavers to imperial pigeons.

Numerous honours and awards have come his way. He was a Fellow of the California Academy of Sciences, a Fellow of the Royal Geographical Society. At least two species names honour Larry Swan- the Nepalese frog, *Rana* (at present *Sphaerotheca*) *swani* and the glacier flea, *Machilanus swani*. Swan's eminently readable autobiography, completed in 1999, and published posthumously in 2000 (with a Foreword by Sir Edmund Hillary), details the world of this high altitude explorer.

Contributions to Larry Swan's memory can be made to the Himalayan Trust, founded by Sir Edmund Hillary, in support of a Sherpa school in Kathmandu, Nepal at: The Himalayan Trust, c/o Larry Witherbee, 267 Exmoor Avenue, Glen Ellyn, Illinois 60137, USA.

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FIGURE 2: Larry Swan on St. Patrick's Day.

FIGURE 2: Stamps issued by the Autonomous Native State of Cooch Nahai.

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The Croc Bank: 25th Birthday Reminiscences

It is a great honor that the venerable editors of *Hamadryad* have asked me to reflect on the Croc Bank in this 25th year of its life. As they well know, there will be no gems of science here, no ruminations on scutes or occipitals or *Osteolaemus tetraspis*. Having spent my whole life, practically from Day One, among scientists, I have managed to remain the generic layman: quite an achievement. My own contribution to the "Bank" has been that of co-initiator, on/off dogsbody, critic and, equally, fan. The actual making of the institution, of developing and steering it through thick and thin, has however been the lot of the many others who for reasons of space will have to remain nameless. Some have come and gone but many- administrators, trustees and other staff- are still here, hopefully a measure of the rewarding and energizing nature of this place.

In excavating its beginnings, one cannot ignore three other institutions which are, willy-nilly, a part of the package. The first is the Madras (now Chennai) Snake Park, set up in the early '70s by the then-American (now naturalized Indian) herpetologist Rom Whitaker in the beautiful and central Guindy Deer Sanctuary. Helped along by a host of local naturalists and friends, the Snake Park was the first reptile-focused conservation/research project in the country. Although its conservation achievements were impressive- it kick-started the movement to save Silent Valley in Kerala and Guindy Deer Park, which was being eye-balled by real estate groups- its magnum opus was to bring reptiles into the realm of animals, so to speak. Public sympathy okayed the protection of lions and tigers, and even a frog or two… but reptiles?

Then, as now, snakes killed a horrific number of people every year. A study done by Dr Yoshio Sawai of the Japan Snake Institute indicated that most of these - almost 90%- are cobras. In India, death from snakebite is a gross possibility: the production of antivenom serum is, sadly, a problem—ridden issue with crucial decisions being made by politicians and novices. The lack of adequate and high-quality antivenom serum is fortunately balanced by the low mortality rates of venomous bites; but understandably, people do not see snake conservation as a priority issue. Equally, the wealth of myth and legend about snakes and the treatment of snakebite is both a colorful and compounding factor. The fact that the Snake Park managed to claw through this forest of brambles and create a solid base of reptile-support, speaks volumes for the band of people, both paid and un, who supported its goals. One positive outcome of the reptile crusade was the banning of the snake skin trade, in 1974: a response to the over ten million snake skins exported annually from India. But as we know, "positive outcomes" often have a flip side and in this case it was the further impoverishment of the Irula tribe of snake-catchers, many of whom depended on the skin trade. They were already victims of another flip side: the increasing protection of the coastal scrub forests of the Eastern Ghats was rapidly depriving them of traditional hunting areas. Thus was the Irula Snake-catchers' Industrial Cooperative Society was born, thanks again to many suffering friends and associates. It is today the main supplier of snake venoms to antivenom production units, and has twice won the Best Cooperative Award for Tamil Nadu State, the Rolex Award for Enterprise and many other accolades. The four common venomous snakes- the cobra, krait, Russell's viper and saw-scaled viper- are caught and kept in captivity during three extractions, then released back into the wild. The entire process, including the lyophilizing of venoms, is carried out by the Irulas. Mr Dravidamani, who has been with the project since its inception, has the pleasure of carrying out the Herculean paper-work, a feat which only those who have worked in this country can truly appreciate.

Not to be outdone by the lowly snake, the three species of Indian crocodililians were begging for attention as well. Surveys conducted by

Snake Park staff and research associates indicated a grim scenario: the gharial and saltwater crocodile, in their rather restricted ranges, were near extinction and the mugger or marsh crocodile following suit. We had begun a program to collect and hatch mugger nests in the few viable habitats in Tamil Nadu, and the findings were that all nests were being collected/destroyed by animal and human predators. The disturbance factor was so high that females were trekking across miles of steep, stony ground in search of nesting sites. I remember sitting on a rocky ledge way above the Bhavani Sagar reservoir, watching a small female struggling up the slope.

While the large reservoirs of this state are administered by the Fisheries Department, the land around belongs to the Forest Department; and the Electricity Board and Waterworks folks also have a say in issuing permits for visitors. Further, there was the question of American-looking spies who protested they were Indian. However it is to the credit of all these departments and many enlightened officials, that our ragged band of croc-egg collectors managed to start a genetically healthy breeding programme.

In 1976 this group of captive-hatched mugger was transferred to a large natural pond in the village of Vadanemmeli, some 35 kms south of Chennai city. Thanks again to beleaguered donors and friends, other species and enclosures rapidly followed and today the Croc Bank has 14 species of the world's crocodilians. Several hundred mugger have been turned over to government for release in the wild. However, since the Government of India/FAO crocodile project began around the same time and on a much larger scale, the Bank's raison d'etre was somewhat hijacked. But like people, institutions must change and flex with changing circumstance and context. As a Centre for Herpetology it has been involved in the captive breeding, study, conservation and management of several species of endangered reptiles including the king cobra, cane turtle, monitor lizards and several rare and endemic amphibians. Much of this has been possible because of a wide range of associates and visitors. We have rubbed shoulders with the likes of Jeff Lang and Ed Moll; Fred Medem and Carl Gans, J. C. Daniel and Binod Choudhury, Wayne King and Grahame Webb, Fritz Huchzermeyer and Harvey Lillywhite. These are the shoulders I can remember at the moment; there are many others as well. In 1984 the Madras Snake Park changed hands and many of us left to concentrate on the crocodiles. The snake venom cooperative was translocated too, by the nervous wife of the American Consul in Madras. It is hard to drive with over 500 venomous snakes behind you, some in rather delicate earthen pots and others in thin muslin bags. Around this time too, Harry Andrews joined the Crocodile Bank wagon and remains its director. The complex skills required to execute this responsibility must, for lack of space, be left to the imagination.

The Crocodile Bank receives some 250,000 visitors a year. Apart from the entertainment value of seeing hundreds of stationary rock-like objects- and being told by anxious staff how fascinating they are- it is becoming an important education center for students. Talks, slide shows and demonstrations help overcome the natural fear of all reptiles, and there are now overnight camps for students which include visits to the venom centre (next door) and another project which is also of the Crocodile Bank network. This is the Irula Women's Society, the female counterpart of the snake venom cooperative. Its three hundred members are involved in a unique scheme for the social and economic empowerment of adivasi (indigenous people) women. One facet is the collection, preparation and sale of herbal products such as teas and shampoos; another, the documentation of Irula knowledge and skills; and a third, the accessing of rights and welfare schemes available to the adivasi peoples of India. Thus, students on camp here at the Croc Bank leave with an integrated idea of the reptile conservation mosaic: the issues of sustainable use of wildlife, the role of indigenous peoples in its study and protection, and the importance of research in managing species and forming strategies (the lack of which is beginning to show at both the state and national levels). The education program has been extended to training zoo personnel in the captive care of reptiles; as when, last year, local zoo-keepers attended a three-day workshop on the husbandry and management of king cobras. In November there will be another one, for environment-educators, in collaboration with the Center for Environment

Education. Perhaps the Croc Bank's most crucial contribution has been the research/conservation/education project in the Andaman and Nicobar Islands. It began in 1975 with the first censuses of the saltwater crocodile and the four species of sea turtles which nest on the beaches of these ethereally beautiful and dismally endangered islands. It is a unique chain of islands, with a multi-level ecosystem of high canopy forest, mangrove, beaches where sea turtles and sea snakes nest, and of course the almost unmatched coral reefs. It is the home of India's last two indigenous peoples who spurn contact with the outside world. Add to this a number of endemics including many reptiles and amphibians, and you have a naturalist's paradise, and one which we should be rushing to cherish and preserve. This, sadly, is not the case.

ANET, the Andamans and Nicobars Environmental Team, with Harry Andrews at the helm, has several ongoing research programs in the Islands including a study, currently, of the status of the sea turtle nesting beaches. Its education program trains school teachers, thus encouraging a broad-based distribution of eco-sensitivity at the local level. Because of its commitment and expertise, ANET is now represented on most of the crucial government and NGO committees concerned with both the development and the protection of the Islands. I must end this with a special mention of the Croc Bank's Canteen. Here, one is likely to be bitten by the most vicious carpenter ants ever evolved. But this is also where you hear the most amazing stories; because people collect here to talk and listen (and gesticulate) after a field trip. Here, one hears that Indraneil Das has found a few more frogs or lizards new to science, or that some extinct crocodile has re-surfaced in Thailand. Or that Rom Whitaker crawled into a croc tunnel in Sri Lanka, forgetting for a moment that it was occupied. One hears, usually from Harry Andrews, the latest episodes about the Jarawa, the Andamans tribe which still answers intrusion with an arrow. More power to them!- and to all the people who bring these experiences to us at the Canteen, and who have made the Croc Bank what it is today.

— *Zai Futehally*

INSTRUCTIONS TO CONTRIBUTORS

Hamadryad publishes original papers dealing with, but not necessarily restricted to, the herpetology of Asia. Reviews of books and major papers are also published.

Manuscripts should be only in English and submitted in triplicate (one original and two copies, along with three copies of all tables and figures), printed or typewritten on one side of the paper. Manuscripts can also be submitted as email file attachments. Papers previously published or submitted for publication elsewhere should not be submitted. Final submissions of accepted papers on disks (IBM-compatible only) are desirable. For general style, contributors are requested to examine the current issue of *Hamadryad.* Authors with access to publication funds are requested to pay US$ 5 or equivalent per printed page of their papers to help defray production costs. Reprints cost Rs. 2.00 or 10 US cents per page inclusive of postage charges, and should be ordered at the time the paper is accepted.

Major papers exceeding four pages (double spaced typescript) should contain the following headings: Title, name and address of author (but not titles and affiliations), Abstract, Key Words (five to 10 words), Introduction, Material and Methods, Results, Discussion, Acknowledgements, Literature Cited (only the references cited in the paper). Appendices follow the main paper. Descriptions of new taxa will be considered as major papers regardless of size. Abstracts (up to 150 words) should summarize the important findings of the paper and should avoid references. In case of descriptions of new taxa, diagnoses should be provided in the abstract. Special attention should be paid to accents and diacritical marks: if fonts are not available in the software or typewriter, these may be put directly on the hard copy of the manuscript by hand.

References should be in the following format:

Papers:
GAULKE, M. 1994. Notes on the herpetofauna of Panaon and Sámar, East Visayans, Philippines. *Hamadryad* 19:1-10.

Books:
RUSSELL, P. 1796. An account of Indian serpents collected on the coast of Coromandel; containing descriptions and drawings of each species; together with experiments and remarks on their several poisons. George Nicol, London. viii + 90 pp + Pl. I-XLVI.

Chapters in books:
KIEW, B. H. 1984. Terrestrial vertebrate fauna of Lambir Hills National Park. *In*: An ecological survey of Lambir Hills National Park, Sarawak. pp: 55-63. E. Soepadmo & K. I. Sudderuddin (Eds). University of Malaya, Kuala Lumpur.

Unpublished reports:
WILKINSON, J. W., J. W. ARNTZEN & R. S. THORPE. 1995. Amphibian populations on organic farms: their role in pest control. M.A.F.F. Report. iv + 48 pp.

Publications in languages other than English:
SZCZERBAK, N. N. & M. L. GOLUBEV. 1986. [The gekkonid fauna of the USSR and adjacent countries.] *Sci. Acad. Ukranian SSR Zool. Inst.* 1986: 1-232. [In Russian.]

Tables should be comprehensive without reference to the text. Tables should follow the main body of the paper, and their desired location within the text indicated on the manuscript. Footnotes are generally not allowed. Line art and half tones are preferred as electronic files saved on compact disks or attached to email files. Black and white photographic prints and slide transparencies are accepted if they are sharp and show good contrast. Black and white photos should be printed on glossy paper at least 152 x 204 mm after being trimmed at right angles and should carry the name of the author and of the manuscript at the back. Illustrations should be preferably done with Indian ink on good quality tracing paper. All lettering should be done using high quality computer printouts or transfers. Illustrations should be planned to fit either one column (6.5 mm) or one page (14 mm) width, after suitable reduction.

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