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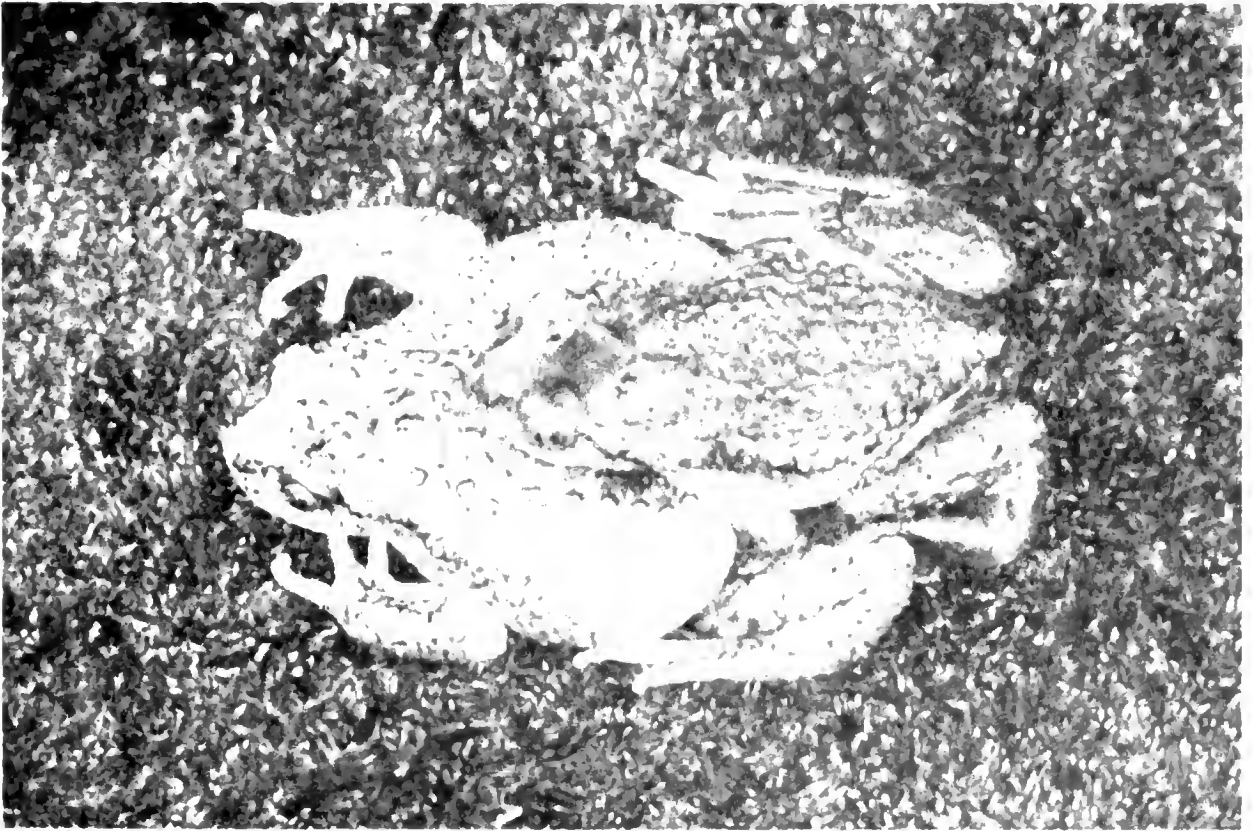


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# ASIATIC HERPETOLOGICAL RESEARCH



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# *Asiatic Herpetological Research*

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Cover: *Scutiger boulengeri* from Wenquan (35° 24' N, 99° 23' E), Qinghai Province, China. Photo by J. Robert Macey.

## Two New Species of the Worm-like Lizard *Dibamus* (Sauria, Dibamidae), with Remarks on the Distribution and Ecology of *Dibamus* in Vietnam

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**Abstract.** -Within Vietnam and the southern part of China there dwell 5 species of worm-like lizards of the genus *Dibamus*, two of them (*D. greeri* sp. nov. and *D. bogadeki* sp. nov.) are new to science. Some new data on the distribution, ecology, morphology, coloration, as well as the structure of hemipenes and the autotomy and regeneration of the tail is given for the species studied. The specific peculiarities of the body and tail coloration in some dibamids may apparently draw the attention of birds of prey, and in connection with this are regarded as the manifestation of attractive coloration and as Batesian mimicry.

**Key words:** Reptilia, Sauria, Dibamidae, *Dibamus*, China, Vietnam, ecology, taxonomy.

### Introduction

According to the current data, the genus of worm-like lizards *Dibamus* Dumeril et Bibron, 1839 includes 9 species widely distributed on the mainland and on a number of big and small islands in Southeast Asia. As to the mainland part proper of this vast area, registered here were only 4 species of which *D. alfredi* is known mainly from the Malay Peninsula, and the three others (*D. bourreti*, *D. montanus*, and *D. smithi*) occur only within Vietnam (Greer, 1985). *Dibamus bourreti* was earlier reported from southern China (Liu and Hu, 1962) and recently was found in Hong Kong (Lazell and Lu, 1990).

From 1982 to 1988, while conducting field herpetological investigations in different regions of mainland and insular Vietnam, the author collected some new material which considerably expands the former views on the distribution as well as the morphological characters and ecology of the genus *Dibamus* within that country. The results of the treatment of the material and the description of the new species are given below.

### Methods

All in all, 12 individuals of the genus *Dibamus* were studied, mainly from Vietnam. They were taken by the author and his colleagues in the course of several

Vietnamese-Soviet zoological expeditions from 1982 to 1988. Different species of the genus from other parts of its range were also examined for comparison. Measurements of snout-vent length (SVL) and tail length (TL) were made by adpressing the animals against a plastic rule taped horizontally to a bench top. All drawings were made under an "Opton" stereomicroscope with a camera lucida attachment. X-ray photos were taken with the Japanese apparatus "Softes". In the description of the elements of scuttellation, I mainly applied the terminology used by Greer (1985).

The following acronyms were used: ZIN- Zoological Institute, Russian Academy of Sciences, St. Petersburg (Leningrad); BM- British Museum Natural History; MNHP- Museum Natural History, Paris; IEMEM- Institute of Animal Evolutionary Morphology and Ecology, Moscow; MCZ- Museum of Comparative Zoology; ZMMU- Zoological Museum, Moscow State University; CAS- California Academy of Sciences.

### Species Accounts

*Dibamus bourreti* Angel  
Figs. 1, 3, 4, 5, and 11.

This species was described by Angel (1935) who had one specimen available from Tamdao, Vinhphu Province, northern

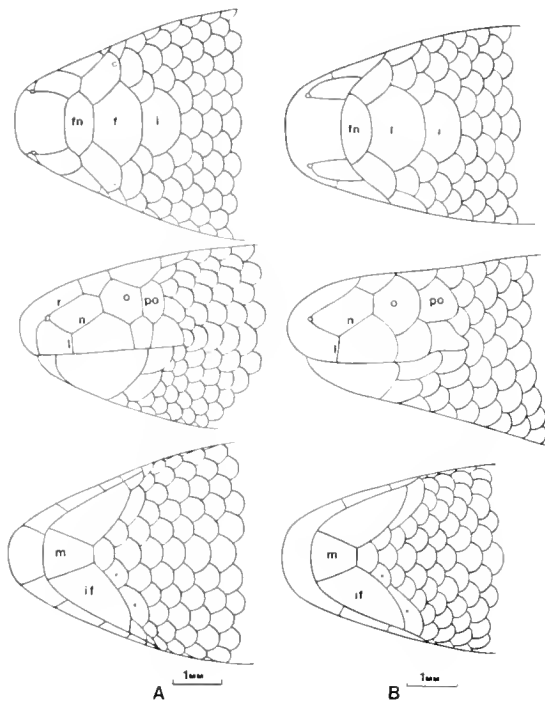


FIG. 1. Head in dorsal, lateral and ventral view of A- *Dibamus bourreti* (ZIN 20012); B- *Dibamus bogadeki* (holotype, MCZ 172041); sutures: r- rostral; n- nasal; l- labial; fn- frontonasal; f- frontal; i- interparietal; o- ocular; po- postocular; m- mental; if- infralabial.

Vietnam. The same type specimen (MNHP 35417) was reexamined by A. Greer in his revision of the family Dibamidae (Greer, 1985). Earlier, Liu and Hu (1962), having three specimens at their disposal, were the first to indicate this lizard for Kwangsi Province (= Guangxi Province) in southern China. Recently a specimen was found in Hong Kong (Lazell and Lu, 1990). In Vietnam, according to the literature, *D. bourreti* is also known from Ninhbinh, Hanamninh Province (Tran et al., 1982) and from the reserve Kukfiong, Hasonbinh Province (Darevsky and Sang, 1983). We also found this lizard in Tamdao, An Lac Shon Dong, Habac Province and on the Vietnam inshore island Katba, Haiphong Province (Darevsky, 1990), (Fig. 2).

The data on the morphology of all specimens we examined are given in Table 1. These data considerably expand the morphological characteristics of *D. bourreti* described by Greer (1985). Already in his

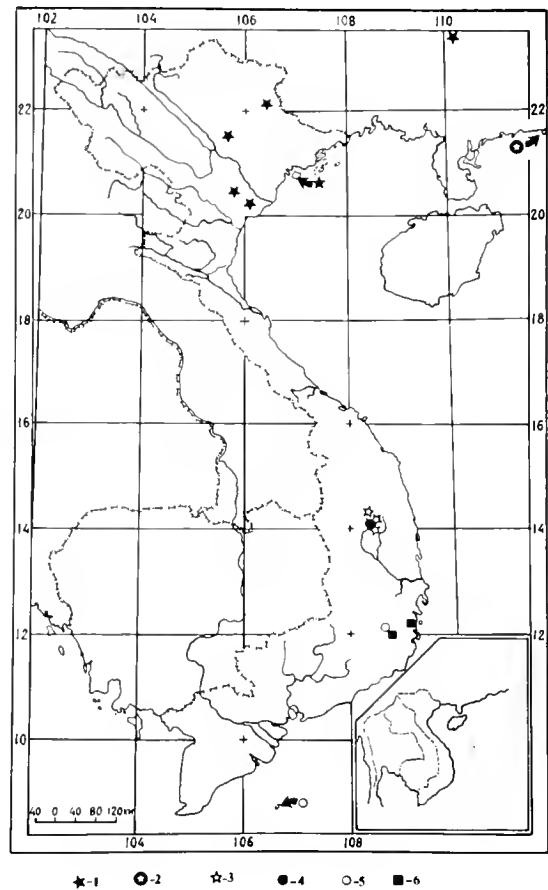


FIG. 2. Distribution of the known localities of *Dibamus* species in Vietnam and southern China: 1- *Dibamus bourreti*; 2- *Dibamus bogadeki*; 3- *Dibamus greeri*; 4- *Dibamus* sp.; 5- *Dibamus montanus*; 6- *Dibamus smüthi*.

first description, Angel (1935) noticed the typical white coloration on the back part of the tail in the specimen available. Lui and Hu (1962) also pointed to the same peculiarity of this species, for individuals from Guangxi Province, China. This distinguishes it from all other representatives of the genus *Dibamus* and the specimen reported from Hong Kong by Lazell and Lu (1990). I noted the bright milk white coloration on the end part of the tail in individuals from Katba Island, but specimens from Tamdao and Kukfiong lacked it, possibly because their tails were regenerated. Attention is also drawn to the fact that the coloration of the tail and the back part of the body in specimens from Katba Island and Hong Kong is not uniform. It is to be accounted for by the



TABLE 1. Investigated morphological characters of *Dibamus* specimens from Vietnam and southern China.

Species	Museum No.	Sex	Locality	SVL (mm)	TL (mm)	% TL of SVL	mid-body scales	sub-caudals	post-oculars	scales on		postsacral vertebrae	hind-limbs (mm)	hindlimbs % of SVL	body diameter	body diameter % of SVL
										posterior edge of infralabial	posterior edge of infralabial					
<i>D. bourreti</i>	MNHIP 35417	F	Tamdao	154	32 cut	20.7%	24	52+	1	2	129	23+	-	-	5.0 mm	3.2%
<i>D. bourreti</i>	ZIL 20278	M	Tamdao	95	25 cut	-	23	16+	1	2	125	12+	2	2.1%	4.2 mm	3.2%
<i>D. bourreti</i>	ZIL 19803	F	Kukfiong	72	9 cut	-	22	30+	1	2	124	19+	-	-	3.2 mm	4.4%
<i>D. bourreti</i>	ZIL 20012	F	Lac Shon	122	52	42.6%	20	88	1	2	115	46	-	-	4.1 mm	3.3%
<i>D. bourreti</i>	ZIL 20014	M	Katba Island	138	51 cut	-	21	73+	1	2	129	40+	3.1	2.2%	4.2 mm	3.0%
<i>D. bourreti</i>	602021	M	Guangxi, China Liu & Hu 1962	130	35 cut	27.0%	23	57+	-	-	-	-	-	-	-	-
<i>D. bourreti</i>	603570	F	Guangxi, China Liu & Hu 1962	150	72	48.0%	23	99	-	-	-	-	-	-	-	-
<i>D. bourreti</i>	603571	M	Guangxi, China Liu & Hu 1962	130	55	42.3%	23	-	-	-	-	-	-	-	-	-
<i>D. bogadeki</i>	MCZ 172041	M	Hong Kong	177	40 cut	22.5%	23	51+	1	2	135	25+	4.7	2.6%	6.0 mm	3.3%
<i>D. greeri</i>	ZIL 20011	M	Kontarang	82	23	-	20	53	1	1 & 3	96	31	1.8	2.1%	4.1 mm	4.9%
<i>D. greeri</i>	ZIL 20016	F	Tram-Lap	84	20	-	20	54	1	1 & 3	111	28	-	-	3.3 mm	3.9%
<i>D. greeri</i>	IEMEM 101	F	Buoenloy	86	5 cut	-	20	-	-	-	99	-	-	-	4.0 mm	4.6%
<i>D. montanus</i>	ZIL 20017	M	Kondao Island	111	23	20.7%	22	59	4	2	137	36	1.8	1.6%	2.7 mm	2.4%
<i>D. smithi</i>	ZMMU R-6567	M	Whatrang	83	5 cut	-	19	13+	2	3	115	11+	2	2.4%	2.6 mm	3.1%
<i>Dibamus sp.</i>	IEMEM 102	F	Buoenloy	?	?	?	19	91	?	?	126	49	-	-	-	-

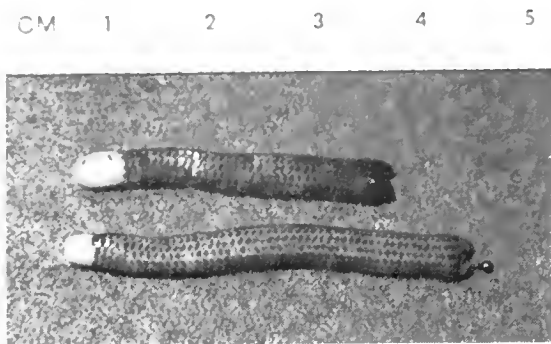


FIG. 3. Two autotomic tails with regenerated tips of *Dibamus bourreti* (upper, ZIN 20014a); (lower, ZIN 20014b).

location of the pigment on every single scale. It is concentrated more compactly in its front part and is poorly marked at the rear (Fig. 3). Greer (1985) mentions the presence of four preanal pores on each side of the anal opening in the only female he examined (MNHP 35417). In this connection it should be noted that these pores were not observed in any of the 5 specimens I examined (3 males and 2 females). This character is apparently not constant in *D. bourreti*.

*Field Notes.*—All the *D. bourreti* specimens currently known were caught under stones or wood debris on the ground of a tropical forest at an elevation of 450-900 m. Liu and Hu (1962) found two specimens in China on the surface of the ground in a hilly forest.

In discussing the milky white coloration on the end part of the tail in *D. bourreti*, it should be observed that this species can also be characterized as having a comparatively very long tail, its length reaching 40% or more of the SVL in both males and females (in other representatives of the genus the length of the tail does not exceed 20-25% of the SVL). The long tail with a bright coloration at its end contrasting sharply with the dark unicolor body of the animal may qualify as a good example of attractive coloration. My observations show that in case of danger (when the stone under which the animal hides is lifted) a *Dibamus* abruptly

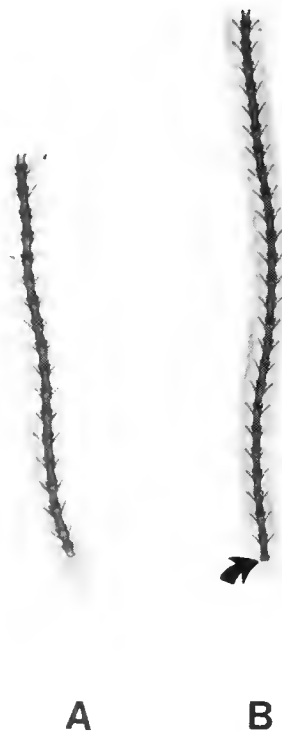


FIG. 4. X-ray photograph of the two autotomic tails with regenerated tips of *Dibamus bourreti* A- (ZIN 20014a); B- (ZIN 20014b). The arrow points to place of the fracture between two neighboring vertebrae.

raises its tail upwards which apparently immediately attracts the attention of a bird of prey, such as ground foraging birds like jungle or pea fowls rummaging about in the forest litter in search of food. Caught by a bird, the fragile tail easily breaks off, and the animal has time to hide itself under the ground. Here it may be noted that out of the 5 specimens examined, 4 had a regenerate tail to some degree. This is seen in the X-ray photo (Fig. 4).

*Comment.*—As Greer (1985) noted, the scales on the regenerate tail in *Dibamus* almost does not differ from the original. But the new tail may be distinguished by the arrangement of the scales on its end part. While a normal tail is somewhat sharp at the end and its point is covered with concentric rows of scales gradually becoming smaller, the regenerate tail ends

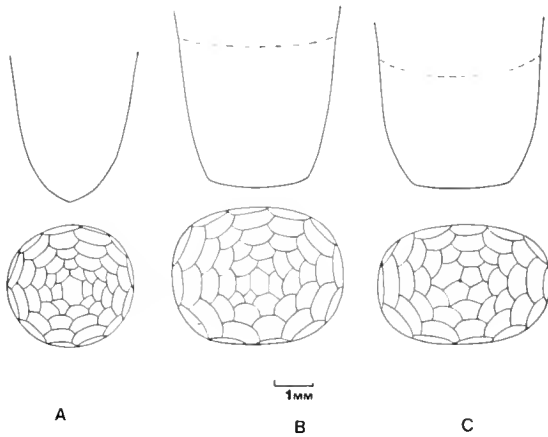


FIG. 5. Scales on the top of original (A) and regenerated (B, C) tails of *Dibamus bourreti*; A- (ZIN 20014a); B- (ZIN 20014b).

bluntly by a plane oval platform occupied by some relatively big irregularly arranged scales (Fig. 5). X-ray photographing clearly shows the fracture which can occur not only across one of the tail vertebrae, as it is in most other lizards, but on the border between two neighboring vertebrae as well. The new tail is longer owing to the fact that the connective tissues spread out both in length and width (Fig. 4). At the same time, a peculiar tail "blade" up to 1 cm long covered with scales is formed, acquiring the bright white coloration described above (Fig. 3).

Judging from the collection material examined and the literature data, *D. bourreti* is characterized by a distinct intraspecific variability. Angel (1935) and Greer (1985) noted the complete absence of labial sutures in the only specimen from Tamdao (MNHP 35417) they studied. The specimen caught by the author in Tamdao (ZIN 20011) is also deprived of labial sutures. In all other examined individuals from Vietnam, as well as from Guangxi Province, China (Liu and Hu, 1962), this suture is well developed. Within wider limits, *D. bourreti* shows variations also in mid-body scale rows (from 20-24). Some coloration differences in various individuals were discussed above. It is possible that the lizards from the type locality (Tamdao) may be isolated in a separate nominate subspecies *D. b. bourreti* Angel. Further

study is needed to settle this question. With respect to this it may be noted that the isolated tracts of forest of the Tamdao mountain ridge show marked endemics among reptiles, as well as some other groups of animals.

*Dibamus greeri* sp. nov.

Figs. 6, 7, 8, 11 and Plate 1.

*Holotype*.—ZIN 20011; Kontarang, Gilai-Contum Province, Vietnam; 850 m; I. S. Darevsky; 21 June 1983; male.

*Paratypes*.—ZIN 20016; Tram-Lap, Gilai-Contum Province, Vietnam; 800 m; A. Gorochoy; 12 December 1988; female. IEMEM 101; Buoenloy, Gilai-Contum Province, Vietnam; 750 m; December 1981; S. Smirnoff; female.

*Diagnosis*.—Differs from all other species of dibamids in the following combination of characters: medial rostral and nasal sutures incomplete; one postocular; two supralabials; frontal much larger than frontonasal and than infraparietal; posteromedial edge of the infralabials bordered by one narrow and long scale; 20 mid-body scale rows; 97-111 presacral vertebrae; 29-31 post sacral vertebrae (number of vertebrae is less than in all other *Dibamus* species).

*Description of Holotype*.—Medial rostral and nasal sutures incomplete and barely extending to anterior edge of rostral pad; the labial suture well developed; frontonasal wider than long; frontal very big, approximately four times bigger than frontonasal; interparietal divided into two, each part bigger than adjacent nuchal scales (in paratype intraparietal not divided); two supralabials posterior to rostral pad; only one narrow scale located along the posteromedial edge of the infralabial with bordering posteromedially by three small scales situated between the second postmental and second infralabial; 20 midbody scales; 54 subcaudals; 97 presacral vertebrae; 32 postsacral vertebrae; SVL 82 mm; TL 23 mm; preanal pores absent; hind limbs very short, 1.4 % of SVL.



FIG. 6. X-ray photograph of *Dibamus greeri* (holotype, ZIN 20011).

*Comment.*—Greer (1985) noted a considerable morphological resemblance between the species of *Anelytropsis* and *Dibamus* and in particular he singled out the species *D. bourreti* which is most close to *Anelytropsis papillosus* in having a complete rostral suture passing through the nostril, a complete nasal suture, and in some other features. As to *D. greeri*, this species resembles *A. papillosus* in the presence of one narrow and long scale bordering on the posteromedial edge of the infralabials (Fig. 7).

*Coloration.*—Living animals (Holotype) uniformly purplish-brown above and below with three distinct brightly blue rings, 6-9 body scale rows wide, two on the body and one on the tail. Shortly after capture, one of the rings on the body disappeared and the two others remained (Plate 1). The two other known individuals (females) had the same coloration as the holotype in life, but

they lacked the blue rings.†

*Hemipenis.*—Everted hemipenes are quite smooth conic formations tapering to the apex with a small hollow near the tip (Fig. 8). The length of the organ is 1.1 mm, and the width is 0.4 mm. No accounts about hemipenes in the family Dibamidae have been given prior to this account (Greer, 1985).

*Distribution.* All three known specimens were taken in the central part of the Gilai-Contum Province in southern Vietnam (Fig. 2). It can be assumed that this

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† I observed whitish-gray rings on the body and the tail in some preserved *Dibamus novaeguineae* specimens from the Philippine Islands (CAS 26647, 26678, 27538, 140218, and others). It is very possible that in living animals the rings were blue as in *D. greeri*.

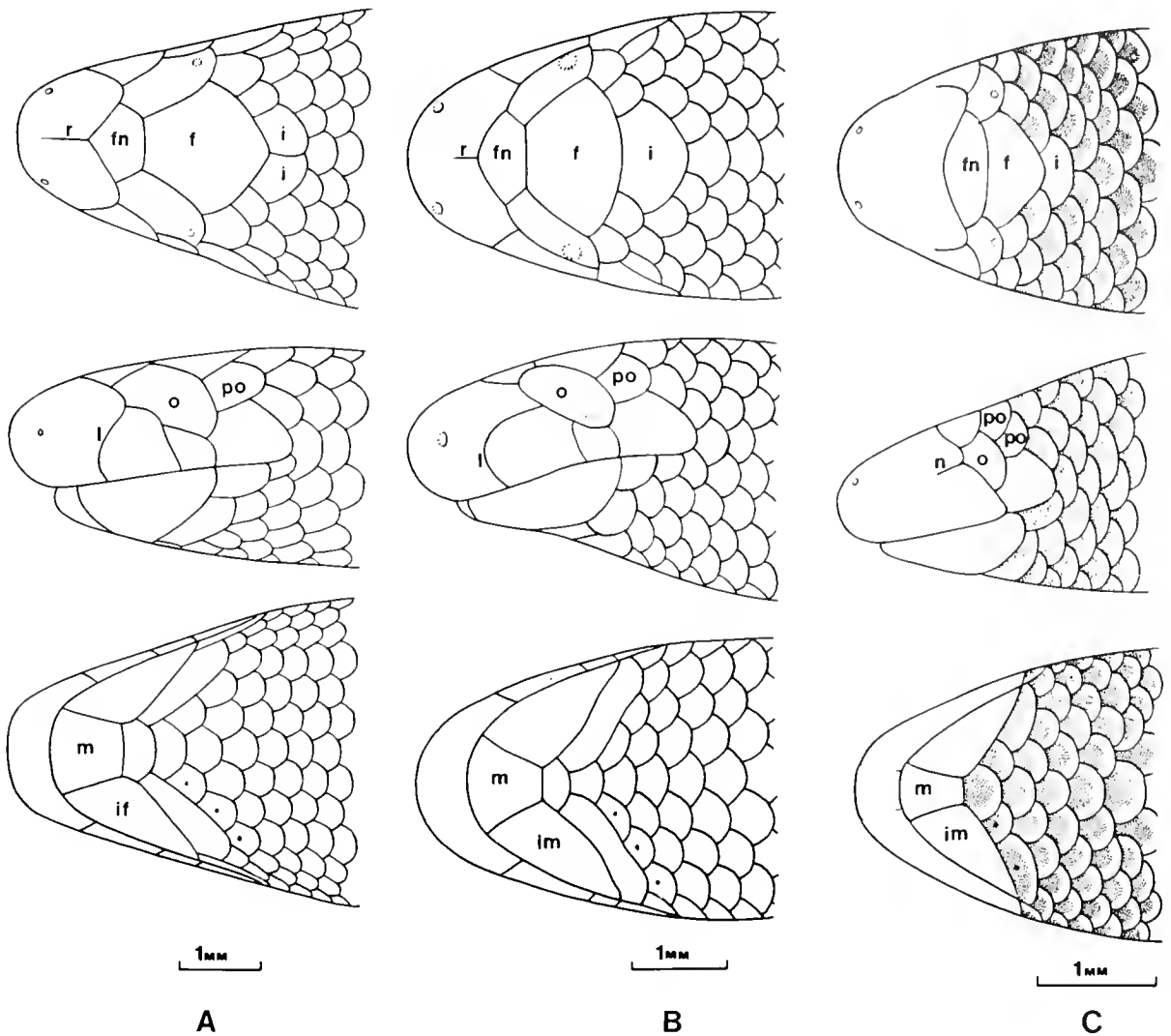


FIG. 7. Dorsal, lateral and ventral view of the head of A- *Dibamus greeri* (holotype, ZIN 20011); B- *Dibamus greeri* (paratype, ZIN 20016); C- *Dibamus smithi* (ZMMU R-6567). For abbreviations see Fig. 1.

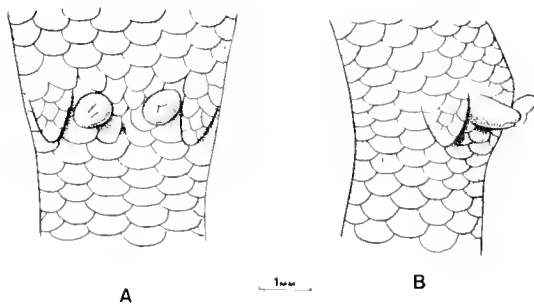


FIG. 8. Everted hemipenes of *Dibamus greeri* (holotype, ZIN 20011). A- Front view; B- Side view.

species widely occurs within the Pleicu Plateau occupying the central part of Gilai-Contum Province.

*Etymology*.—Named for Allen E. Greer, the author of numerous works in the field of taxonomy of various groups of lizards, including the fundamental study of the family Dibamidae.

*Field Notes*.—The type specimen was found in a big lump of the so-called “suspected” soil. The lump, which pierced through with plant roots of epiphytes, had fallen down from a tree at a height of about

three meters. It was torn to pieces by the author right after it fell to the ground. The trunk of the tree was twisted with liana up to three meters height and it was thickly overgrown with moss. The animal seems to have worked its way up under the cover of the moss. After capture the lizard behaved very aggressively, struggled to break loose, and opened its mouth to bite. The two other specimens were discovered in the wood litter under the cover of the forest. Specimens of two new species of lizards, *Sphenomorphus rufocaudatus* and *Ophisaurus sokolovi* (Darevsky and Sang, 1983) were found at the same locality.

The bright blue coloration in the form of separate spots, stripes or ocelli is known to occur in many species of diurnal lizards. It is usually regarded as one of the features of sexual coloration. But it is evident that the blue rings in worm-like lizards which live in the soil and are practically blind cannot play this role. Some other explanation must be found for it. Hence, it is of interest to note that the bright blue rings on the body of *Dibamus greeri* make the animal outwardly resemble some tropical motley colored earth worms of the Megascolicidae family living in the forest litter. If such worms are not edible or venomous, it may be assumed that this represents a peculiar case of Batesian mimicry. The ground-foraging birds, such as jungle fowl, spur fowl and pea fowl may have been important selective agents in the evolution of such a memetic resemblance as was shown for some species of uropeltid snakes (Gans, 1987). This assumption, however, must be supported experimentally, especially because the blue rings are capable of appearing and disappearing, and were found by the author only in one male. They were absent in females and have never been observed in other species of the genus *Dibamus*.

*Dibamus bogadeki* sp. nov.  
Figs. 1, 9 and 10.

*Dibamus* cf. *bouretti* Lazell and Lu, 1990

*Holotype*.—MCZ 172041; Hei Ling

Chau, ca. 10 km southwest of Victoria, Hong Kong; A. Bogadek; 1 April 1987 (Fig. 10).

*Diagnosis*.—Differs from all other *Dibamus* in the following combination of characters: medial rostral suture absent; nasal sutures not complete; labial sutures present; interparietal large; one postocular; two supralabials; 23 midbody scale rows.

*Description of Holotype*.—Nasal suture incomplete; not present from lip to nostril and extending from nostril to the ocular only; the labial sutures well developed; frontonasal wider than long; fontal approximately 3 times bigger than frontonasal; interparietal larger than frontonasal; 2 supralabials posterior to rostral pad; one postocular; two scales bordering posterior edge of the first infralabial, one of them wider than the other; 23 midbody scales; 51+ subcaudals; 134 presacral vertebrae; 25 postsacral vertebrae in incomplete tail; SVL 177 mm; TL 40 mm; preanal pores absent; hindlimbs well developed, 2.7% of SVL. According to Lazell and Lu (1990) and the description by Dr. J. D. Lazell (pers. comm.) the living animal was lilac or lavender-gray, irregularly mottled lighter and darker, at darkest, light plumbeous. Tail ash-white; head flecked with ash-white, but not as much as tail. As in *D. bouretti*, the white coloration of the back part of the tail apparently demonstrates a characteristic case of attractive coloration.

*Distribution*.—It is known only from the type locality. The only finding of this species during all the research history of the Hong Kong herpetofauna indicates that it occurs very rarely on this island (Fig. 2). According to J. D. Lazell (pers. comm.) the following reptiles are known from the type locality of *Dibamus bogadeki*, Hei Ling Chau: *Hemidactylus bowringi*, *Gekko chinensis*, *Typhlops braminus*, *Pareas margaritophorus*, *Python molurus*, *Ptyas corros*, *Trimeresurus albolabres*, *Naja haja* and other snake species.

*Etymology*.—The species is named for its first collector Fr. Anthony Bogadek,

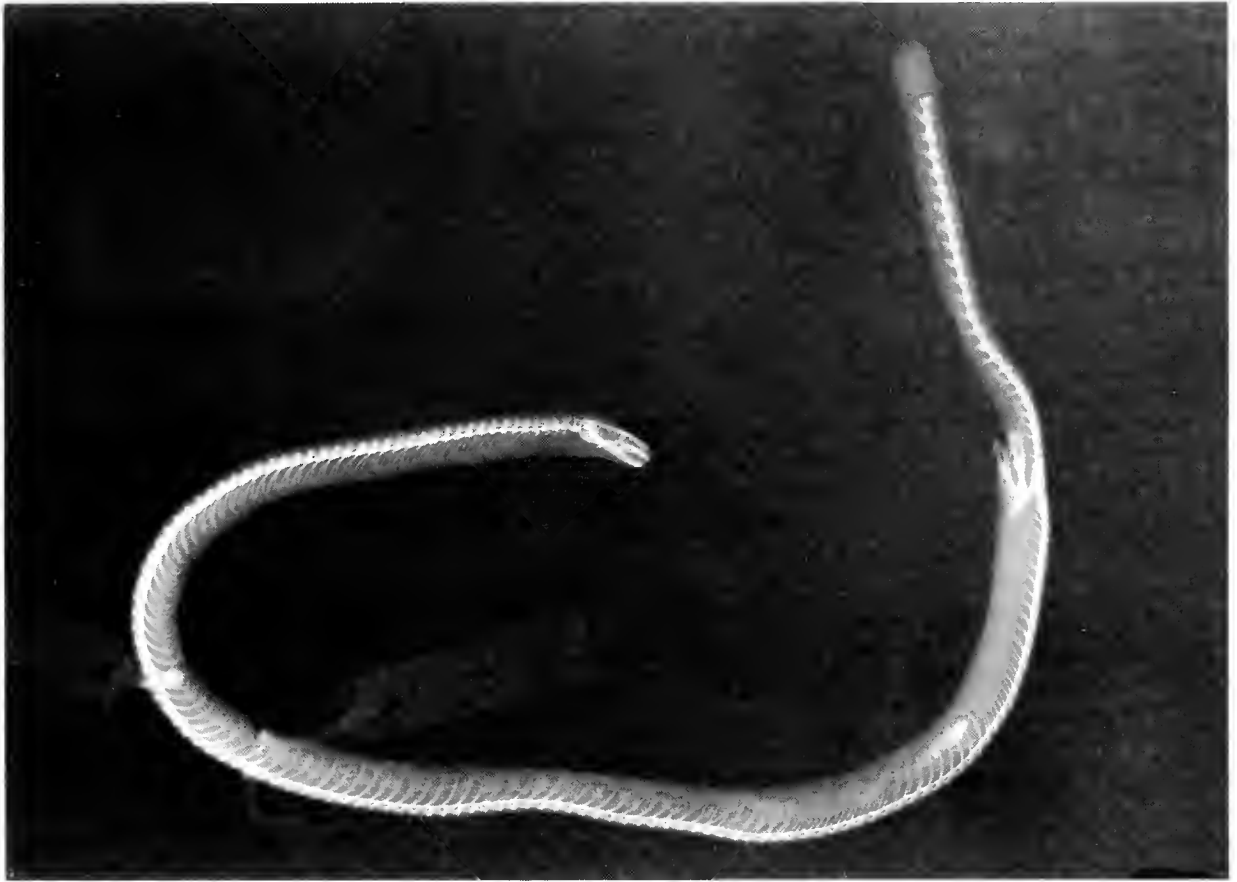


FIG. 9. X-ray photograph of *Dibamus bogadeki* (holotype, MCZ 172041).

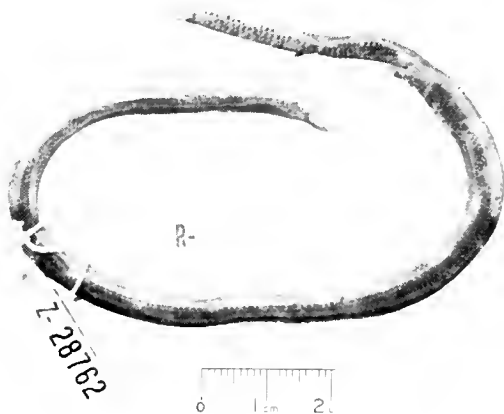


FIG. 10. Photograph of *Dibamus bogadeki* (holotype, MCZ 172041).

biologist at the St. Louis School, Victoria, Hong Kong, and coauthor of the book, *Hong Kong Amphibians and Reptiles* (Urban Council, 1986).

*Comment.*—On a number of characteristics, coloration included, this insular species is most close to *D. bourreti*, which drew the attention of Lazell and Lu (1990). At the same time, there is a clear-cut difference between *D. bogadeki* and *D. bourreti*, such as the important character of an incomplete nasal suture. It is also characterized by a large size of SVL 177 mm and by a markedly greater number of presacral vertebrae (136). See also Table 1.

#### *Dibamus montanus* Smith

Smith (1921) described this species having at his disposal a few specimens from the Langbian Plateau in the present Lamdong Province in southern Vietnam. All the type series has been recently reexamined by Greer (1985) who singled out the Lectotype (BMNH 1946.8.3.2) out of two specimens from Le Bosquet.

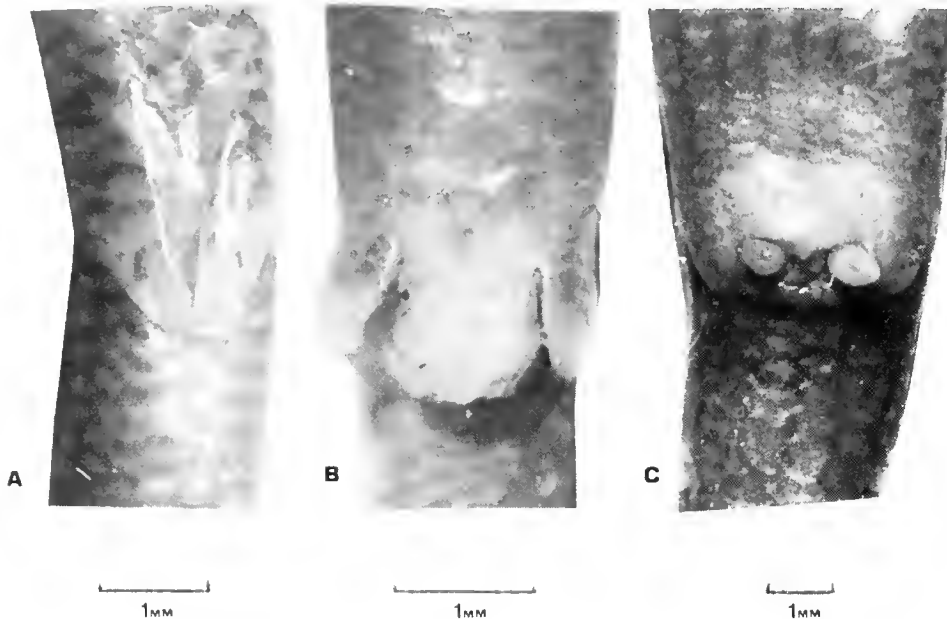


FIG. 11. Anal area with the male's hindlimbs of three *Dibamus* species: A- *Dibamus smithi* (ZMMU R-6567); B- *Dibamus bourreti* (ZIN 20278); C- *Dibamus greeri* (holotype, ZIN 20011).

Two specimens of *D. montanus* were captured by the author in April, 1987 at an elevation of about 500 m in a tropical forest on Condao Island (formerly Pulo Condore)<sup>†</sup>

*Dibamus smithi* Greer  
Figs. 7 and 11.

Smith (1921) was the first to notice the differences between a part of the specimens from the Langbian Plateau he had at his disposal and the typical individuals of *Dibamus montanus*. Greer (1985) studied these specimens again and showed that they refer to the new species *Dibamus smithi* he had described. This species is known only from the type locality (Daban, Lamdong Province, Vietnam). I also had at my disposal a specimen (ZMMU R-6467) captured in April, 1985 by V. F. Goncharov from Nhatrang, Phykhanh

Province, Vietnam.

*Comment.*—*Dibamus smithi*, as well as the closely related species *D. montanus*, has a non-uniform body coloration. On each of the body scales the dark pigment is located more compactly in its front part forming a peculiar reticulate pattern (Fig. 11, A). On the whole, both of these species differ from the other representatives of the genus *Dibamus* in having a more slender body (see Table 1).

*Dibamus* sp.

I had at my disposal one headless specimen (a female) from Buoneloy, Gilai-Contum Province, Vietnam (IEMEM 102) identified by Iordansky (1985) as *D. bourreti* and used by him for studying the head muscles. The absence of the head prevents us from identifying the species of this specimen. But it should be noted that the 19 midbody scale rows clearly distinguish it from its sympatric species, *D. greeri* and the large number of postsacral vertebrae (49) makes it different from all

<sup>†</sup> Earlier these specimens were mentioned for Condao under the name *D. smithi* (Darevsky, 1990).



other species in the genus *Dibamus* from Vietnam. It is of interest to note that in this headless specimen, as was shown by Iordansky (1985), some rudiments of postfrontal bones are preserved. According

to Greer (1985), *Anelytropsis papillosus* also have such bones, while the specimen of *D. greeri* examined by Iordansky, as well as *D. novaeguineae* (Rieppel, 1984) lack them.

Key to the species of *Dibamus* from Vietnam and southern China.

1 (7). Mid-body scale rows 20-24.

2 (8). Medial rostral suture absent or incomplete (barely extending to anterior edge of the rostral pad).

3 (4). Nasal suture complete and extending between the nostril and the posterior edge of the rostral pad.....*D. bourreti*.

4 (3). Nasal suture absent or incomplete (not extending to the posterior edge of the rostral pad).

5 (6). Nasal suture reduced; medial rostral suture present.....*D. greeri*.

6 (5). Nasal suture present and extending from the nostril and ocular.....*D. bogadeki*.

7 (1). Mid-body scale rows 18-19.....*D. smithi*.

8 (2). Medial rostral suture complete extending to the tip of the snout .....*D. montanus*.

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## A New Subspecies of the Dwarf Snake *Calamaria lowi ingermarxi* ssp. nov. (Serpentes, Colubridae) from Southern Vietnam

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**Abstract.** -The Indo-Malay species of the dwarf snake *Calamaria lowi* Boulenger was discovered for the first time in Vietnam, where it is represented by the subspecies *Calamaria lowi ingermarxi* spp. nov. Some other examples pointing to the historical links between the herpetofaunas of Vietnam and the insular regions of Southeast Asia are given. A key to the subspecies *Calamaria lowi* and to other *Calamaria* species from Vietnam is given.

**Key words:** Reptilia, Serpentes, Colubridae, *Calamaria*, Vietnam, biogeography, distribution, taxonomy.

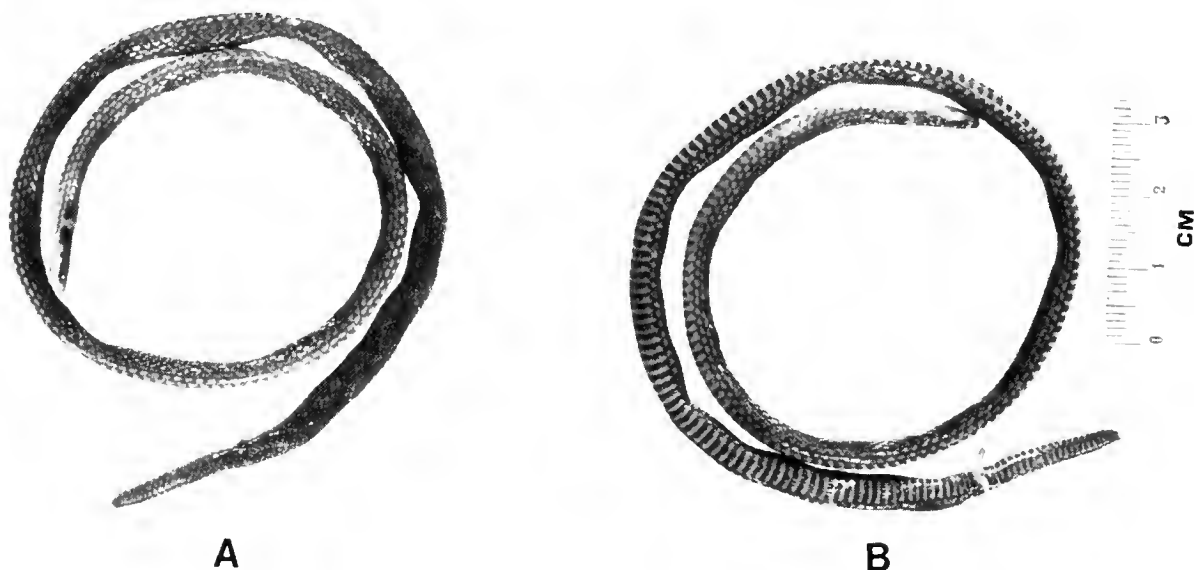


FIG. 1. A- Dorsal and B- lateral view of ZIN 20006, the holotype of *Calamaria lowi ingermarxi*.

### Introduction

According to the last revision of the genus of oriental colubrid dwarf snakes *Calamaria* H. Boie, 1827, the widely distributed species *Calamaria lowi* Boulenger, 1877 forms three well distinct subspecies. Of them, the nominative subspecies *C. l. lowi* Boulenger occurs on Kalimantan Island, Thailand, *C. l. wermuthi* Marx and Inger is known from a single specimen from the western part of Java Island, Indonesia, and *C. l. gimletti* Boulenger is distributed on the Malay Peninsular mainland and the two adjoining

small islands of Aor and Riouw (Inger and Marx, 1965). The northern most location of this subspecies on the Malay Peninsula is Kalantan where the holotype comes from.

In 1982, during field herpetological work in Vietnam, a specimen of *C. lowi* was taken by the authors for the first time in Indochina, more than 1000 km to the northeast of the known mainland distribution of the species. A detailed study of this specimen showed that it belongs to a subspecies new to science. Its description is given below.



FIG. 2. Dorsal and lateral view of the head of ZIN 20006, the holotype of *Calamaria lowi ingermarxi*.

*Calamaria lowi ingermarxi* spp. nov.  
Figs. 1, 2, 3, and 4.

*Holotype*.—Zoological Institute, Russian Academy of Sciences, St. Petersburg (Leningrad), ZIN 20006; Buoenloy, Gilai-Contum Province, Vietnam; 750 m; I. S. Darevsky; 18 June 1982; male (Fig. 1).

*Diagnosis*.—Differs from all other subspecies of *Calamaria lowi* in the following combination of characters; maxillary teeth modified; second and third supralabials enter orbit; mental touching anterior chin shields; ventrals uniformly dark gray colored with light posterior edges; 205 ventrals; 23 subcaudals.

*Description of holotype*.—Rostral wider than high, portion visible from above more than half length of prefrontal suture;

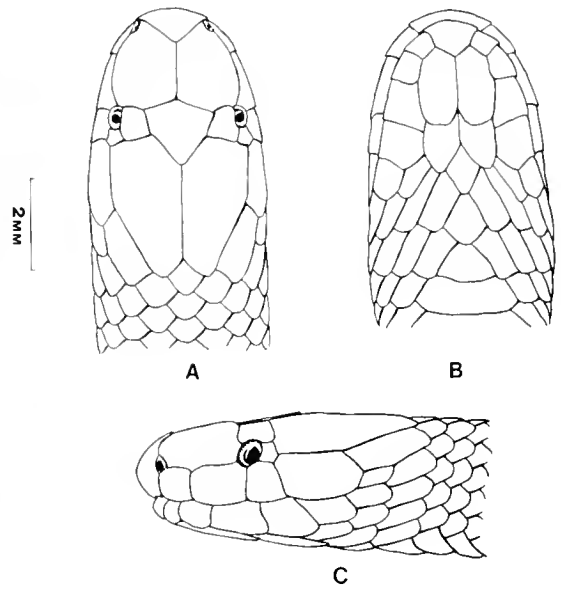


FIG. 3. Head: A- dorsal view; B- ventral view; C- lateral view; ZIN 20006, the holotype of *Calamaria lowi ingermarxi*.

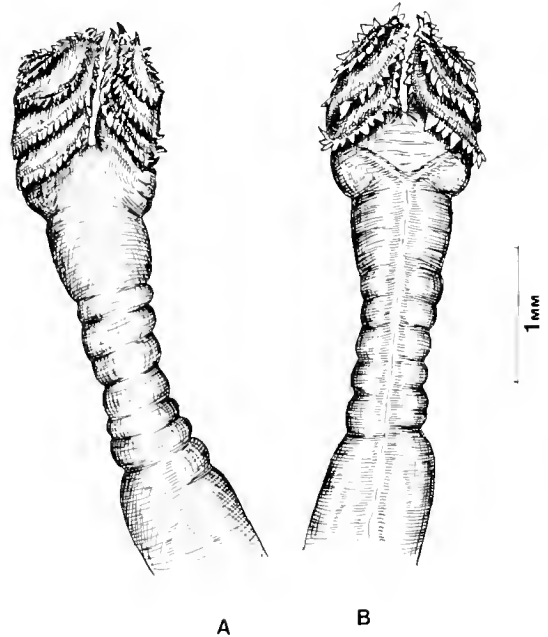


FIG. 4. Left hemipenis of *Calamaria lowi ingermarxi*. A- lateral; B- dorsal view.

prefrontal longer than frontal, touching first two supralabials; frontal 2 times width of supraocular, length about two thirds that of the parietal; paraparietal surrounded by 6 shields and scales; nasal smaller than

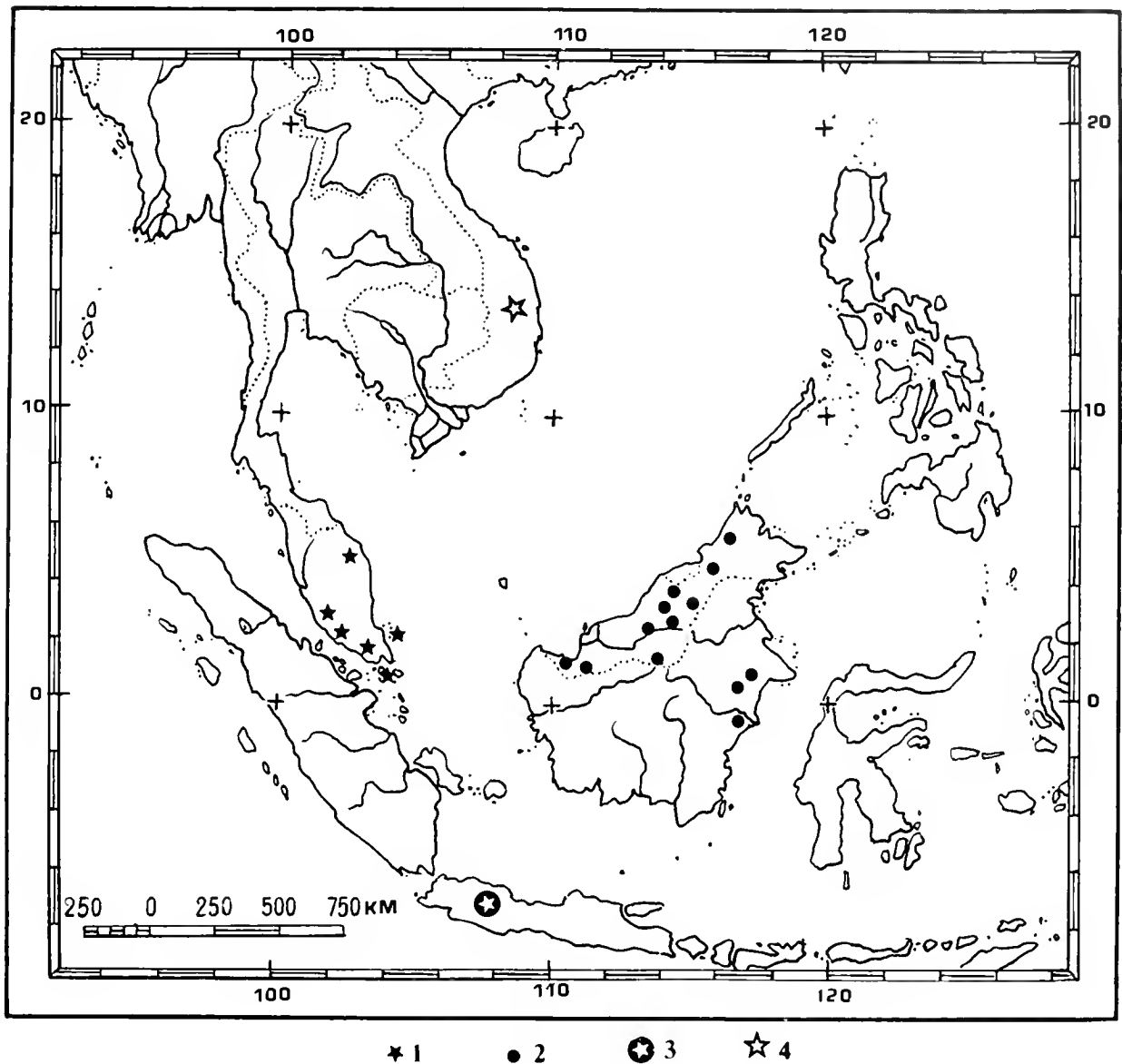


FIG. 5. Map of the main known localities of *Calamaria lowi* subspecies: 1- *C. l. lowi*; 2- *C. l. gimletti*; 3- *C. l. wermuthi* (after Inger and Marx, 1965); 4- *C. l. ingermarxi*.

postocular; no preocular; postocular as deep as eye; 4 supraoculars, second and third entering orbit, fourth longest, first not longer than third; mental triangular, touching first pair of chin shields; both pair of chin shields meeting in mid-line; 3 gulars in midline between posterior chin shields and first ventral (Figs. 2 and 3). Tail short, not tapering, tip blunt; dorsal scales reduce to 4 rows on tail opposite first to fifth subcaudal anterior to terminal scute. Eight modified maxillary teeth. Thirteen scale

rows, 205 ventrals, 23 subcaudals; SVL 296 mm; TL 22 mm; ratio of tail to total length is 0.074.

The hemipenis is 4 mm in length, forked on the top, calyces papillate (Fig. 4). Body grown gray-bluish, immaculate; light spots on each side of neck covering 4 scales; lower halves of supralabials yellowish. Ventrals and subcaudals uniformly dark gray except for light borders at the extreme posterior edge of the ventrals (Fig. 1).

*Distribution.*—Known only from the type locality in central Vietnam (Fig. 5). Probably occurs widely within the Pleicu Plateau in the central part of Gilai-Contum Province in central Vietnam.

*Etymology.*—This subspecies is named for Robert F. Inger and Hymen Marx who have made a great contribution to the study of the herpetofauna of Southeast Asia. Among other works, they are the authors of an important summary on the taxonomy and evolution of the snake genus *Calamaria*.

### Discussion

This specimen of *Calamaria lowi* from Gilai-Contum Province in central Vietnam was found a considerable distance from the main distribution of this species, which is the Malay Peninsula in Malaysia and the islands of Kalimantan and Java, in Thailand and Indonesia respectively. However, *C. lowi* is not the only species suggesting some historical link between the herpetological faunas of Vietnam and the

insular regions of Southeast Asia. For example, in central Vietnam at the type locality of *C. l. ingermarxi* we collected a specimen of the skink, *Sphenomorphus stellatus* (Boulenger). This species is also found in Thailand on Kalimantan Island (Bacon, 1967). This region of Vietnam is also the type locality of the glass lizard *Ophisaurus sokolovi* Darevsky and Sang (1983). This species is closely related to *Ophisaurus buetticoferi* Mertens from Kalimantan Island, Thailand. In the same area a specimen of *Calamaria septentrionalis* was collected. This species is widely distributed in Vietnam and also on the Malay Peninsula.

The present day disjunction in the ranges of these and some other species of reptiles and amphibians are apparently of secondary formation, as a result of the changes occurring in the paleogeographic conditions in this region. In particular, the sinking of the water level during the Pleistocene, which led to the separation of both Kalimantan and Java from the mainland (Beaufort, 1951).

Key to the species of *Calamaria* from Vietnam.

- 1 (6). Preocular present.
- 2 (3). Ventrals yellow, immaculate .....*C. buchi* Inger et Marx.
- 3 (2). Ventrals yellow, with dark lateral tips.
- 4 (5). Tail as thick as body, not tapering, end broadly rounded .....  
.....*C. septentrionalis* Boulenger.
- 5 (4). Tail not as thick as body, tapered, pointed .....*C. pavimentata* Dumeril et Bibron.
- 6 (1). Preocular absent .....*C. lowi* Boulenger.

Key to the subspecies of *Calamaria lowi*.

- 1 (2). Mental not touching anterior chin shields .....*C. l. gimletti* Boulenger.
- 2 (1). Mental touching anterior chin shields.
- 3 (4). Ventrals uniformly cream colored .....*C. l. wermuthi* Inger et Marx.
- 4 (3). Ventrals colored otherwise.
- 5 (6). Anterior ventrals cream, posterior ventrals almost uniformly dark brown; or ventrals yellow with large, irregular brown squares .....*C. l. lowi* Boulenger.
- 6 (5). Ventrals all uniformly dark gray with light posterior borders .....  
.....*C. l. ingermarxi* ssp. n.

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## A New Species of the Genus *Tropidophorus* (Reptilia: Lacertilia) from Guangxi Zhuang Autonomous Region, China

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**Abstract.** -A new species of *Tropidophorus* is described from Guangxi Zhuang Autonomous Region, China. This new species (*Tropidophorus guangxiensis*) is characterized by having an undivided postmental, that differs from *T. sinicus* which is divided. Though the postmental is undivided in *T. thai*, the new species is separated from *T. thai* in having an undivided frontal, which is similar to *T. sinicus*.

**Key words:** Reptilia, Lacertilia, Scincidae, *Tropidophorus*, China, Guangxi, taxonomy.



FIG. 1. Holotype of *Tropidophorus guangxiensis*, GMC 85-032 from Daming Hill, Wuming (23° 23' N 108° 30' E), Guangxi Zhuang Autonomous Region, China.

*Tropidophorus guangxiensis* sp. nov.  
Figs. 1, 2, 3, 4 and 5.

**Holotype.**—GMC 85-032 (Fig. 1), a juvenile from Daming Shan (23° 23' N

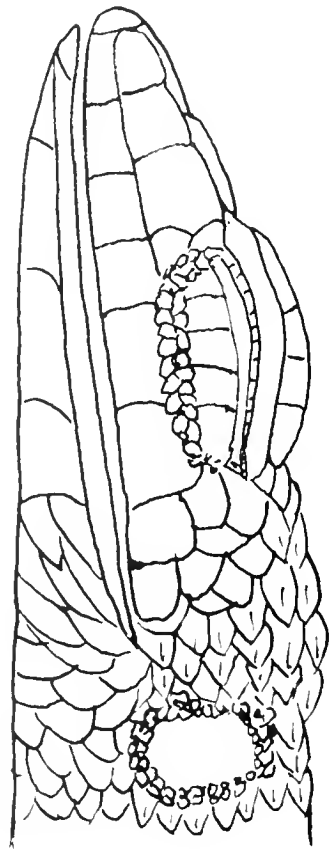


FIG. 2. Lateral scutellation of the head of the holotype (GMC 85-032).

108° 30' E), Wuming Xian (County), Guangxi Zhuang Autonomous Region, China, altitude 1240 m (Fig. 6). The specimen was collected on June 15, 1985 by Zhaoxiang Yang and is deposited in Guangxi Medical College (GMC).



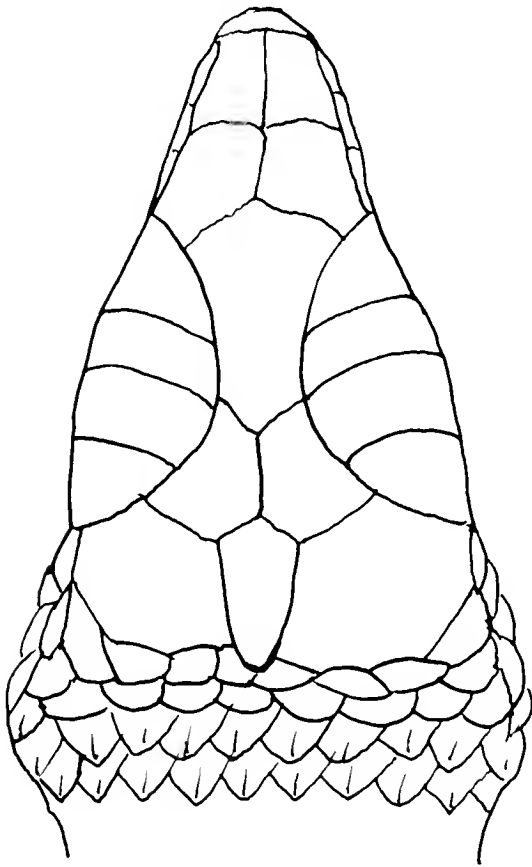


FIG. 3. Dorsal scutellation of the head of the holotype (GMC 85-032).

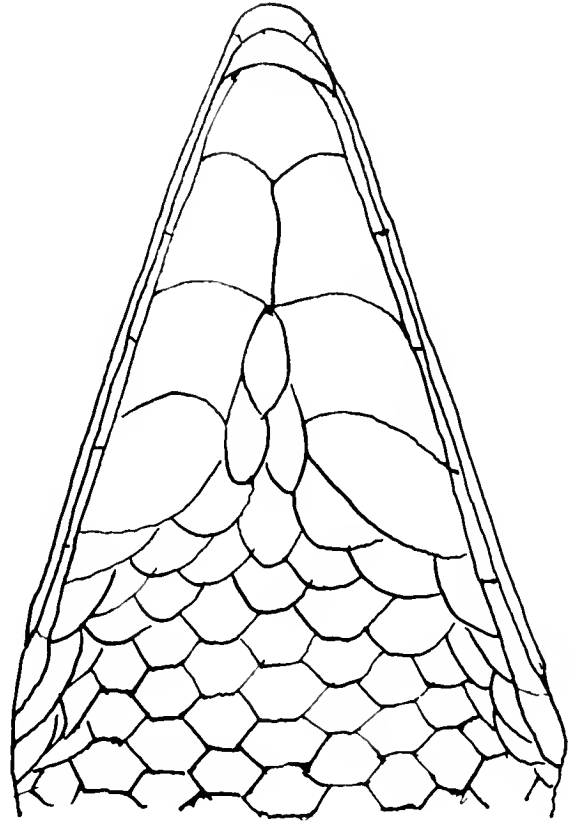


FIG. 4. Ventral scutellation of the head of the holotype (GMC 85-032).

*Paratypes*.—GMC 85-029 and GMC 85-030, two adult males collected with the holotype.

*Diagnosis*.—This new species closely resembles *Tropidophorus sinicus* Boettger, but differs from the latter by the following characters: a single postmental, head nearly triangle, interparietal separating parietals (Boulenger, 1887; Smith, 1935; Tian and Jiang, 1986).

*Description of holotype*.—A juvenile with a SVL of 39 mm and complete tail length of 46 mm. See Table 1 for the other measurements.

Head nearly triangle in dorsal aspect; snout obtusely pointed, portion of rostral visible from above, rostral wider than high; upper head shields strongly striated; frontonasal divided medially into two

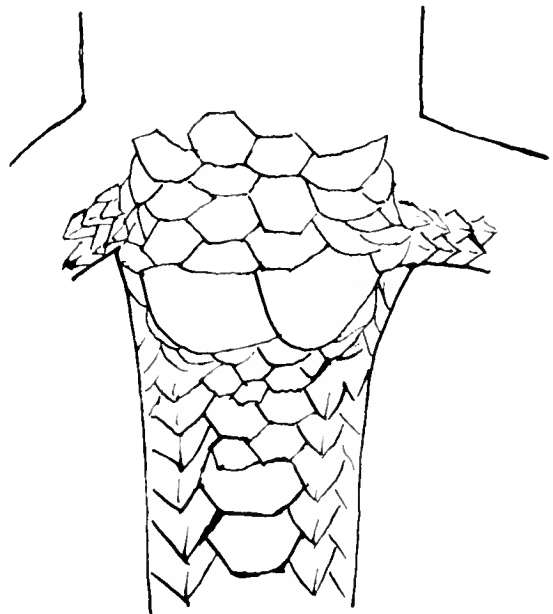


FIG. 5. Ventral view of anal and base of tail scutellation of the holotype (GMC 85-032).

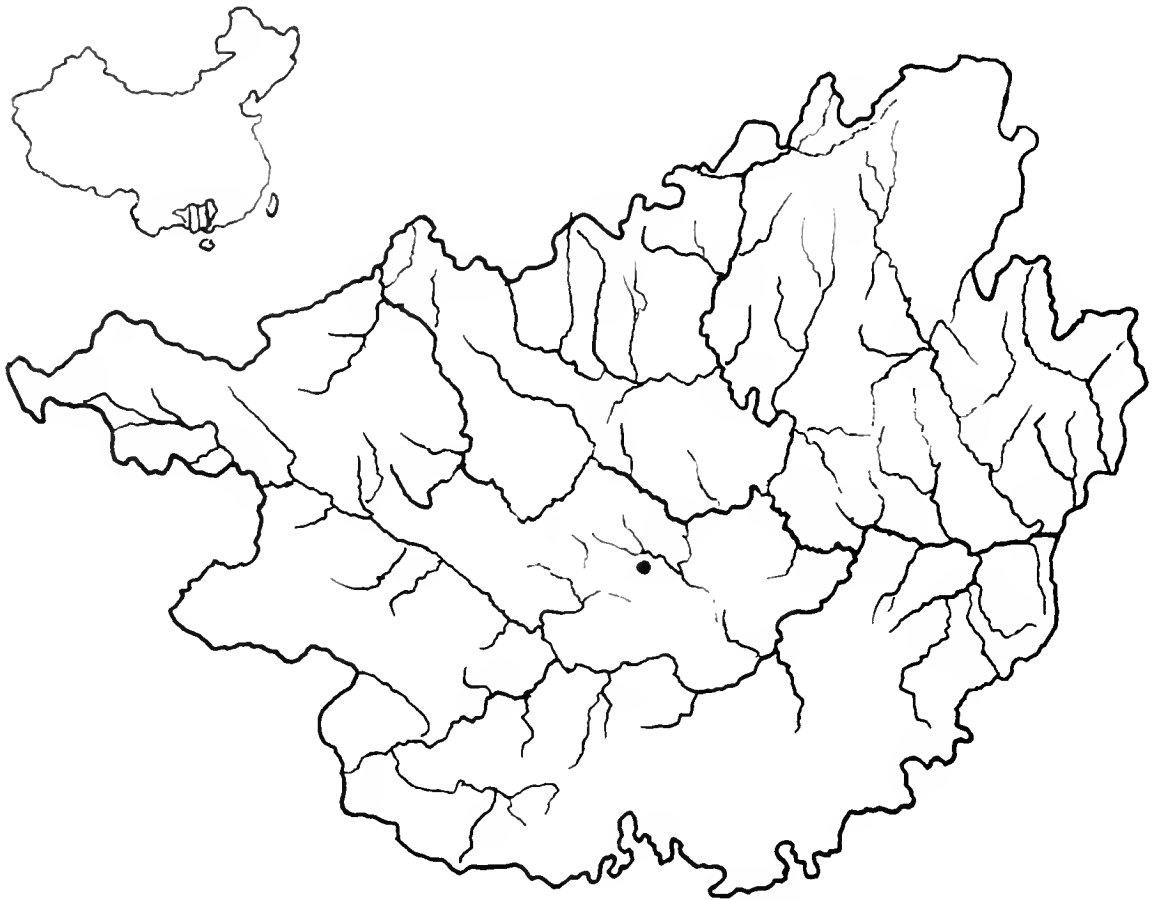


FIG. 6. Type locality (dot) of *Tropidophorus guangxiensis* at Daming Shan ( $23^{\circ} 23' N$   $108^{\circ} 30' E$ ), Wuming Xian (County), Guangxi Zhuang Autonomous Region, China.

longitudinal parts, longer than wide, suture of frontonasals longer than suture between prefrontals; prefrontals pentagonal, in contact with anterior and posterior loreals; frontal narrower posteriorly, length 1.44 times width at widest point, 1.4 times length of interparietal; frontoparietals pentagonal, broader posteriorly, in contact medially; interparietal slightly narrower posteriorly, rounded behind, separating parietal; parietal large, polygonal, border five shields on each side; supraoculars four, anterior two touching frontal; superciliaries eight, anterior two largest, first touching prefrontal; anterior loreal nearly rectangular, 1.2 times higher than wide; posterior loreal 1.1 times higher than broad; nasal undivided, 1.5 times wider than high, nostril opening just behind center; lower eyelid transparent (clouded), separated from supralabials by two rows of

granular scales; presubocular one; preocular small; postocular two; temporals majority, some striated or with keels; primary temporal large; supralabials eight, fifth longest, sixth highest; infralabials six, first longest; mental enlarged with labial border much greater than rostral; postmental undivided, pentagonal, wider than long; three pairs of chinshields, first in broad medial contact, posterior two separated by pregulars; body scales parallel on side of dorsum, dorsal scales slightly larger than lateral scales, imbricated, scales of first two rows following interparietal not keeled, sharply keeled with acute to normal points posteriorly by third row; scale rows around middle of body 29 (9 dorsal, 7/7 lateral, 6 ventral); 46 transverse rows between interparietal and rear edge of hindlimbs, 30 rows between forward edge of forelimbs and rear edge of hindlimbs; ventrals slightly

TABLE 1. Measurements (mm) of *Tropidophorus guangxiensis* sp.nov.

sex and measurements	GMC85-032	GMC85-029	GMC85-030
sex	unknown	male	male
snout-vent length	39.0	64.0	59.0
snout length	3.8	4.2	4.1
head length	9.0	12.0	11.2
head width	6.0	9.0	8.6
eye diameter	2.1	2.9	3.0
snout to ear length	9.2	11.0	11.5
internasal space	1.7	2.0	2.1
interorbital space	0.8	1.0	1.0
axilla to groin length	19.0	35.0	31.0
tail length	46.0	53.0*	44.0*
fore limb length	9.0	15.0	14.0
hind limb length	14.0	21.0	19.0

\* tail regenerated.

larger than dorsals, smooth, 27 transverse rows between rear edge of forelimbs and preanal scales; preanal scales four, central two very large; supracaudals like dorsals, but keels forming continuous ridges; subcaudals strongly widened, smooth, in single row except anterior four rings, 13 scale rows encircle tail at level of tenth subcaudal, 58 scales in a longitudinal series; scales of fore- and hindlimbs keeled above and below as dorsal; finger lamellar formula 5-9-11-15-7, toe lamellar formula 6-8-13-17-12 on each side, terminal lamella tightly bound about claws; limbs adpressed along flank toes in contact with fingers.

*Color in preservative.*—Head rusty brown above and on side, with yellowish, blackish cloudy spots; dorsum brown with irregular cream transverse bands and spots from neck to middle of body, middle of body to base of tail pale (corneal epithelium

TABLE 2. Scutellation (Left/Right) of *Tropidophorus guangxiensis* sp.nov.

Scale counts	GMC85-032	GMC85-029	GMC85-030
upper labials	8/8	8/8	7/8
lower labials	6/6	6/7	6/6
super-cilliaris	8/8	8/8	8/8
mid-body scale rows	29	29	28
scale rows on 10th subcaudal	13	12	12
paravertebral scales	46	45	46

shed); tail-like torso, cream bands narrower, lost on posterior three fourth; limbs and digits marked in same manner as body; upper and lower labials black, each scale with white spot center; chin and throat dark brown with longitudinal greyish white stripes; venter yellowish white; underside of tail white, subcaudals darken on both sides forming longitudinal white stripes.

*Habitat.*—The species is restricted to high mountains where mixed forest is present. The specimens were collected under fallen, rotten wood beside a lumberman's domitory.

*Variation.*—The specimen, GMC 85-029, has an azygos shield between the frontonasals and the prefrontals; other characters are listed in Tables 1 and 2.

*Comparison.*—This new species is similar to *T. sinicus* with the frontal entire, but differs from the latter in having the postmental undivided. It is similar to *T. thai* with the postmental single, but the frontal of *T. thai* is divided (Smith, 1935; Taylor, 1963; Tian and Jiang, 1986).

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## A Preliminary Report on the Reptile Fauna of the Kingdom of Bhutan with the Description of a New Species of Scincid Lizard (Reptilia: Scincidae)

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**Abstract.** -The herpetofauna of the Kingdom of Bhutan has been poorly studied and few collections of Bhutanese reptiles have been made. Reptiles collected by the 1972 expedition of the Naturhistorisches Museum Basel (Switzerland) are presented as a basis for a preliminary species list for this eastern Himalayan country. Specimens representing seven families and 18 species were examined. Included is a new species of scincid lizard of the genus *Mabuya*. An additional five species have been reported from Bhutan and numerous other taxa are known from adjacent regions of Sikkim and Assam. Most of the fauna is pan-oriental in derivation and is widespread to the east, west and south. A number of species, however, are primarily Indo-Chinese in their affinities and extend only as far west as eastern Nepal. Collections from eastern Bhutan and from elevations over 1500 m are particularly small and additional field work will be required to provide a complete picture of the reptiles of the country.

**Key words:** Reptilia, Sauria, Scincidae, *Mabuya*, Bhutan, Himalayas, biogeography, zoogeography.

### Introduction

Acharji and Kripilani (1951) reported that the herpetofauna of the western Himalayas was poorly researched in comparison with that of the eastern portion of the range. Since the time of their publication this condition may be said to have reversed, with several major and many minor expeditions reporting on the herpetofauna of the Kingdom of Nepal, particularly the region from Annapurna to the west (Cox, 1985; Dubois, 1974a, 1974b; Leviton et al., 1962; Mrsic, 1980; Nanhoë and Ouboter, 1987; Sura, 1987, 1989; Swan and Leviton, 1958). In the eastern Himalayas, numerous workers have reported on the reptiles of Sikkim and West Bengal (e.g., Annandale 1912; Günther, 1864; Inglis et al., 1920) reviewed the herpetofauna of the Abor district (= central Arunchal Pradesh), some 225 km east of Bhutan. Nonetheless, no comprehensive works on the region have been compiled.

The Kingdom of Bhutan has long remained a gap in the knowledge of eastern Himalayan zoology, especially that of the herpetofauna (Annandale, 1912; Ouboter 1986; Swan and Leviton, 1962). Bhutan occupies approximately 47000 km<sup>2</sup> in the

eastern Himalayas (Fig. 1). To the north it is bordered by Tibet (Xizang Zizhiqu), to the east by Arunchal Pradesh, to the south by Assam, and to the west by Sikkim and the Darjeeling district of West Bengal. Government policy severely limiting foreign travel and research in the Kingdom has, until quite recently, left Bhutan as a zoological terra incognita in south central Asia. Fortunately, a great deal of Bhutan lies within national parks, sanctuaries or reserves (Hawkins, 1986) so that there may yet be opportunities to study its fauna in a relatively undisturbed state.

To date only four papers have been published on the herpetofauna of Bhutan. Bustard (1979, 1980a, 1980b) published a conservation document and two short notes on the status of the gaviial (*Gavialis gangeticus*) in Bhutan. Biswas (1975) reported on a small collection of reptiles from Bhutan and described a new taxon, *Calotes bhutanensis*. We here report on a much more extensive collection of reptiles and amphibians from Bhutan collected by the Zoologische Expedition des Naturhistorischen Museums Basel (NMBA) in 1972. This material is supplemented by additional information from literature sources.

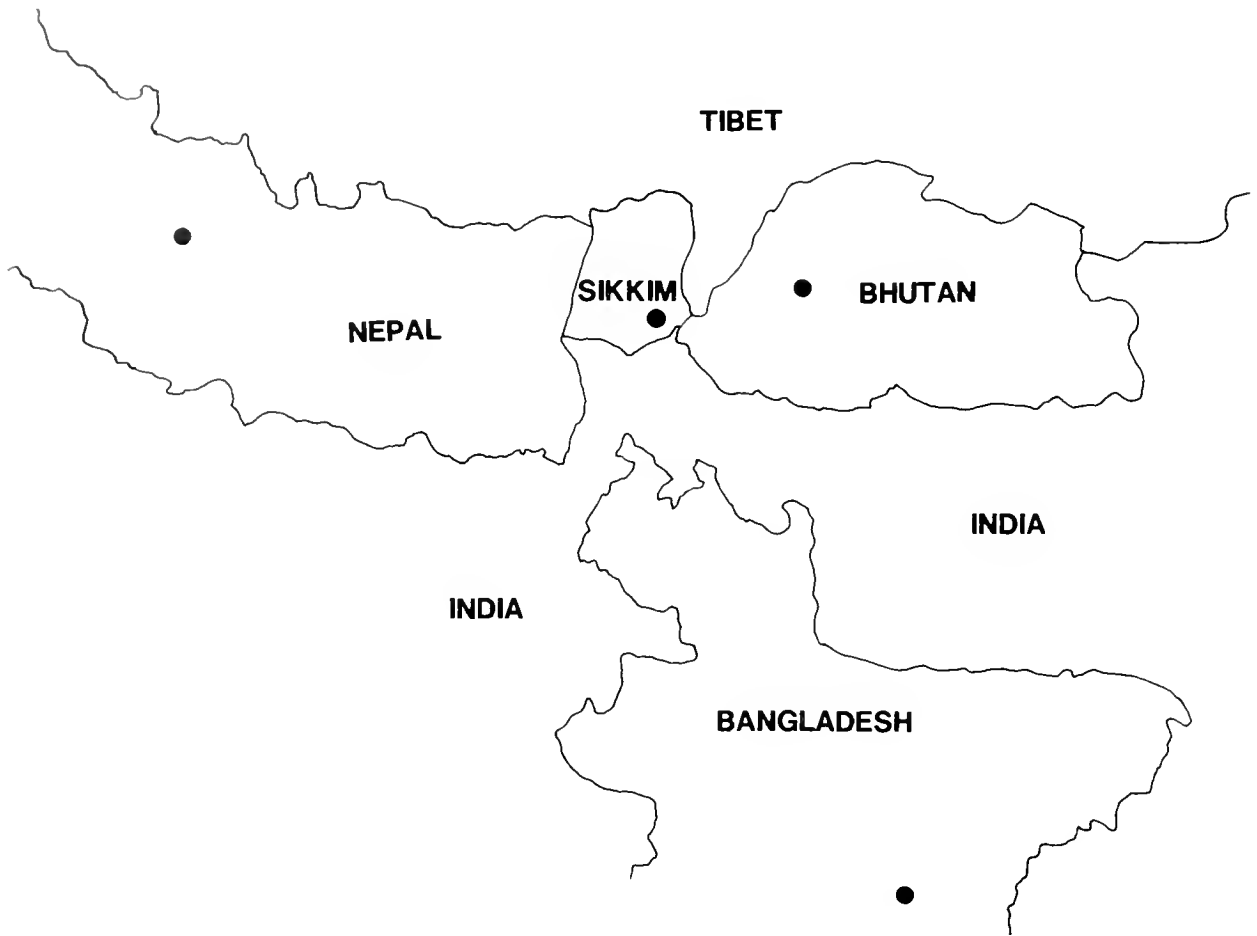


FIG. 1. Map of the eastern Himalayas and adjacent regions showing the position of Bhutan. Closed circles indicate the capitol cities of each country.

### Methods

Specimens were collected in the Kingdom of Bhutan in April-May 1972 by the Zoologische Expedition des Naturhistorischen Museums Basel (NMBA), primarily by Drs. O. Stemmler and M. Würmli. Specimens were examined while on loan at the Museum für Naturkunde, Berlin. Other material referred to is from the collections of the Academy of Natural Sciences of Philadelphia (ANSP), the U.S. National Museum (USNM) and the Zoological Survey of India (ZSI). Live weights for some specimens were obtained from the field notes of the collectors. The following abbreviations are used throughout this paper: LW = live weight, SC = subcaudal

scales, SVL = snout-vent length, TL = tail length, V = ventral scales. Measurements were taken only from representative specimens of each taxon and samples generally reflect typical individuals from each series.

All of the localities represented by the NMBA expedition are in southwestern Bhutan. Literature records from other collections also include several localities in the central and eastern regions of the country. Localities of the NMBA expedition have already been characterized in the literature (Baroni-Urbani et al., 1973). To avoid repetition only the latitudes, longitudes, and elevations of those localities at which reptiles were collected are provided below, along

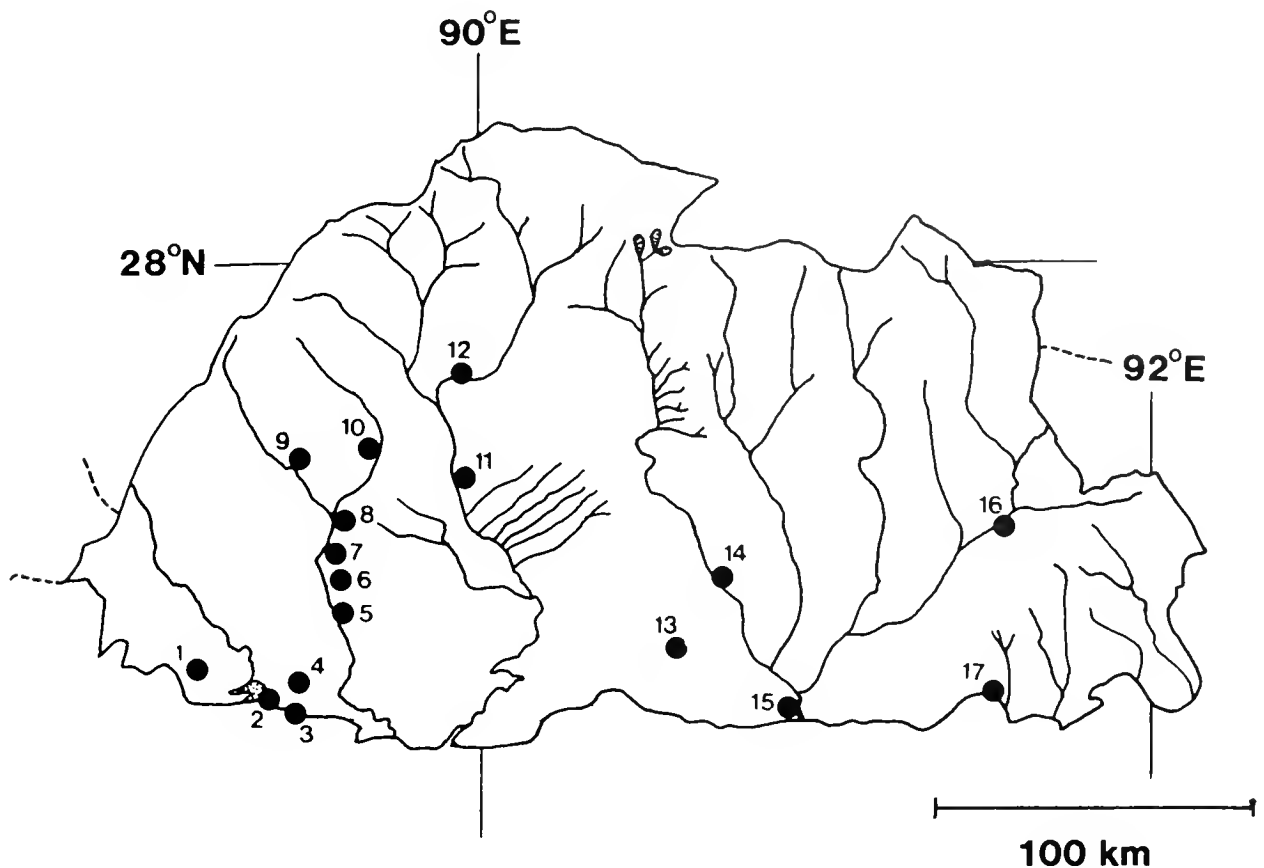


FIG. 2. Map of the Kingdom of Bhutan showing the localities referred to in the text. See **Methods** for names, elevations and coordinates of numbered localities.

with the same information for literature and other specimen localities. Latitudes and longitudes are approximate as no adequate gazetteer exists for Bhutan and several localities not appearing on any available maps could only be bracketed between known places by reference to collectors field notes. The following numbered localities are marked on Figure 2:

1. Samchi (400 m),  
26° 54' N 89° 14' E.

2. Phuntsholing (200-400 m),  
26° 51' N 89° 26' E.

3. Khala and Balu Jhura (200 m),  
26° 50' N 89° 26' E.

4. 14 km N of Phuntsholing,  
(850-950 m), 26° 53' N 89° 27' E.

5. 87 km N of Phuntsholing (1700 m),  
27° 05' N, 89° 35' E.

6. Chimakothi (2200 m),  
27° 10' N 89° 34' E.

7. 110 km N of Phuntsholing (2000 m),  
27° 12' N 89° 34' E.

8. 125 km N of Phuntsholing (2100 m),  
27° 15' N 89° 35' E.

9. Paro (2300 m),  
27° 26' N 89° 25' E.

10. Thimphu (2300-2500 m),  
27° 29' N 89° 37' E.

11. Wangdi Phodrang (1400 m),  
27° 29' N 89° 54' E.

12. Tamji (2450 m),  
27° 40' N 89° 54' E.

13. Batase (1500 m),  
27° 00' N 90° 37' E.
14. Panjurmane (1525 m),  
27° 10' N 90° 43' E.
15. Manas River,  
26° 50' N 90° 59' E.
16. Rongtong (2042 m),  
27° 16' N 91° 32' E.
17. Samdrup Jhongkhar (300 m),  
26° 52' N 91° 28' E.

### Species Recorded from the Kingdom of Bhutan

Reptilia

Crocodylia

Family Gavialidae

*Gavialis gangeticus* (Gmelin, 1789)

Ross (1989) included Bhutan in his list of the recent distribution of the gharial. Bustard (1979, 1980a, 1980b) reported that this species had recently been extirpated from its primary habitat in the Kingdom of Bhutan, the Manas River. The last specimens were seen in the 1960's. Bustard (1980a, 1980b) and Groombridge (1987) have suggested reintroducing the species into suitable habitat. At present a small population survives in the Indian portion of the Manas River (Whitaker, 1987).

Sauria

Family Agamidae

*Calotes bhutanensis* Biswas, 1975

Biswas (1975) described this endemic species on the basis of a single specimen (ZSI 22480) from Panjurmane (listed as Janjurmane by Biswas). Although he provided mensural characters to distinguish *C. bhutanensis* from the very similar *C. versicolor*, the validity of this taxon must remain in doubt. The values provided by

Biswas (1975) suggest that the single specimen falls within the range of variation displayed by *C. versicolor*. Moody (1980) in his systematic revision of the Agamidae was apparently unaware of this description and did not recognize the species either as distinct or as a junior synonym. Until such time as *C. bhutanensis* is reevaluated in the context of the genus *Calotes* as a whole we tentatively recognize it a taxon distinguishable from *C. versicolor* on the basis of the minor scalation and color features delineated by its describer.

*Calotes versicolor* (Daudin, 1802)

(17 specimens examined): Phuntsholing NMBA 22582-92, ZMB 48784-85; Balu Jhura NMBA 22593; Wangdi Phodrang NMBA 22594-6.

LW adult males 27.0-36.4 g ( $\bar{x}$  = 31.68 g, n = 4), LW females and juveniles 5.8-21.1 g ( $\bar{x}$  = 9.96 g, n = 8).

In addition to the specimens examined, Biswas (1975) reported a specimen from Samdrup Jhongkhar, Bhutan. *Calotes versicolor* is widespread throughout the Oriental region, including all of the southern slopes of the Himalayas. Smith (1935) and Cox (1985) recorded the species as common up to 1980 m in the Himalayas. It is widespread in most of Nepal and in adjacent regions of Sikkim and the Darjeeling District (Acharji, 1961; Acharji and Kripilani, 1951; Leviton et al., 1956; Mrcic, 1980; Nanho and Ouboter, 1987; Rendahl, 1937; Sura, 1987, 1989; Swan and Leviton, 1962). Barbour (1912) recorded this species from the Tista Valley near the Bhutanese frontier of Sikkim.

*Japalura variegata* Gray, 1853

(2 specimens examined): 87 km N of Phuntsholing NMBA 22597-8. Biswas (1980) obtained a specimen from Batase, Bhutan. Günther (1865) recorded this taxon from Sikkim, and Hora (1926) and Smith (1935) reported that this species was common throughout the eastern Himalayas at elevations of 330-2970 m. Annandale (1906) initially reported *J. yunnanensis*



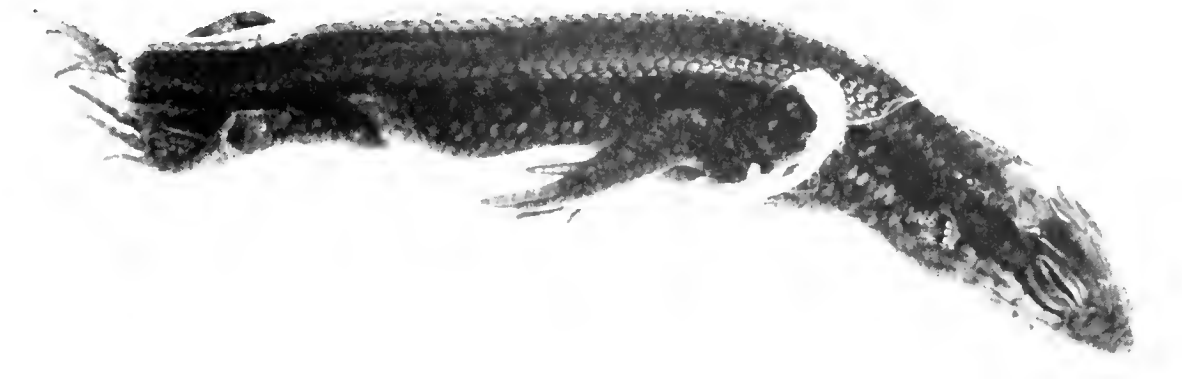


FIG. 3. Holotype of *Mabuya quadratolobus* Baur and Günther (NMBA 10275). Note general coloration pattern.

from Buksa (=Buxa), near the Bengalese/Bhutan frontier, but later described the same specimen as *J. bengalensis*, now regarded as a synonym of *J. variegata*.

Family Gekkonidae

*Hemidactylus brookii* Gray, 1845

(1 specimen examined): Samchi NMBA 22599.

Swan and Leviton (1962) did not record this species among the fauna of Nepal, but it has since been reported as locally common at lower altitudes (Mrsic, 1980; Nanhoe and Ouboter, 1987). Mitchell and Zug (1988) found it to be the most abundant gecko at their locality in the Terai of Nepal as did Cox (1985) at his central Nepalese sites.

*Hemidactylus frenatus*  
Duméril and Bibron, 1836

(39 specimens examined): Samchi NMBA 22600-7; Phuntsholing NMBA 22608-34; ZMB 48786-89.

LW 1.0-6+.2 g ( $\bar{x}$  = 3.16 g, n = 32), LW males ( $\bar{x}$  = 3.43 g, n = 13), LW females ( $\bar{x}$  = 2.97 g, n = 19).

Leviton et al. (1956) and Swan and Leviton (1962) recorded this species from Dharan (ca. 330 m) in Eastern Nepal and Cox (1985) found it common in Tharu, in

central Nepal. Annandale (1912) regarded the species as common at low altitude throughout the eastern Himalayas.

*Platyurus platyurus* (Schneider, 1797)

(5 specimens examined): Phuntsholing NMBA 22635; Wangdi Phodrang NMBA 22636-7; no precise locality NMBA 22638-9.

LW 2.5-5.2 g ( $\bar{x}$  = 3.63 g, n = 3).

Annandale (1912), Cox (1985), Leviton et al. (1956), Mrsic (1980), and Swan and Leviton (1962) recorded this species from central and eastern Nepal at elevations up to 1500 m and Smith (1935) and Taylor (1962) recorded it from Sikkim. The species is also known from southeastern Tibet (Kraig Adler, pers. comm.).

Family Scincidae

*Mabuya quadratolobus*  
Bauer and Günther, n. sp.  
Figs. 3 and 4.

*Holotype*.—NMBA 22681, lowest terrace on the right bank of river valley west of Samchi, Bhutan (26°54'N, 89°14'E), elevation 450 m. Collected by M. Würmli and C. Baroni-Urbani, 12 May 1972.

*Paratypes*.—(11 specimens): NMBA 22682-87, ZMB 48769, 48775-78 all from Samchi, Bhutan. Collected 8 May 1972 by

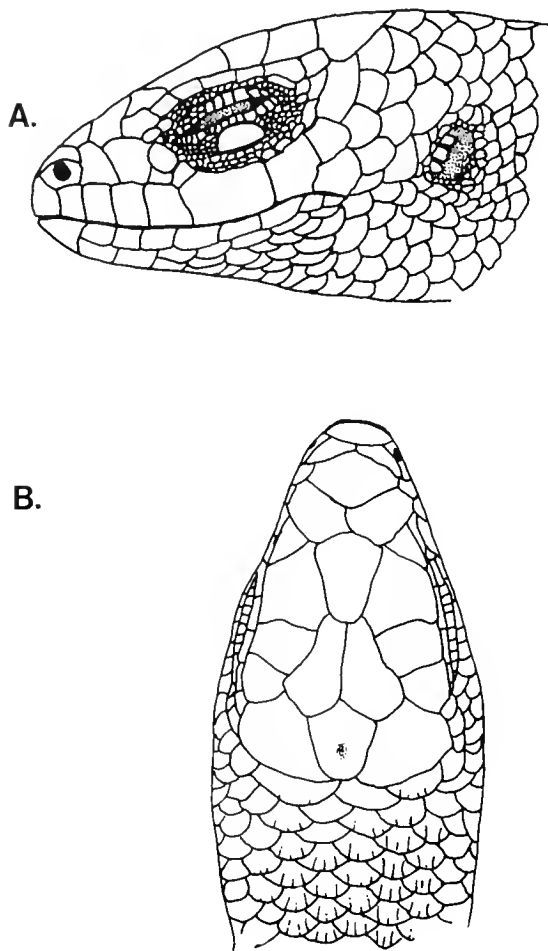


Fig. 4. A) Lateral and B) dorsal views of the head of *Mabuya quadratolobus* (NMBA 10275). Note the ear lobules, enlarged fifth supralabial and carinate dorsal scales.

O. Stemmler (NMBA 22682, 22688) and 11 May 1972 by O. Stemmler and M. Würmli (NMBA 22683-87, ZMB 10281-84).

**Diagnosis.**—*Mabuya quadratolobus* is distinguished from all other Asian members of the genus by the following combination of characters: lower eyelid with transparent disk; three large, squared lobules at anterior margin of ear; seven supralabials with fifth approximately 2.5 x length of first; dorsal scales tricarinate.

**Description of holotype.**—A juvenile, 36.0 mm SVL, LW 1.3 g. TL (incomplete) 25.8 mm (TL of intact paratype NMBA

48777 = 130% SVL). Axilla-groin length 14.2 mm. Hindlimb length 13.8 mm.

**Scalation (Fig. 4).**—Frontonasal broader than long; prefrontals large, in broad contact; frontoparietals large, paired; distinct interparietal; parietals each bordered posteriorly by a single nuchal (unilaterally fragmented in holotype); nostril entirely within nasal; small supranasals present, in narrow contact dorsally; two loreals, anterior larger than posterior; lower eyelid with central transparent disk (diameter approximately 50% of eye); four supraoculars, decreasing in size in the order 2>3>4>1; six supracilliaris; seven supralabials, fifth and sixth under eye; sixth supralabial separated from orbit by series of small suboculars; fifth supralabial 2.5 x length of anteriormost supralabials; seven or eight infralabials, roughly equal in size; first and second infralabials contact postmental; two enlarged pairs of chin shields, first pair in narrow contact.

Ears moderately large; tympanum sunken; anterior margin of ear with three flattened, distinctly squarish lobules; remainder of scales on anterior margin of ear slightly raised.

Dorsal scales tricarinate, with lateral carinations more well developed than medial; medial ridge limited to posterior scale edge on many lateral and posterior scales; carinated scales continue on to proximal region of tail; dorsal scales approximately equal in size, decreasing slightly on flanks; 35 scale rows around mid-body.

Limbs pentadactyl; scales on dorsal surface of limbs weakly tricarinate; palmar scales spinose; 14 unkeeled lamellae under fourth toe.

**Color (in preservative).**—Dorsum olive brown with series of dark brown marks on distal edges of scales, forming irregular spots on nape and broken transverse bands at every second scale row on body. Light dorsolateral stripe, one and one half scale rows wide, from level of ear to tail. Dark brown stripe beneath light stripe, extending

from anterior corner of eye on to tail, passing beneath eye as a narrow dark line, disrupted and diffuse through ear, flecked with blue-white scales ventrally and fading towards flanks. Venter white. Dorsal surfaces of limbs brown, scales edged with dark brown, forming a diffuse, irregular reticulate pattern.

*Variation.*—The paratypes resemble the holotype in all major features. All specimens appear to be juveniles and possess yolk scars. Some specimens show minor fragmentation of some head scales. LW 0.5-1.3 g ( $\bar{x}$  = 0.85 g, n = 11); SVL 28.9-36.0 mm ( $\bar{x}$  = 32.1 mm, n = 8).

*Etymology.*—The name derives from the Latin lobus (lobe) and quadratus (square) and is in reference to the striking ear lobules characteristic of this species.

Unfortunately the phylogeny of the lygosomine skinks in general, and *Mabuya* in particular, is not well resolved. Greer (1974, 1979) regarded *Mabuya* as ancestral to other skink lineages and suggested that the south-east Asian species of the genus exhibited the greatest number of plesiomorphic features. If this is true, then this group must also be paraphyletic. The only comprehensive treatment of *Mabuya* as a whole has been that of Horton (1973), who provided a key to the species and an overview of the evolution and biogeography of the numerous species groups by geographic region. More than 20 Asian *Mabuya* were recognized by Horton (1973), but no unified picture of relationships among these taxa was presented. In most existing keys to the herpetofauna of the greater Indian region (e.g., Smith, 1935) the new species falls out most closely with *Mabuya dissimilis*, a species from the western Himalayan region. Comparison with the types (ANSP 9537-8) and other specimens of the latter taxon, however, reveal major differences and the two taxa are clearly distinct, if closely related at all. With the material at hand we are unable to offer any meaningful suggestion as to the close relationship of *Mabuya quadratilobus*.

*Scincella sikkimensis* (Blyth, 1853)

(45 specimens examined): Phuntsholing NMBA 22640; 87 km N of Phuntsholing NMBA 22641; Chimakothi NMBA 22642-51, ZMB 48779-83; 110 km N of Phuntsholing NMBA 22652-60; 125 km N of Phuntsholing NMBA 22661; Paro NMBA 22662-67; Thimphu NMBA 22668-76; Tamji USNM 166443; no specific locality NMBA 22667-80.

LW 0.6-3.5g ( $\bar{x}$  = 1.62g, n = 35), SVL (larger specimens only) 45.8-55.8 mm ( $\bar{x}$  = 49.48 mm, n = 6), TL 144-148% SVL (n = 3).

Ouboter (1986) reported a maximum SVL of 55.7 mm and an average of 39.1 mm. Although only larger individuals of the Bhutanese sample were measured, it appears that populations from the northeastern extent of the range may be slightly larger than average. Specimens examined in detail revealed at least three different head scale patterns, reflecting fusions and fragmentation of the standard pattern reported by Ouboter (1986). For example, NMBA 22668 possessed a fragmented frontonasal, NMBA 22663 had both prefrontals fused to the frontal, and NMBA 22662 had unilateral prefrontal-frontal fusion.

Hora (1927) recorded the species from Sikkim and other neighboring areas of India, and Cox (1985), Mrcic (1980), Sura (1987), and Swan and Leviton (1962) reported specimens from central Nepal. Gruber (1981) and Ouboter (1986) highlighted the confusion surrounding the identity of the Himalayan species of *Scincella* in general, but demonstrated that *S. sikkimensis* is the characteristic species of eastern Himalayas. As defined by Ouboter (1986) it appears to be limited chiefly to mesic oak forest regions on the southern flanks of the range. Nanhoe and Ouboter (1987) characterized this species as a common inhabitant of forest clearings or edges, generally below 3000 m throughout the Himalayan region to the east of Jaljala Pass in central Nepal. Ouboter (1986)

stated that the species was not known from localities below 1200 m. However, Mrcsic (1980) recorded specimens below 1000 m in Nepal and the Bhutanese localities reported here, especially Phuntsholing, clearly indicate that the species may occupy the entire elevational range of the tropical-subtropical belt of the foothills. The presence of such low altitude specimens give some credence to occurrence of *Scincella sikkimensis* at Parasnath Hill, south of the Gangetic Plain in Bihar, the type locality of *Mococa sacra*, a junior synonym of *S. sikkimensis*.

*Sphenomorphus indicus* (Gray, 1853)

(5 specimens examined): 87 km N of Phuntsholing NMBA 22689-92, ZMB 48768.

LW 9.4-26.5g ( $\bar{x}$  = 17.58, n = 5), Maximum SVL 104.7 mm (NMBA 22689, a large female containing embryos), TL 128-130% SVL (n = 2)

Hora (1927) reported this species from "the eastern Himalayas below Darjeeling" and Smith (1935) and Taylor (1962) mentioned material from Sikkim. Although literature records in the region are few, the species is widespread in the eastern Himalayas (Annandale, 1912; Rendahl, 1937).

*Sphenomorphus maculatus*  
(Blyth, 1853)

(4 specimens examined): Samchi NMBA 22693; Phuntsholing NMBA 22694. In addition the Basel Expedition collected two specimens, NMBA 22695-6, from 23 km N of Siliguri (ca. 150 m) in the Jaipalguri District of India.

LW 3.0-4.0 g ( $\bar{x}$  = 3.5 g, n = 2), SVL 45.0-58.8 mm ( $\bar{x}$  = 50.6 mm, n = 4), TL 144-200% SVL, n = 4).

Nanhoe and Ouboter (1987) concluded that this Indo-Chinese species was limited in its distribution to low altitude riverine

forests. The Bhutanese localities reported here support this. Smith (1935) mentioned specimens from Sikkim.

Family Varanidae

*Varanus bengalensis* (Daudin, 1802)

(3 specimens examined): Phuntsholing NMBA 22697-8, 22740. Specimens were also sighted at Samchi.

This species is common throughout much of the eastern Himalayas as well as Assam (Annandale, 1912). Cox (1985) reported a specimen from central Nepal at Patan.

Serpentes

Family Typhlopidae

*Ramphotyphlops braminus*  
(Daudin, 1803)

(24 specimens examined): Samchi NMBA 22699-713; Phuntsholing NMBA 22714-17, ZMB 48770-74, 48774.

LW 0.3-1.0 g ( $\bar{x}$  = 0.72 g, n = 21). Largest specimen ZNB 48771, SVL 146.0 mm, TL 2.0 mm. All specimens have 20 scale rows around mid-body and show the head scale suture pattern typical of this species.

This widespread and easily transported snake has also been recorded from Nepal (Kramer, 1977; Mrcsic, 1980; Nanhoe and Ouboter, 1987) and Sikkim (Rendahl, 1937).

Family Pythonidae

*Python molurus* (Linnaeus, 1758)

Although we know of no Bhutanese specimens in collections, the statement of Harris et al. (1964) that "pythons" were common inhabitants of the Duars Plains of Bhutan, must surely refer to this species. It has been recorded from comparable habitats

in Nepal (Kramer, 1977).

Family Colubridae

*Amphiesma platyceps* (Blyth, 1854)

(1 specimen examined): Wangdi Phodrang NMBA 22741 (475 + 184 mm, 186 V, 98 SC).

This species has previously been recorded from Sikkim, Assam and Nepal (Kramer, 1977; Mrcic, 1980; Nanhoe and Ouboter, 1987; Smith, 1943; Swan and Leviton, 1962) and is widely distributed in the Himalayas.

*Amphiesma stolata* (Linnaeus 1758)

Biswas (1975) collected a single specimen from Samdrup Jhongkhar in eastern Bhutan. This is a widely distributed pan-oriental species that appears to thrive in disturbed areas (Nanhoe and Ouboter, 1987).

*Boiga ochracea ochracea*  
(Günther, 1868)

(2 specimens examined): Phuntsholing NMBA 22730, juvenile (280.5 + 73.8 mm, 4 g, 234 V, 108 SC); NMBA 22731, adult male, badly damaged (925 + 284 mm, 241 V, 118 SC).

This species is common in the eastern Himalayas and is known from the Buksa Duars along the southern boundary of Bhutan (Smith, 1937).

*Pseudoxenodon macrops* (Blyth, 1854)

(2 specimens examined): 125 km N of Phuntsholing NMBA 22738, male, head and neck severely damaged (975 + 227 mm, 164 V, 63 SC); Wangdi Phodrang NMBA 22739 (710 + 183 mm, 169 V, 67 SC).

Nanhoe and Ouboter (1987) regarded this species as an Indo-Chinese form, extending through the eastern Himalayas as far west as Jaljala Pass in west central Nepal.

*Trachischium guentheri* Boulenger, 1890

(4 specimens examined): 87 km N Phuntsholing NMBA 22732-35. Largest specimen (NMBA 22735), 226.3 + 38.6 mm.

Kramer (1977) and Swan and Leviton (1962) reported this species from Nepal, and Smith (1943) from Sikkim and Darjeeling.

*Xenochrophis piscator*  
(Schneider, 1799)

(12 specimens examined): Phuntsholing NMBA 22718-29. The specimens are all neonates (typical individuals 140.5 + 64.8 mm) and were collected along with 16 egg shells. Smith (1943) reported clutch sizes of 8-87 in this species. Nanhoe and Ouboter (1987) reported this species as common at low altitudes in association with water and Annandale (1912) reported its presence at elevations as high as 1450 m in the western Himalayas. The species range extends throughout the Oriental region. Kramer (1977) and Swan and Leviton (1962) reported Nepalese localities.

*Zaocys nigromarginatus* (Blyth, 1854)

(1 specimen examined): 87 km N Phuntsholing NMBA-Field Number 10258, total length 1980 mm, badly damaged.

This large snake is an eastern form, ranging from Yunnan to the eastern Himalayas (Smith, 1943). It is known from elevations of up to 2500 m.

Family Elapidae

*Bungarus niger* Wall, 1908

(1 specimen examined): Phuntsholing NMBA 22736 (667 + 120 mm, 221 V, 56 SC).

Although this taxon has long been known from the eastern Himalayas and Assam (Smith, 1943), it has not been recorded from eastern Nepal by any of the

recent reviewers of the fauna of that region.

### *Ophiophagus hannah* (Cantor, 1836)

Biswas (1975) reported a juvenile specimen from Rongtong in the Manas Valley. This species has recently been recorded from as far west as eastern Nepal (Nanhoe and Ouboter, 1987).

### Species Likely to Occur in Bhutan

In addition to the 23 species listed above, it is certain that a great many more reptile species are yet to be found in Bhutan, both in the more well-known, but richer lowlands, and the less-well collected higher elevations. No turtles have been reported from Bhutan, but several species are likely to occur. Among the batagurine emydids the range of *Kachuga tecta* brackets Bhutan, with records from Sikkim in the west (Moll, 1987) and the Dihang River in the east (Annandale, 1912). *Kachuga drongoka* has been collected in the Brahmaputra River in the Kamrup District of Assam (Moll, 1986) and was illustrated in a distribution map as occurring in Bhutan by Tikader and Sharma (1985). *Cuora amboinensis*, *Melanochelys tricarinata*, *M. trijuga*, *Kachuga smithii*, *K. tentoria* and *K. sylhetensis* have been reported from the Manas Tiger Reserve in Assam (Das, 1988) and *Hardella thutjii*, *Indotestudo elongata* and *Lissemys punctata* also approach the borders of Bhutan. The freshwater turtles are known either from the Tista to the west or the Brahmaputra to the south (Das, 1985; Iverson, 1986; Smith, 1933; Tikader and Sharma, 1985) and might be expected to occur at lower elevations in the Torsa, Wong Chu, Sankosh, and Manas drainages of southwestern and south central Bhutan.

It is highly probable that additional lizard species may also be found in Bhutan. The gekkonid *Hemidactylus flaviviridis* occurs in Nepal (Cox, 1985; Sura, 1987, 1989) but apparently does not reach the eastern Himalayas. *Hemidactylus garnotii*, on the other hand, extends only as far west as central Nepal (Cox, 1985; Nanhoe and Ouboter, 1987; Sura, 1989), where it has only recently become established. The

latter species almost certainly occurs at lower elevations in Bhutan. *Hemidactylus bowringii* was recorded by Barbour (1912) from the Tista Valley near the Bhutanese frontier with Sikkim, but no more recent remarks on this species in the area in question have appeared in the literature. Among agamids, *Japalura tricarinata* occurs in eastern Nepal, Sikkim, and the Darjeeling area, it may be expected to occur in the southwestern corner of Bhutan, although the Basel expedition found no specimens despite their intense collecting effort in and around Phuntsholing. *Japalura andersoniana* was described from the Dafla Hills, near the eastern border of Bhutan and is another potentially indigenous agamid. Annandale (1906) suggested that *Ptyctolaemus gularis* might be found in the Buksa Duars along the southern frontier of Bhutan. There are a great many snake taxa that might be expected to occur in Bhutan. Over 40 species have been recorded from Nepal (Kramer, 1977). In the family Typhlopidae at least *Ramphotyphlops jerdoni* and *R. oligolepis* and possibly *R. diardi* extend to the border regions of Bhutan. The colubrid fauna of adjacent Sikkim and Assam is exceptionally rich (Smith, 1943). Welch (1988) listed *Ahaetulla p. prasina*, *Boiga gokool*, *Boiga multifasciata* and *Rhabdophis himalayana* as well as *Boiga o. ochracea* as taxa occurring in Bhutan. However, these records were purportedly derived from Smith (1943), who, in fact, listed no material from Bhutan. Welch's (1988) apparent criterion for inclusion in the Bhutanese fauna was Smith's (1943) mention of the "eastern Himalayas" in his distributional comments. In addition, at least four species of *Oligodon* occur in Sikkim or the Jaipalguri District of India and may also be found in Bhutan. Additional specimens and species almost certainly exist in museum collections, but have never been reported in the literature. It is also likely that the cobra, *Naja naja kaouthia*, occurs in Bhutan. Smith (1943:434) presented a distribution map showing most of Bhutan within the range of the subspecies. The nominate subspecies is illustrated as just reaching the southwest corner of the country. The true

status of these forms relative to one another remains unclear. They occur in sympatry in a number of areas and are probably specifically distinct (Wüster and Thorpe, 1989). To date, however, there have been no specimens to confirm the presence of either form in Bhutan, although there are records from Nepal (Acharji, 1961; Kramer, 1977).

### Discussion

Himalayan zoogeography has been reviewed extensively by previous authors (e.g., Annandale, 1912; Blanford, 1901; Dubois, 1981; Hora, 1948; Nanhoë and Ouboter, 1987; Smith, 1933; Swan and Leviton, 1962). All have used approximately the same divisions in identifying the affinities of the faunal elements of the region. Bhutan lies primarily within the Eastern Himalayan province of the Indo-Chinese subregion of the classically-defined Oriental region. The herpetology of the eastern Himalayas in general is known from a number of faunal reports from eastern Nepal (e.g., Leviton et al., 1956) and northeastern Bengal (Annandale, 1912), as well as from descriptions of new species, especially amphibians (see Dubois, 1974a). Swan and Leviton (1962) recorded 85 snake and lizard species from Sikkim and the adjacent Darjeeling area of India. As yet material is insufficient to compare the similarity and richness of the Bhutanese fauna with these figures. Bhutan is characterized by north-south flowing rivers that ultimately drain into the Brahmaputra and thence to the Bay of Bengal. To the north the higher peaks of the Himalayas form a barrier to reptile movement. Mountain ridges also form partial barriers to the west and east. Only to the south is there low altitude access to Bhutan. The mountains further subdivide the country into a series of valleys between which communication is likely only in the subtropical south. As a consequence, the majority of the species recorded are pan-oriental in their distribution or, like *Platyurus platyurus*, *Sphenomorphus maculatus*, and *Pseudoxenodon macrops*, are primarily Indo-Chinese species that extend only as far west as eastern or central

Nepal. Eastern Himalayan endemics include *Trachischium guentheri* and *Scincella sikkimensis*. The distribution of the two putatively endemic forms described from Bhutan, *Calotes bhutanensis* and *Mabuya quadratilobus* n. sp., remains poorly known, but it is probable that at least the latter may be found in adjacent Sikkim or Assam. None of the taxa reported here reflect Tibetan or Mediterranean influences as reported for the Nepalese reptile fauna by Swan and Leviton (1962) and Nanhoë and Ouboter (1987). At least in part, this is a reflection of the limitation of previous collecting efforts to the valleys and lower elevations of Bhutan. This same factor precludes a meaningful elevational analysis of herpetofaunal distribution at this time. In Bhutan, as elsewhere in the Himalayas, there appears to be a strong correlation between zonation of vegetation and that of amphibians and reptiles (Dubois, 1974a, 1974b, 1981; Nanhoë and Ouboter, 1987). The elevational profiles provided by Baroni-Urbani et al. (1973) characterized the native vegetation of the lower elevations of Bhutan as: moist sal forest (200-800 m), evergreen montane forest (700-1600 m), evergreen deciduous forest (1600-2800 m), and Rhododendron - conifer forest (2800-3500 m). Dubois (1974b) regarded elevations below 1000 m in neighboring Nepal as tropical, those to 2000 m as subtropical and those to 3000 m as temperate, with higher elevations subalpine or alpine in their climate and floral characteristics. Although each of the vegetation types is represented by at least one collecting site, all are within the tropical or subtropical zones, biasing the fauna sampled against Tibetan or Mediterranean taxa which would be expected to occur at higher, more temperate elevations (Swan et al., 1962). On the basis of the known fauna of other areas of the Eastern Himalayas only a fraction of the expected species have as yet been recorded. Further, phylogenies have not been proposed for the majority of the known taxa, precluding the application of cladistic biogeographic methods (Humphries and Parenti, 1986) in the analysis of pattern. It would thus be premature to speculate about long-term

historical biogeographical patterns of the Bhutanese reptile fauna and a more detailed analysis is deferred to a later date.

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## First Records of the Pipe Snake (*Cylindrophis*) in China

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**Abstract.** -*Cylindrophis ruffus* (Laurenti, 1768), the red-tail pipe snake, previously known from Burma through Indochina and the East Indies, is reported from three localities in southern China (Hainan, Hong Kong, and Xiamen). These are the first Chinese records for this snake family (Aniliidae or Uropeltidae, according to different classifications). Justification is given for spelling the specific epithet *ruffus* and not *rufus*.

**Key words:** Reptilia, Serpentes, snakes, Aniliidae, Uropeltidae, *Cylindrophis*, China, Indochina.

### Introduction

The genus *Cylindrophis* is comprised of eight species of snakes distributed in Sri Lanka and from Burma through Indochina and the East Indies. Until now, there were no records for China. Historically, this genus has been placed in the primitive family Aniliidae (e.g., Goin et al., 1978; Rieppel, 1979; Underwood, 1967), which also includes *Anomochilus* of western Malaysia and Sumatra, and *Anilius* of South America; *Loxocemus* of Mexico and Central America is sometimes also included in this family. McDowell (1975, 1987), however, separated the two Asian genera from the Aniliidae, and placed them in the subfamily Cylindropheinae of the family Uropeltidae, which includes the shield-tailed snakes (subfamily Uropeltinae), a group of seven genera of burrowing snakes restricted to Sri Lanka and peninsular India.

### Chinese Records

We wish to report the first specimens of this genus (and family) from China. All appear to be referable to the most widely distributed species in the genus, *Cylindrophis ruffus* (Laurenti, 1768), which ranges from Burma to Vietnam, south through peninsular Malaysia and Indonesia (Fig. 1). The published records nearest to China are for Bhamo, Burma (Boulenger, 1888) and Myitkyina, Burma (Wall, 1926), both of which localities are

about 50 km from the western border of China's Yunnan Province. The species is also known from northern Thailand: Chiang Mai in the northwest and Sakon Nakhon in the northeast (Cox, pers. comm.). Deuve (1970) reported *C. ruffus* from several localities in western Laos as far north as Vientiane. Bourret (1935) described four specimens in the collection of the University of Hanoi, but none of these has precise locality data; there are no recent records from northern Vietnam (Tran et al., 1981).

Our new records are from three widely-separated localities in southern China (see Fig. 1), as follows:

**Fujian Province:** Xiamen (Amoy Island); Department of Biology, Xiamen University, two unnumbered specimens, collected at Xiamen by a farmer who dug them out of the soil, date unknown but prior to 1969.

**Hainan Province:** Hainan, no further locality data; Zoological Institute, St. Petersburg (Leningrad), (ZIN 7509), collected in 1888 by Alfred Otto Herz.

**Hong Kong:** No further locality data; Museum of Comparative Zoology (MCZ), Harvard University, (MCZ 5489), collected by a "Capt. Muller," and received in exchange with Peabody Museum, Salem, in 1886.

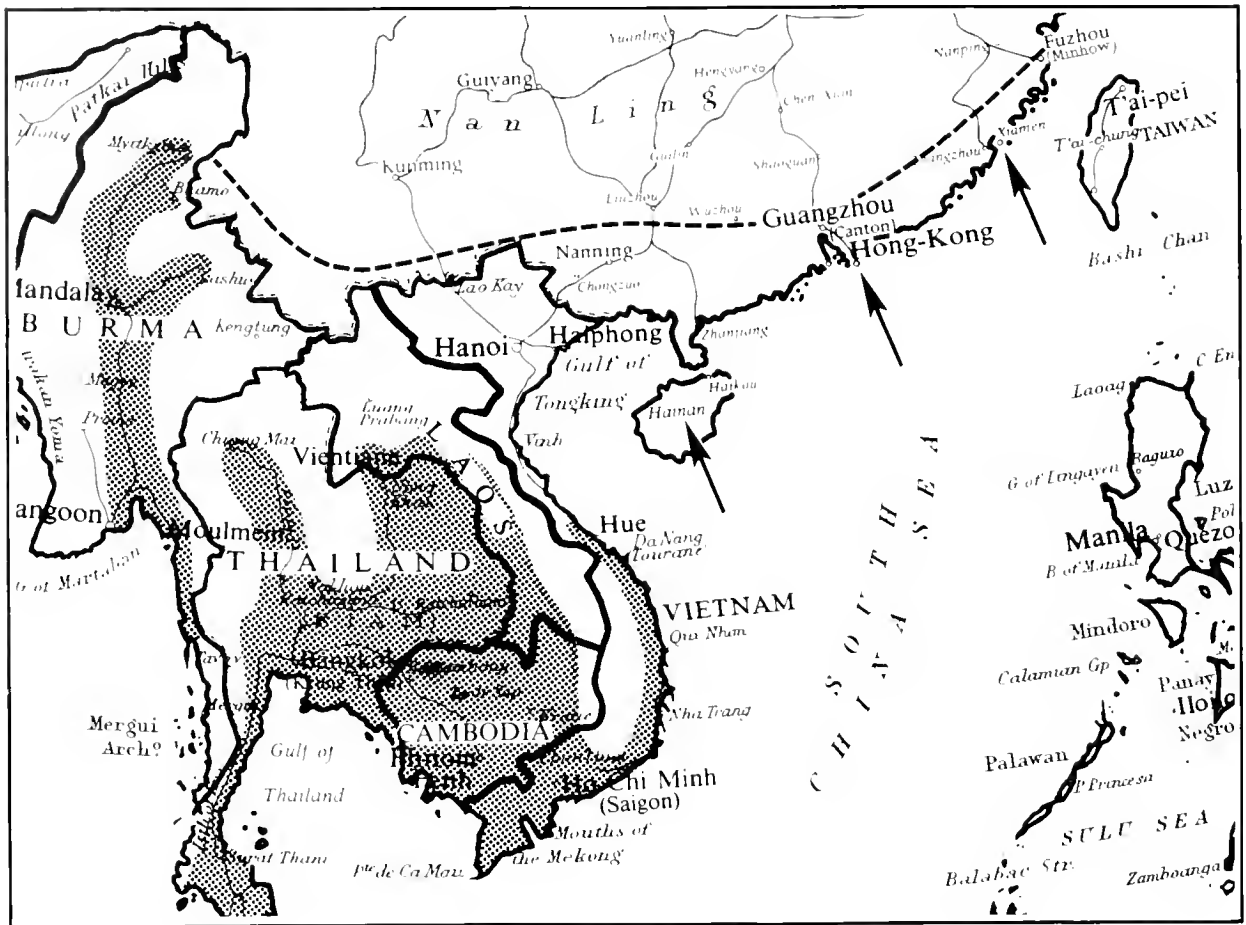


FIG. 1. Distribution of *Cylindrophis ruffus* in Indochina and southern China. The range extends through Indonesia (including Sumatra, Java, and Borneo) as far east as the Celebes and nearby Batjan and Sangihe islands. The new localities in China are Hainan, Hong Kong, and Xiamen (arrows). There are no known authentic records from northern Vietnam. The dashed line indicates the northernmost limit of the South China Biogeographic Region. (Base map adapted from New York Times Atlas of the World, 1985).

All of these localities are in that part of China designated, on biogeographic grounds, as the "South China Region" (China Natural Geography Editorial Board, 1979), an area in southern China that extends from western Yunnan eastward to Fujian Province and includes Hainan and Taiwan (Fig. 1). These records are all the more surprising since this part of China has been collected by herpetologists for many decades. Clifford H. Pope and Malcolm A. Smith failed to find *Cylindrophis* during their extensive field work in Hainan in the 1920s, and Rudolf Mell, who resided in Canton (=Guangzhou) from 1908 to 1921 and made comprehensive collections from southern China, never found it. It is unreported in Fujian by Ting and Zheng

(1974) in their survey of the snakes of that province and also from Hong Kong (Karsen et al., 1986; Romer, 1979). It is possible, of course, that our specimens from Hainan and Hong Kong, being old records and without precise locality data, merely were shipped from these places and the specimens actually originated elsewhere, but the newer records from Fujian, even further north along the Chinese coast and more distant from the main range of the species, are undoubtedly authentic.

On geographic grounds, the Chinese specimens are referable to the nominate subspecies, *C. r. ruffus*. For the record, we provide some meristic data for the

TABLE 1. Meristic data for the Hainan Island and Hong Kong *Calamaria*.

	Hainan	Hong Kong
	ZIN	MCZ
	7509	5489
Sex	female	female
Snout-vent length (in mm)	430	350
Tail length (in mm)	10	8.5
Dorsal scale rows (midbody)	21	21
Ventrals	195	187
Subcaudals	7	7
Upper/lower labials	5/6	6/6
Preoculars/postoculars	0/1	0/1
Anterior/posterior temporals	1/2	1/2

Hainan and Hong Kong specimens (Table 1); unfortunately, we have been unable to reexamine the Fujian specimens to obtain comparable data.

Further descriptive details are given elsewhere (Zhao and Adler, 1989; Zhao and Darevsky, 1990).

#### Natural History

Insofar as is known, all species of pipe snakes, as they are commonly called, are live bearing, inoffensive, and secretive in nature, often being collected beneath fallen vegetation or dug up by farmers from their subterranean burrows. In Thailand, *C. ruffus* is locally common and has been collected in rice fields (it takes readily to water) and in gardens near houses, where it easily burrows in soft earth (Smith, 1943). Schmidt (1928) reported a specimen found in a salt water lagoon.

This is a distinctive snake, both morphologically and behaviorally, and should be easily recognized by collectors. Members of the genus *Cylindrophis* are heavy-bodied snakes, with no neck constriction and a very short tail (Fig. 2A). They reach a total length of nearly one meter. The body of *C. ruffus* is banded and boldly so on the venter. Males have pelvic vestiges with tiny hind limbs terminating in a claw-like spur on each side of the vent. According to literature reports, these snakes make little attempt to escape



FIG. 2. *Cylindrophis ruffus*. A: Hong Kong specimen (MCZ 5489); note absence of neck constriction and the very short tail (arrow marks location of vent). B-C: Adult specimens, probably from Thailand, in defensive posture. When threatened, the head typically is hidden beneath the body (B) or in debris (C) and the posterior end of the body and tail are flattened, held over the body, and sometimes aimed at the intruder, as shown in B.

when exposed, but flatten the entire body and curl the posterior end of the body and the tail over the body, thus exposing the bright red bands on their ventral surface (Fig. 2B-C). Persons collecting in southern China, including Taiwan, should make a special effort to look for this snake.

### Correct Spelling of *ruffus*

Laurenti (1768, p. 71) originally named this taxon *Anguis ruffa* (two fs). His original description is brief: "CXXXVIII. *Anguis ruffa*. DIAGN. Corpore æquali, ruffo, lineis transversalibus albis interruptis; abdomine vario. *Habitat Surinami; hospitatur in Museo Gronoviano,*" or in translation, "[Species] 138. *Anguis ruffa*. Diagnosis. Body uniform, red, broken white transverse bands; abdomen various. Lives in Surinam; housed in Gronovius's Museum." The description apparently is based on *Anguis* species number 6 in Gronovius (1756, p. 54), where fuller details are given. Gmelin (1789) apparently was the first to cite Laurenti's new species, which he called *Anguis rufus* (one f). Wagler (1828) associated this species with his new genus *Cylindrophis*, although he called his new species *C. resplendens*, now regarded as a synonym of *ruffus*. There can be little question that Laurenti intended the spelling with two fs and not as emended by Gmelin. Laurenti used the two-f spelling twice in his description (in both printings of the book; for details of these editions, see Adler, 1989, pp. 12-13) and this spelling was not corrected on his errata page. In classical Latin, rufus is invariably spelled with a single *f*, which probably led to Gmelin's emendation. However, in late Latin inscriptions and manuscripts, doubling of consonants was often used to preserve the length of the preceding vowel, here a long *u*, for purposes of pronunciation (Grandgent, 1907); thus, the alternate spelling *ruffus* is a perfectly acceptable form. Laurenti, in fact, routinely doubled consonants before and after vowels in the names of species throughout his book. The International Code (1985, article 32) states that an author's original spelling must be

preserved unless it contravenes provisions of Articles 27-31 (*ruffus* does not) or there is evidence in the original publication of an inadvertent error (there is none). Thus, "*Anguis ruffa*" is the correct original spelling in the sense of the Code. The Code makes no explicit statement about doubling of consonants, but *in passim* there are several instances of such names used as examples in that book.

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## A New Species of Grass Snake, *Natrix megalcephala*, from the Caucasus (Ophidia: Colubridae)<sup>†</sup>

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**Abstract.** -A new species of Grass Snake, *Natrix megalcephala*, is described from the Caucasus Mountains, of Azerbaijan, Georgia, and Russia. It differs from *Natrix natrix* in having a very thick massive body, a large broad head, and enlarged frontal and temporal scales. *Natrix megalcephala* is found in habitats with Colchida refugia vegetation.

**Key words:** Reptilia, Serpentes, Colubridae, *Natrix*, Azerbaijan, Caucasus, Georgia, Russia, USSR, biogeography, distribution, taxonomy.

### Introduction

In studying museum specimens of the genus *Natrix* Laurenti and working with Colchida snakes in the wild, we came to the conclusion that three species of grass snakes inhabit the Caucasus. This is based on a morphological analysis of specimens in collections. The possible genesis of the species and the formation of their present-day habitats is discussed.

### Methods

We examined 15 specimens of *Natrix natrix persa* Pallas, 15 specimens of *N. natrix scutata* Pallas, and 19 specimens of *Natrix* from the western Caucasus which were thought to be a new species. The following characters were used: 1- snout vent length in mm (L); 2- tail length in mm. (L. cd.); 3- number of scales around the middle of the body (Sq.); 4- number of ventrals (Ventr.); 5- number of subcaudals (S. cd.); 6- number of upper labials (Lab.); 7- number of lower labials (Sublab.); 8- length and width of the frontal; 9- length and width of the parietals; 10- length, height, and width of the head.

A comparative description of skulls in

*Natrix n. scutata* and the new species was done. For a number of characters we calculated mean numbers ( $\bar{x}$ ), error of mean (m), and standard deviation ( $\sigma$ ) using statistics from Lakin (1968).

### Results

An analysis of the data show that the grass snake which occurs within the western Caucasus (known as the Colchida) refugia may be regarded as a separate species. This species, due to a very big head, was given the name *Natrix megalcephala* (Orlov and Tuniyev, 1986a). The common English name is the Colchida Grass Snake.

### Nomenclature Remarks

A number of synonyms were proposed for the Caucasus Grass Snake. However, after a detailed study, we came to the conclusion that none of the proposed synonyms fits the form described.

Nordmann (1840) mentioned two forms for the Caucasus: *Tropidonotus natrix* var. *colchica* and *Tropidonotus natrix* var. *nigra*. The description and the drawing of the first form agrees with *Natrix natrix persa* (Pallas). That of the second form agrees with *Natrix natrix scutata* (Pallas). Derjugin (1899) regarded the form *Tropidonotus natrix* var. *nigra* as a color variation of *T. natrix*. Radde (1899) also

<sup>†</sup> This publication combines material previously published in Russian by Orlov and Tuniyev (1986a) with additional information.



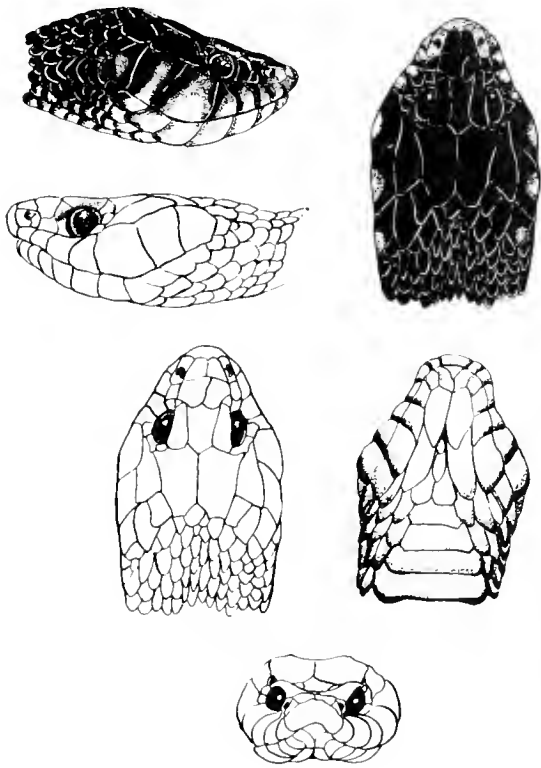


FIG. 1. Various views of the head of the holotype (ZIN 11846) of *Natrrix megalcephala* from Pitsunda, Abkhazia, Georgia.



FIG. 3. Ventral view of the holotype (ZIN 11846) of *Natrrix megalcephala* from Pitsunda, Abkhazia, Georgia.

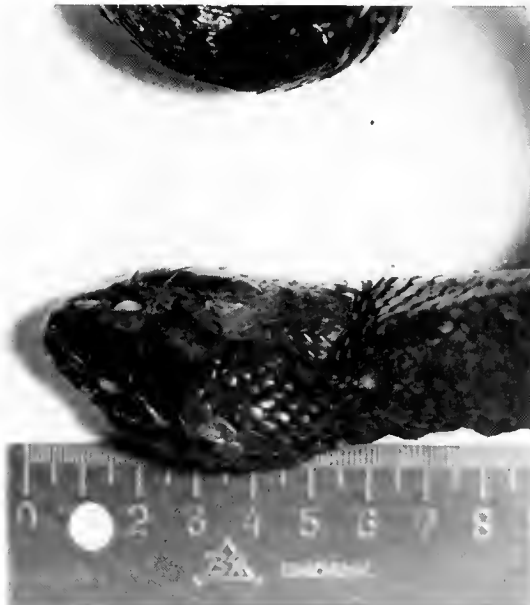


FIG. 2. The head of the holotype (ZIN 11846) of *Natrrix megalcephala* from Pitsunda, Abkhazia, Georgia.



FIG. 4. Dorsal view of the holotype (ZIN 11846) of *Natrrix megalcephala* from Pitsunda, Abkhazia, Georgia.

mentioned that the form, *T. natrix* var. *scutata* Pallas, which had black coloration, occurred in Likani in the vicinity of Borjomi. Dinnik (1902) observed *Tropidonotus natrix* var. *ater* Eichwald, which actually are melanistic specimens of *N. natrix*. Nikolsky (1913, 1916) gives three forms of *Tropidonotus natrix* with regard to the Caucasus: a typical form, *Tropidonotus natrix natrix*; *T. n.* var. *scutatus* Pallas; *T. n.* var. *ater* Eichwald. The latter corresponded to melanistic specimens of *Natrix natrix*.

The synonym "ater" cannot be used as the name for the new species because Eichwald (1831) employed it with regard to melanistic individuals of the valid species *N. n. scutata* (Pallas) from the suburbs of Astrakhan, Russia. Terentyev and Chernov (1949) and Milyanovsky (1957) suggested that *N. n. persa* and *N. n. natrix* occurred in the Caucasus. The overwhelming majority of authors have named two forms for the Caucasus: *Natrix n. scutata* (Pallas) and *N. n. persa* (Pallas), (see, Bischoff and Engelmann, 1976; Mertens and Wermuth, 1960).

The three forms, *N. n. natrix*, *N. n. persa* and *N. n. scutata* which inhabit the USSR territory are given in the field guide of the herpetofauna of the USSR regarding the Caucasus (Bannikov et al., 1977).

To date there is no definite conception about the distribution and interaction of *Natrix natrix* subspecies, particularly in the western portion of its range. Presently from 3 to 9 subspecies are recognized (Thorpe, 1975). In his recent work Thorpe (1980) suggested two initial centers of *Natrix* speciation for the mainland: western European and eastern European centers.

*Natrix megalcephala*  
Orlov and Tuniyev, 1986

*Holotype*.—ZIN 11846, an adult female from Pitsunda, Abkhazia, Georgia, western Caucasus. The specimen was collected in 1909 by K. Satunin (Figs. 1, 2, 3 and 4).

*Description of holotypes*.—SVL 960

mm, tail length 240 mm. Head is covered by large regular scales. Upper labials 8 on the right and 7 on the left. Lower labials are 11 on the right and 9 on the left. One preocular and 3 postoculars on both sides. The nasal touches 2 upper labials. Parietals are large, 17 mm in length and 6 mm in width. Large anterior chin shields are set in two rows. Between posterior chin shields are 3 rows of small scales 1+1+2. Two rows of greatly enlarged irregular scales follow temporals and parietals. The width of the anterior chin shields are greater than their height. The width of internasals equals their length. The length of prefrontals is greater than their width. Nineteen scales surround the mid-body. On the level of the 6th ventral scale from the head and the 6th ventral from the tail there are 19 and 17 scale rows respectively. There are 172 ventrals. Two rows of subcaudals, 68 scales each. The anal plate is divided. The first row of lateral scales bordering the ventrals has a smooth surface. The scales of the second row are barely keeled. The remainder are distinctly keeled. Lateral and dorsal coloration is bright black. The first half of ventrum is spotted with alternating black and white spots. Towards the tail white coloration vanishes. White spots become smaller. Subcaudals are black. Unspotted head is black from above and white from below. White coloration extends onto the lower portion of upper labials. Black stripes go along the edge of lower labials.

*Description of paratypes*.—ZIN 9039, 18794, 21535, 11243, 18794, 11247, 11862, 9594, 18211, 16653, 5273 (Fig. 5 and Table 1).

*Diagnosis*.—This snake differs from the various subspecies of the closely related species *Natrix natrix* Laurenti in having 1) a very thick massive body; 2) a remarkable big broad head; 3) enlarged frontal and temporal scales.

Unlike the subspecies of *N. natrix*, in *N. megalcephala* sutures between closely adjacent head shields are not that well defined. In *N. natrix* scales which cover the head from above (prefrontal, frontal,

TABLE I. Morphological characters of *Natrix megalcephala*.

N	sex	Locality	L	Lcd	ventr	scd	A	lab	sublab	sq1	sq	sq2	prorb	postorb
9093	F	Kheba	640	189	162	63	1-1	7-7	10-10	20	19	17	1-1	3-3
18794	F	Chernali	498	154	167	61	1-1	7-8	10-10	20	19	17	1-1	3-3
11585	F	Lagodekhi	940	205	175	59	1-1	7-7	10-10	19	19	17	1-1	3-3
11846	F	Pitsunda	960	240	172	68	1-1	7-8	9-11	19	19	17	1-1	3-3
11243	F	Makanse River	845	220	171	66	1-1	7-7	10-10	19	19	17	1-1	3-3
Caucasian Reserve	F	Laura River	-	-	172	66	1-1	7-7	9-9	19	19	17	1-1	3-3
Caucasian Reserve	F	Achipse River	830	204	178	62	1-1	7-7	10-10	19	19	17	1-1	3-3
18794	M	Chernali	677	-	169	-	1-1	7-7	10-10	20	19	17	1-1	3-3
11247	M	Lasorevskoye	860	195	172	61	1-1	7-7	10-10	20	19	17	1-1	3-3
11862	M	Sochi	780	215	165	61	1-1	7-7	10-10	19	19	17	1-1	3-3
9591	M	Sochi	720	193	169	65	1-1	7-7	10-10	19	19	17	1-1	3-3
18211	M	Borjomi	530	160	178	80	1-1	7-7	10-10	20	19	17	1-1	3-3
16653	M	Vartashen	360	102	179	77	1-1	7-7	10-10	19	19	17	1-1	3-3
5273	M	Sukhumi	490	160	172	76	1-1	7-7	10-10	19	19	17	1-1	3-3

preocular and parietals) form a smooth surface. In *N. megalcephala* head scales are relieved. The hatchlings of *N. megalcephala* have two light blotches on the head. This character, which is present in a number of *Natrix* species, is an ancestral feature (Fig. 6). While maturing, the light blotches vanish and the snakes acquire strong black coloration. All adult specimens of *N. megalcephala* are pure black dorsally, having no light blotches.

*Comparative Description of Skulls in Natrix megalcephala and Natrix natrix scutata.*—The skull of *N. megalcephala* is relatively higher and broader than that of *N. n. scutata* (Fig. 7). There is a sharp grade going from the frontal to the nasal. Whereas in *N. n. scutata* the two bones lie in one plane. In *N. megalcephala* the parietal is slightly concave, whereas in *N. n. scutata* it is slightly protuberant laterally. In *N. megalcephala* the scaled bone

increases towards the ocular hole, whereas in *N. n. scutata* it is rectangular. The quadrate is very broad at the junction with the squamosum bone. The articular bone is less concave than in *N. n. scutata* at the junction with the pterygoid. In *N. megalcephala* the articular bone is concaved inward to the skull. In *N. n. scutata*, however, dental and articular bones form an exteriorly smoothly concaved arc. On the lower surface of the basisphenoid there is a well expressed longitudinal crest. In *N. n. scutata* it is feebly expressed. On the transversum of the basioccipital there is a hollow which is absent in *N. n. scutata*.

*Geographic Distribution.*—The species' range covers the western Transcaucasus. It occurs from the suburbs of Tuapse, Krasnodarsky Territory, Russia in the west to the Chorokh River of Georgia and Turkey in the southwest. From Tuapse, the border of the distribution goes over the

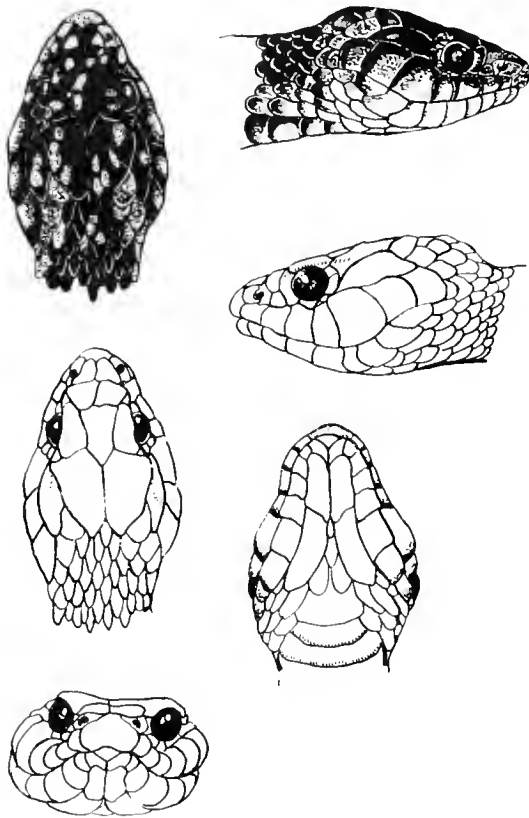


FIG. 5. Various views of the head of *Natrix megalcephala* from Lagodekhi, Georgia.

Great Caucasus Ridge and then stretches along the foothills up to the area where the Urushten and Malaya Laba rivers merge in Krasnodarsky Territory, Russia.

Isolated populations are found along the southern slope of the western Caucasus in the vicinity of Lagodekhi, Georgia and Vartashen, Azerbaijan. Isolated populations are also found on the eastern slope of Adjaro-Imeretinsky Ridge, in the vicinity of Borjomi, Georgia (Fig. 8).

The species habitat is associated with the Colchida or western Transcaucasian botanico-geographical province (Kuznetsov, 1891, 1909). Distributions of isolated populations of *Natrix megalcephala* coincide with vegetation refugia of the Colchida type in Belo-Labinsky district, in the canyon of mid-flow of the Kura River and a number of refugia on the southern slopes of the Eastern Caucasus.



FIG. 6. Juvenile specimen of *Natrix megalcephala* (ZIN 19967).

*Biotopic and Elevational Distribution.*— In western Transcaucasia *Natrix megalcephala* ranges from the Black Sea slope of the Great Caucasus Ridge up to the subalpine belt. On the northern slope and in the eastern refugia this species occurs in the mountains up to 1000 m (Table 2). The biotypes of *N. megalcephala* are represented by forests of the Colchida type: evergreen secondary trees, *Fagus orientalis*, *Quercus iberica*, *Taxus baccata*, *Buxus colchica*, *Laurocerasus officinalis*, *Fagetum nudum*, *Castanetum colchicum*, *Alnetum strutiopteridosum*, *Fageto-Abieta athirio-mixtogerbosa*. More seldom *Quercetum azaleosum*. This snake also occurs in transformed areas such as forest edge meadows, tea plantations, and secondary hornbeam woods. *Natrix megalcephala* is a mesophyllic species, but unlike *Natrix natrix* and *Natrix tessellata*, it is well adapted to swift montane rivers. In case of danger, this species can hide in swift waters.

*Abundance.*—It is a common but not numerous species. It never forms such dense populations as are found in *N. natrix* and *N. tessellata*. The highest density is observed in mixed Alder and Willow forests along river beds, where up to three specimens per kilometer walked may be

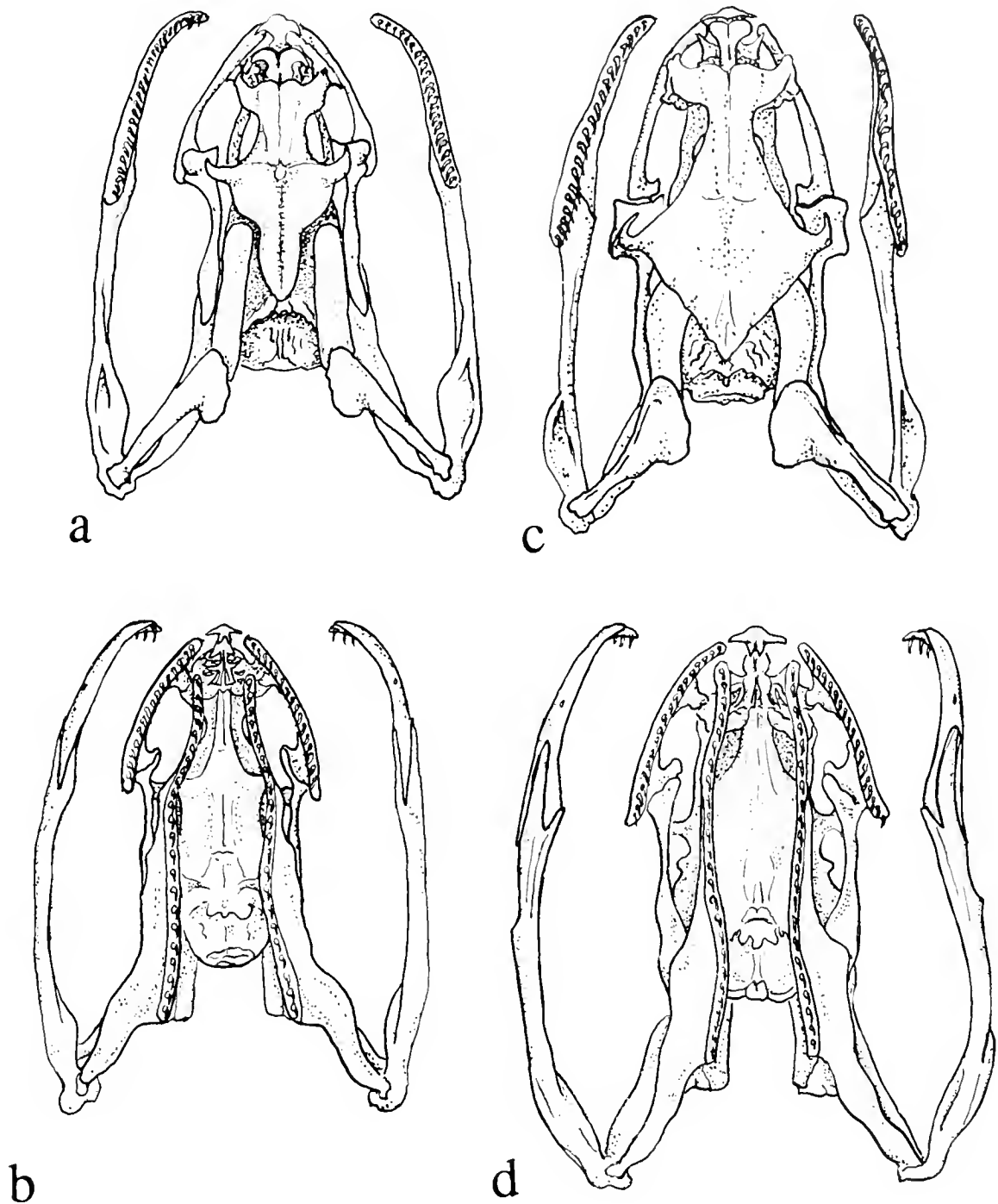


FIG. 7. Skulls of *Natrrix natrrix scutata* (a, b) and *Natrrix megalcephala* (c, d).

encountered.

*Seasonal and Daily Activity.* —On the Black Sea coast of the Caucasus near Sochi, *N. megalcephala* comes out of hibernation in March and remains active until November or early December. At

elevations of 600 to 1600 m the activity period is shorter. For instance, in a gorge of the Achipse River, we have observed active snakes from the end of April to the end of September. In the spring and fall *N. megalcephala* is active in the afternoon. In these seasons snakes may be encountered

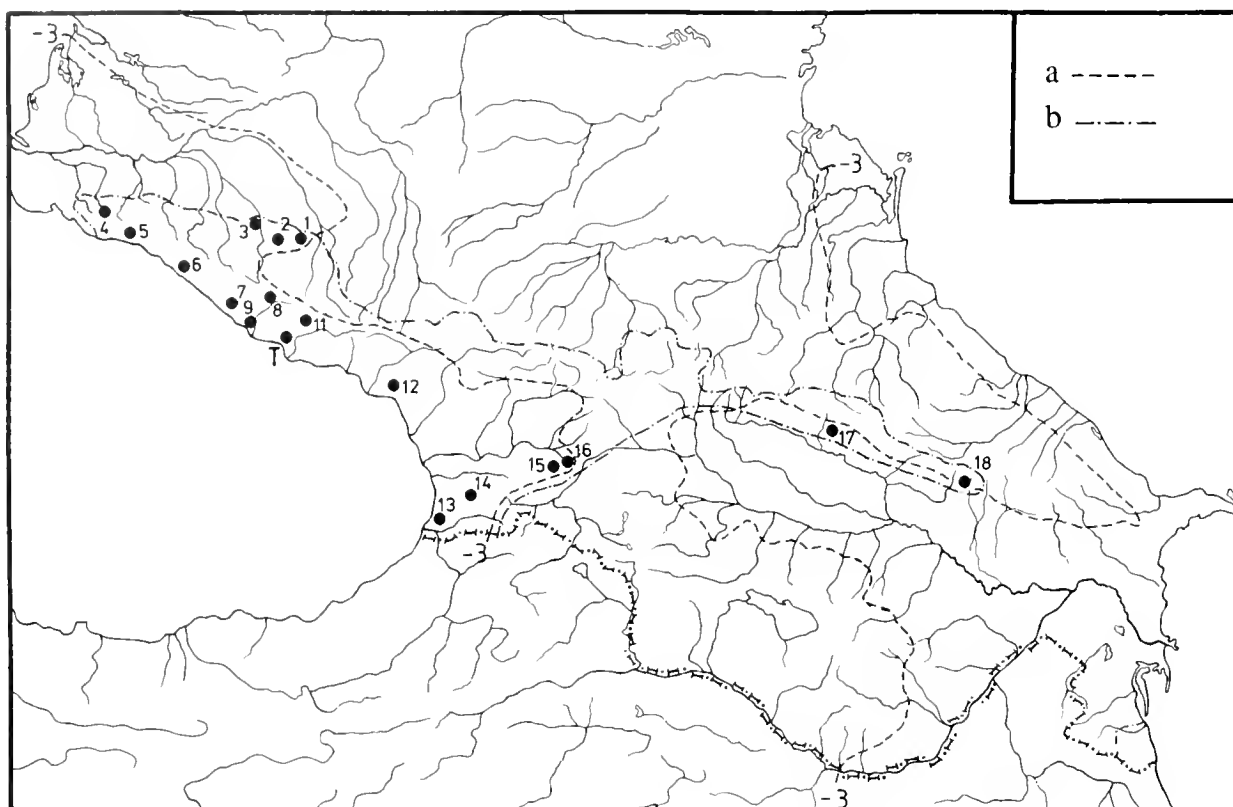


FIG. 8. Distribution of *Natrrix megalcephala*. Russia, Krasnodarsky Territory: 1- mouth of the Urushten River; 2- Kisha Cordon, Caucasian Reserve; 3- Stanitsa (a small settlement in the country side) of Khamyshki; 4- Tuapse; 5- Lazorevskoye; 6- Sergei-Pole; 7- Sochi; 8- Malaya Khosta River; 9- Yew-box Grove; 10- Achipse River. Georgia: 11- Lake Ritza; 12- Sukhumi; 13- Batumi; 14- settlement of Kheba; 15- settlement of Likani; 16- Borjomi; 17- Lagodekhi. Azerbaijan: 18- settlement of Vartashen. T- Type locality, Pitsunda, Abkhazia, Georgia. a- Isotherm of the coldest month, above  $-3^{\circ}\text{C}$ . b- Amount of precipitation not less than 800 mm (after Gerasimov, 1966).

basking up to 1000 m away from a water source during the warmest hours. In the summer along the Black Sea coast *N. megalcephala* is active in the morning, during the late afternoon, and at night. For instance, in the Yew-box Grove of the Caucasus Preserve in the Labirintovaya Wash, Sochi, Krasnodarsky Territory, Russia, we observed *N. megalcephala* hunting for *Pelodytes caucasicus* in July from 2100 until 2330 hours. Summer activity at mid-elevations has a daily two peaked pattern: from 0900 until 1130 hours, and from 1630 until 1800 hours. It is interesting to note that in the summer *N. natrrix* and *N. tessalata* are active strictly during the day along the Black Sea coast of the Caucasus.

*Breeding.*—A female *N. megalcephala*,

collected in the canyon of the Achipse River on 11 August 1985, laid 13 eggs. Table 3 gives comparative data on size of the eggs and hatchlings of *N. megalcephala*, *N. natrrix*, and *N. tessalata*. These data show that *N. megalcephala* lays much bigger eggs and its hatchlings are bigger in size compared to the other representatives of the genus. A female, which was collected in the Yew-box Grove of the Caucasus Preserve in the Labirintovaya Wash, Sochi, Krasnodarsky Territory, Russia during June 1990, laid a clutch of 11 eggs in captivity on 20 August, 1990. The eggs were incubated at  $26-29^{\circ}\text{C}$  and hatched on 29 September, 1990.

*Diet.*—*Natrrix megalcephala* feeds mainly on amphibians. Adults prey actively on adult *Bufo verrucosissimus*. In

TABLE 2. Habitat descriptions of *Natrix megalcephala* populations.

Location of Population	Short description of biotopes	Elev.
1. The Zapadny Dagomys River	Dwarf scrub-like creeping vegetation near river bed	0 m
2. Yew-box Grove	Washes in box woods	50 m
3. Lake Agurskoye	A reservoir in a cherry-laurel- oak grove	150 m
4. Settlement of Sergei Polye	Agrocenosises, azalea oak grove	200 m
5. Settlement of Golitsino	Oak grove	300 m
6. Malaya Khosta River	Alder and willow groves near river bed	350 m
7. Settlement of Solokh-Aul	Willow groves near river bed	350 m
8. Settlement of Krasnaya Polyana	Alder groves	550 m
9. Settlement of Esto-Sadok	Hornbeam groves, alder groves	550 m
10. Laura Cordon, Caucasian Reserve	Post-forest meadows in forest near river bed	570 m
11. Settlement of Rudnik	A post-forest meadow in an alder grove	570 m
12. Guzeripl Cordon, Caucasian Reserve	A post-forest meadow in an oak grove	600 m
13. Assara River	Alder grove near river bed, <i>Alnetum struthiopteridosum</i>	600 m
14. Vylomannaya Balka, Caucasian Reserve	Alder grove near river bed <i>Alnetum corylosum-sambulosum</i>	600 m
15. Kisha Cordon, Caucasian Reserve	A meadow in the "Cherkessky Forest"	700 m
16. Suvorovsky Cordon, Caucasian reserve	A post-forest meadow in a peach grove	700 m
17. Goreloye Urochische	<i>Abies</i> grove	800 m
18. Achipse Stationary, Caucasian Reserve	Mountain waste with scrub communities, <i>Fagetum nudum</i>	970 m
19. Turovaya River	An <i>Abies</i> -peach grove	970 m
20. Engelmannova Meadow, Caucasian Reserve	A hornbeam and beach grove near river bed	1200 m
21. Beryosovaya River	An alder grove near river bed	1300 m

TABLE 3. Size of eggs and hatchlings of *Natrix natrix*, *Natrix tessellata* and *Natrix megalcephala*.

Character	<i>N. natrix</i>		<i>N. tessellata</i>		<i>N. megalcephala</i> min-max $\bar{x} \pm m$
	1	2	1	2	
Egg length mm	12-23	12-19	32-35	24-38	<u>37.5-47</u> 41.38±0.60
Egg width mm	23-25	18-24	15-16	14-23	<u>21.0-24.0</u> 22.46±0.23
Total length of hatchlings	-	222	-	182	<u>254-337</u> 287±10.47

Note: 1- according to data of Bannikov et al. (1977); 2- according to data of Scherbak and Scherban (1980).

June, 1982 we collected a specimen in a canyon of the Achipse River. It was 850 mm in length and contained a toad 120 mm in length. In the Achipse Station within the Caucasus Preserve this species was observed to prey on *Triturus vittatus*, and in the Yew-box Grove, on *Pelodytes caucasicus*. Hatchlings feed mostly on tadpoles and small specimens of *P. caucasicus* and *Rana macrocnemis*. We

have observed juvenile *N. megalcephala* preying on these amphibians in water puddles of meadows and former river beds of swift rivers in the vicinity of Sergei-Pole (Serge Field), Krasnaya Polyana (Red Meadow), Guzeripl, Yew-box Grove, Achipse River Valley and a number of other spots in the western Caucasus.

*Shedding.*—We observed snakes

TABLE 4. A comparison of morphology and pholidosis in *Natrix natrix scutata*, *N. natrix persa*, and *N. megalocephala*.

Character	<i>Natrix n. scutata</i>			<i>N. n. persa</i>			<i>N. megalocephala</i>		
	n	min-max	$\bar{x} \pm m$	n	min-max	$\bar{x} \pm m$	n	min-max	$\bar{x} \pm m$
Body Length	12	512-720	608.3±20.6	12	520-745	645±22.4	10	530-940	778±40.9
Tail Length	11	130-178	148.3±3.46	12	130-200	165±6.35	10	154-240	198.1±7.5
Ventrals	12	164-178	171.9±1.55	12	177-183	178.2±0.97	14	162-181	172.0±1.26
Subcaudals	12	52-79	64.16±2.36	12	46-75	65.9±2.53	14	59-80	67±1.93
Scale Rows	12	17-20	18.91±0.18	12	18-19	18.85±0.12	14	18-19	18.93±0.06
Relative Head Length	12	0.027-0.031	0.028±0.001	9	0.027-0.030	0.028±0.001	10	0.03-0.05	0.04±0.002
Relative Head Width	12	0.019-0.027	0.022±0.001	9	0.020-0.023	0.021±0.001	10	0.026-0.041	0.031±0.001
Relative Head Depth	12	0.013-0.016	0.014±0.001	9	0.013-0.016	0.014±0.001	10	0.018-0.024	0.020±0.001
Frontal Length	12	4.0-6.0	5.38±0.15	9	4.5-7.0	5.50±0.25	10	6-10	7.77±0.37
Frontal Width	12	3.0-4.5	3.75±0.15	10	3.5-4.5	3.95±0.08	10	4.5-7	5.44±0.26
Pareital Length	12	6.0-9.0	7.08±0.31	10	6-10	7.35±0.33	10	8-17	12.25±0.77
Parietal Width	12	4.0-6.0	4.75±0.40	10	4.0-6.0	4.70±0.16	10	5-9.5	7.30±0.40

shedding skin on the southern slope of the Great Caucasus Ridge at an elevation of 850 m from late June to early July.

### Discussion

*Natrix megalocephala* differs from other *Natrix* species in external morphology, skull composition, size of eggs and hatchlings. There are also ecological differences. These differences suggest an ancient separation of *Natrix megalocephala* (Tables 1 and 4). In the east and southeast *N. megalocephala* is sympatric with *N. natrix persa*. Sympatry has been observed near Borjomi and Batumi, Georgia. In the west and northwest portion of its distribution, in the suburbs of Tuapse, Goryachy Kluch (Hot Springs), Khamychki and the Urushten River bed, of Krasnodarsky Territory, Russia *N. megalocephala* lives sympatrically and often symbiotopically with *Natrix natrix scutata*. In the collections of the Zoological Institute St. Petersburg (Leningrad) there are

specimens (see ZIN 18744 and ZIN 11284) collected from near Chornaly (suburbs of Batumi, Georgia) and from Stanifsa (a small settlement in the country side) of Khamyshky, Krasnodarsky Territory, Russia. Both *Natrix* species lived sympatrically (Fig. 9).

Within the town of Pitsunda, Abkazia, Georgia there is an isolated population of *Natrix natrix scutata*. Apparently, it is a relict of the holocene xerothermal epoch. *Natrix megalocephala* may also be encountered at this spot (Fig. 10). Radde (1899) thought that melanistic *Natrix* from the Borjomi Canyon, Georgia were *Tropidonotus natrix* var. *scutatus* Pallas. He wrote: "It is interesting that this variety occurs in Likani where it lives together with *T. natrix* L, typ". Nikolsky (1913, 1916) also wrote about sympatric occurrence of *N. natrix* typ., *N. natrix scutatus* and *Natrix natrix ater* on the southern side of the Great Caucasus Ridge. In the areas where *N. megalocephala* lives sympatrically with



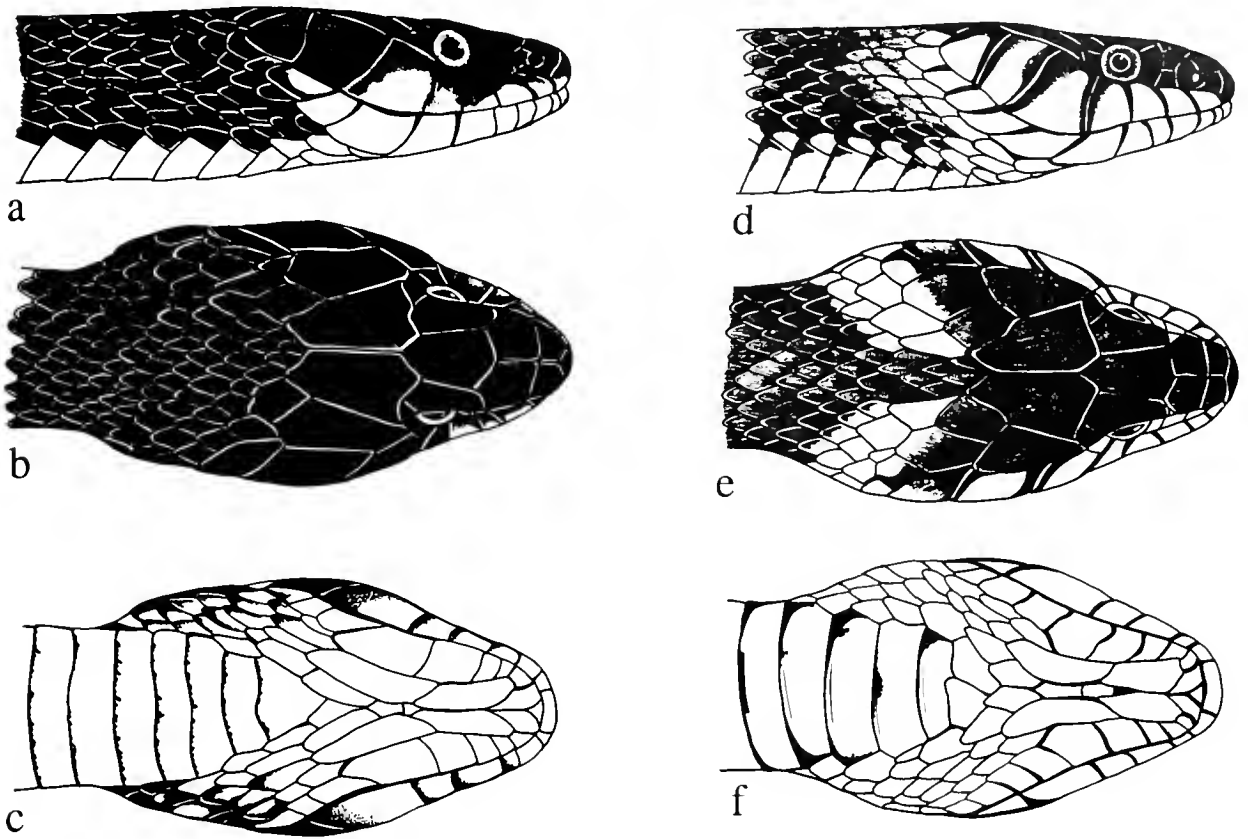


FIG. 9. The heads of *Natrrix megalcephala* (a, b, c) and *Natrrix natrix scutata* (d, e, f) from sympatric populations at Stanitsa of Khamyshki, Krasnodarsky Territory, Ruissia.

other subspecies of *Natrrix natrix* we did not find hybrid characters in morphology (Intergrading features). In all areas where *N. megalcephala* comes into contact with *N. natrix* and *N. tessalata* it has a distinct morphological isolation (Table 4). Despite evident phylogenetic relationship between *N. megalcephala* and *N. natrix* it is probable that these species diverged from some ancient ancestral form not on the territory of the Caucasus Isthmus, but rather beyond it, when the Caucasus had been an island. Supposedly, not less than three faunogenetic centers contributed to the invasion of *Natrrix* species to the Caucasus Isthmus in the Miocene: Asia Minor, Kirkand-Elbursk, and South Europe (Vereshchagin, 1958). Apparently the time of invasion and distribution differed. The fact is supported by the entire location of habitats and interaction of such forms as *N. natrix persa*, and *N. natrix scutata* which form intergrading populations in the

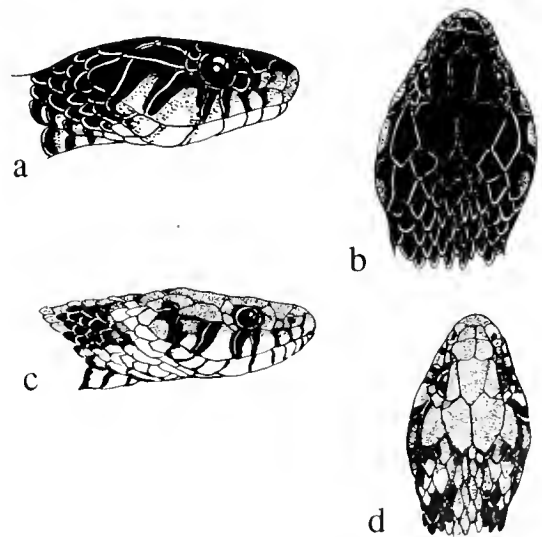


FIG. 10. The heads of *Natrrix megalcephala* (a, b) and *Natrrix natrix scutata* (c, d) from sympatric populations in the vicinity of Pitsunda, Abkhazia, Georgia, the type locality for *Natrrix megalcephala*.

Caucasus, and *N. megalcephala*, which in each overlapping area is distinctly separated from *N. natrix* and *N. tessellata*.

It is evident that an ancestral form of *N. megalcephala* came from Asia Minor in the Miocene at the time the island of Caucasus joined Asia Minor (Vereshchagin, 1958). The Pleiocene was the time of apparent general invasion of *N. megalcephala* to forested subtropic areas of the Great Caucasus and the western portion of the Small Caucasus. At that time, this territory was covered with moisture loving vegetation similar to the type that presently exists in the Colchida refugia (Kharadze 1974; Kholyavko et al., 1978). *Vipera kaznakowi* Nikolsky invaded the Caucasus in a similar way. Its present habitat coincides with the range of *N. megalcephala* (Orlov and Tuniyev, 1986b, 1990). Abundant food items like various Anura (Chkhikvadze, 1984) also contributed to the broad distribution of this species under the favorable conditions of damp subtropics. It is evident that at the end of the Pleistocene, *N. natrix persa* colonized the Talysh Mountains, presently the Azerbaijan-Iran border. This species is to a great extent associated with a xerothermal regime. This is suggested by the present range of the form which covers semideserts and the dry steppes of eastern Transcaucasus, Dagestan, and northern Iran. During Pleistocene glaciation, which covered high elevations of the Great and Small Caucasus (Gvozdetsky 1954, 1958; Markov et al., 1965), the habitat of *N. megalcephala* had apparently split into: 1) the Colchida portion where subtropical vegetation was preserved even in the most severe periods of glaciation (Adamyants, 1971; Vereshchagin, 1958) and 2) other smaller spots lying between the Belaya Laba (White Laba) and Malaya Laba (Small Laba) rivers, in Borjomi Canyon and in the area of Lagodekhi-Zakataly, all in Georgia.

In the Pleistocene *N. natrix scutata* invaded the Precaucasus. Previously it was probably ousted by glaciers from the European Plain to the lower areas of the Don and Volga rivers. The Manychsky Strait, which occasionally used to connect

the basins of the Black and Caspian seas (Kvasov, 1975) would not have been able to be a barrier for such water-loving forms as *N. natrix scutata* to invade the Precaucasus. Alternation of regressions and transgressions of these seas (Kvasov, 1975; Vereshchagin, 1958) might provide a wave shaped invasion for *N. natrix scutata* to the Caucasus. During interglacier and particularly the postglacier Holocene period, a shift of all vegetation belts in the Caucasus occurred (Vereshchagin, 1958). This contributed to the isolation of *N. natrix scutata* and probably *N. natrix natrix*. In the Holocene, formation of habitats occupied by *Natrix* species and subspecies had apparently been finished. The habitats acquired contours similar to those presently existing. Arid areas of eastern Transcaucasus did not allow *N. megalcephala* to restore the eastern portion of its former distribution.

Analysis of the recent range of *N. megalcephala* shows that the species does not exceed the limits where the January isotherm is  $-3^{\circ}\text{C}$  and precipitation is not less than 800 mm yearly (Gerasimov, 1960). This along with the preference of Colchida subtropical vegetation in general support the fact that this warm and water dwelling species is ancient. Bartenev and Reznikova (1935) observed a higher degree of melanism in representatives of the Colchida fauna, some snakes included. In this area melanistic specimens of *Coluber najadum* (Maimin and Orlov, 1977) and *Vipera kaznakowi* are found. Black color is also prevalent in the coloration of *N. megalcephala* from the Colchida.

It is interesting to note that apart from melanism both *V. kaznakowi* and *N. megalcephala* from the Colchida are characterized by: 1) a big head, 2) a massive body, and 3) a very small population density compared to their closely related species.

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*Cyrtodactylus madarensis* Sharma (1980), a junior synonym of *Eublepharis macularius* Blyth (1854)

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**Key words:** Reptilia, Sauria, Gekkonidae, *Cyrtodactylus madarensis*, *Eublepharis macularius*, systematics.

*Cyrtodactylus madarensis* was described by Sharma (1980) based on a single juvenile male from near Madar (alt. 263 m), approximately 5 km north-west of Ajmer City, Rajasthan, in north-western India. No diagnosis of the new species was provided and the author compared his new find, for reasons uncited, only with the gekkonid, *Cyrtodactylus stoliczkai*, which is restricted to the extreme northern parts of India (Kashmir and Ladakh) and north-western Pakistan (North-West Frontier Province) and adjacent China (Welch et al., 1990).

Examination of the photographs and a close scrutiny of the type description of *Cyrtodactylus madarensis* revealed that the generic assignment of this taxon has been erroneous. The plate (No. IV: A) accompanying the paper clearly shows thick upper eyelids that are pale in color, which have been considered diagnostic of another gekkonid genus, *Eublepharis* (see Smith, 1935; Minton, 1966; Daniel, 1983). In general, the color pattern of the dorsum of the type is strikingly similar to Daniel's (op cit.) *Eublepharis macularius* (Blyth, 1854) juvenile (Plate 16, top).

Other generic characters of *Eublepharis* that were present in the type of *Cyrtodactylus madarensis* include the presence of lamellae under the digits; a segmented, cylindrical tail; dorsum of body with small granular scales intermixed with large subtriangular tubercles; and imbricate ventral scales. Specific characters of *Eublepharis macularius* noted in *Cyrtodactylus madarensis* include a large head with a distinct, narrow neck; pointed snout; prominent tubercles on the dorsum;

nine upper labials; ten lower labials; hind limbs reaching axilla; tail cylindrical, segmented, tapering to a point and tail length (36 mm) shorter than snout-vent length (50 mm). The description of coloration of dorsum agrees with that of *Eublepharis macularius* provided by Smith (1935) for juveniles (dark brown with bands and a white nuchal loop), and as previously noted, the type of *C. madarensis* is virtually identical in coloration to the juvenile of *E. macularius* illustrated in Daniel (1983). Adults of *E. macularius* are dark brown or reddish brown above, with the bands breaking up into spots.

Underwood (1954) revived the genus *Cyrtodactylus* Gray (1827), whose members are widespread from the shores of the Mediterranean eastwards through the Indian subcontinent, to Australia and the islands of the south-west Pacific. The subsequent splitting up of the genus by Szczerbak and Golubev (1986) has been criticised by Bauer (1987), but none of the members of this taxonomically complex group of padless geckos possess thick movable eyelids. Eyelids among gekkonids, in fact, are restricted to the eublepharines.

Males of *Eublepharis macularius* possess 9-18 preanal pores (Smith, 1935), which were not present in the type of *Cyrtodactylus madarensis*, according to the type description. However, the type was a juvenile male (snout-vent length 50 mm). *Eublepharis macularius* is known to reach about 250 mm in total body length, the 300 mm length supposedly attained by the species according to Theobald (in Smith, 1935) may refer to a third species of Asian

eublepharid, *Eublepharis angramainyu* (G. Benyr, pers. comm.).

Bhati (1989) synonymised *Eublepharis macularius* (Blyth, 1854) with *E. hardwickii* Gray (1827) after claiming to have examined a large series from Rajasthan. However, no evidence of this opinion was presented in the communication. In fact, another recent worker, Grismer (1988) has shown both species of Indian eublepharids to be valid and that the ranges of the two species of Indian eublepharine geckos are separated by the plains of north-central India. *Eublepharis macularius* enters India in the north-west, with an apparently isolated population in northern Maharashtra State in western India, whereas *E. hardwickii* is restricted to north-eastern peninsular India and probably Bangladesh. The locality of Sharma's *Cyrtodactylus madarensis* therefore falls within the known range of the first named species.

Thus, I consider *Cyrtodactylus madarensis* a junior synonym of *Eublepharis macularius*, a gekkonid lizard found in north-western India, Pakistan, and Afghanistan.

In the description of his new species, Sharma claimed that the skin of his specimen exhibited luminescence. No explanation for this observation could be given in the present note, except that the pale bands on the dorsal aspect of the body of *Eublepharis macularius* juveniles appear extremely conspicuous against the dark brown background, a color pattern that may be aposematic.

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## The Type Locality of *Agkistrodon halys caraganus*

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Wolfgang Böhme (1991) called attention to an error in the designation of the type locality for *Agkistrodon halys caraganus* (Eichwald). Inasmuch as Böhme's correction appears in German in the midst of his long, detailed review of the *Agkistrodon* complex by Gloyd and Conant (1990), and thus may be overlooked, it seems advisable to summarize the facts briefly in English. Eichwald (1831), in describing *caraganus*, wrote "Hab. in ora orientali caspii maris Tjuk-karaganensi ..." In 1969, when Dr. Gloyd transferred his major attention from the North American members of the genus to those of the Old World, he searched diligently but failed to find any locality on any map of Asia available to him that matched the one given by Eichwald (*fide* Kathryn J. Gloyd, who assisted him with his bibliographical work). He eventually interpreted the locality as Karaganda, north of Lake Balkhash, because of its similar spelling and its location within the range of the taxon as implied from the list given by Paraskiv (1956). The type locality for *caraganus* was thus stated and mapped in Gloyd and Conant (1990) as Karaganda. It is unfortunate, during my own lengthy and much later study on *caraganus*, that I did not compare Eichwald's original statement with more recently published maps. In the (London) Times Atlas of the World, on

plate 46, Mys Tjub Karagan (Cape Karagan Hill) appears at the tip of the Mangyshlak Peninsula on the eastern side of the Caspian Sea. This is certainly the equivalent of Eichwald's "Tjuk-karaganensi," as Bohme pointed out. The type locality for *Agkistrodon halys caraganus* is on the eastern edge of the Caspian Sea in Kazakhstan and not at the city of Karaganda.

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## Evaluation of Snake Venoms among *Agkistrodon* Species in China†

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**Abstract.** -Venom toxicity and enzymatic activities were examined in six species of Chinese *Agkistrodon* and *Deinagkistrodon acutus*. The venom toxicity of *A. intermedius* is the strongest, ten times that of *Deinagkistrodon acutus*. The venoms of *A. blomhoffii brevicaudus*, *A. blomhoffii ussuriensis*, and *A. shedaoensis* are the next strongest. *Agkistrodon saxatilis* venom had a similar toxicity as *A. strauchii* venom and they are more similar to *Deinagkistrodon acutus* in toxicity.

**Key words:** Reptilia, Serpentes, Viperidae, *Agkistrodon*, *Deinagkistrodon*, China, venom, toxicity.

### Introduction

*Agkistrodon* snakes are widespread and abundant in China. According to Zhao et al. (1981) and Chen et al. (1984) they should be classified as: (1) *Agkistrodon blomhoffii brevicaudus* Stejneger, (2) *A. b. ussuriensis* Emelianov, (3) *A. intermedius* (Strauch), (4) *A. saxatilis* Emelianov, (5) *A. shedaoensis* Zhao, (6) *A. strauchii* Bedriaga (Plate 1), (7) *A. monticola* Werner, and (8) *Deinagkistrodon acutus* (Gloyd, 1979). The later was formerly regarded as *Agkistrodon acutus*.

The components and properties of venoms from these species are strikingly different from each other (Zhao et al., 1981). From the standpoint of venoms the general designation of Chinese *Agkistrodon* as only one species, *A. halys* Pallas, should not be accepted. Recently in China, *Agkistrodon* venoms have been used to make medicines to cure thrombotic disease and cancers. SVATE (Snake Venom Anti-thrombotic Enzymes) was first prepared from the venom of *A. shedaoensis* from Snake Island in Dalian, and was effective in curing thrombosis. Since there was a shortage of *A. shedaoensis* venom, the venom of *A. b. brevicaudus* from Zhejiang in eastern China was also used. However the product of *A. shedaoensis* seemed

better than that from *A. b. brevicaudus*. Later, two products, one named Qin Suan Mei using the venom of *A. b. ussuriensis*, and the other named Defibrinogenase using the venom of *D. acutus* also appeared in clinical application, but their efficiency and side reactions differed from each other. 787 Snake Venom Capsules, made by Shanghai Xin-Le District Hospital using the crude venom of *A. b. brevicaudus* for treatment of cancers has a magically inhibitory effect on the growth of malignant tumour cells. These observations aroused our interest to understand the differences of *Agkistrodon* venom properties. In this paper we determined the toxicity (LD<sub>50</sub>), and enzymatic activities of arginine esterase, proteolytic and fibrinolytic enzymes to evaluate the quality of selected pit-viper venoms.

### Methods

#### *Snake Venoms*

*Agkistrodon b. brevicaudus* were purchased from the Shanghai Experimental Animal Supply Station. *Agkistrodon b. ussuriensis*, *A. shedaoensis*, and *A. strauchii* were kindly provided by Professor Ermi Zhao of the Chengdu Institute of Biology. *Agkistrodon intermedius* was kindly provided by Mr. Jinbao Yu from Xinjiang Institute of Chemistry. *Deinagkistrodon acutus* were purchased from Jindezeng Snake Institute, Jiangxi.

† This publication was previously published in Chinese by Chen et al. (1990).



### Chemical Reagents

BAEE (N-benzoyl arginine ethyl ester hydrochloride), are products of the Dongfeng Factory of Biochemical Reagents. Human fibrinogen and thrombin are products of the Shanghai Institute of Biological Products and casein is a product of the Factory of Chemical Reagents, Shanghai. All other chemical reagents are analytical grade.

### Toxicity ( $LD_{50}$ )

Toxicity ( $LD_{50}$ ) was assayed (Litchfield and Wilcoxon, 1949). We dissolved 3-5 mg of snake venom in physiological saline, and then diluted the venom solution to 1-5 concentrations. Swiss mice of 18-20 grams of body weight, were divided into five groups, with six individuals each. Mice were injected intra-abdominally with 0.4 ml of venom solution. After injection observations were made within 48 hours. The death rate ( $LD_{50}$ ) was then calculated.

### Enzymatic Activities

1. *Arginine esterase* (United States Pharmacopea, 1980).—BAEE solution (0.8 mm moles) was prepared by dissolving BAEE in 0.05 M pH 8.0 tris-HCl buffer solution. Three ml of BAEE solution was inserted into a cuvette and 0.1 ml of snake venom solution was added. Spectrophotometric measurements were made at 253 nm and 25°C. The unit of activity is calculated according to the formula,  $U/mg = (A_1 - A_2) / (0.003 \times T \times W \times A_1)$ . The last value is at the linear part of the curve, where  $A_2$  is the initial value, T is the time tested, and W is the weight of venom in milligrams.

2. *Proteolytic enzyme* (Rick, 1963).—One gram of casein was dissolved in 100 ml of 0.05 M Tris-HCl pH 7.8 buffer in a boiling water bath and the undissolved materials were filtered. We transferred 2 ml of filtrate to a test tube and incubated it in a 37°C water bath. Then two ml of venom solution (2 mg/ml) was added. After 15

minutes we added 15 ml of 15% trichloroacetic acid and mixed it thoroughly, filtering after 30 min. The filtrate was measured at 280 nm. We calculated the tyrosine released from the standard curve of tyrosine. The unit of activity is denoted by  $\mu g$  of Tyr/15 x mg of venom.

3. *Fibrinolytic enzyme* (Deogny et al., 1975).—We dissolved 0.5 grams of human fibrinogen in 10 ml of pH 7.75 barbiturate buffer and transferred 5 ml of the solution into each of two petri dishes (8 cm diameter). We subsequently added 1 ml of thrombin (about 4 units) and mixed it thoroughly. Then we immediately added 5 ml of 2% agar solution (below 60°C) and mixed it again to get a uniform plate. Wells were punched in the plate into which was put 10  $\mu l$  of venom solution; incubated at 37°C for 18 hours. One unit of activity is equal to 1 mm<sup>2</sup> of lysis on the plate. The activity is denoted by units = mm<sup>2</sup>/mg of venom.

### Results

The venom toxicity of *A. intermedius* is the strongest, ten times that of *Deinagkistrodon acutus* (Table 1). The venoms of *A. b. brevicaudus* and *A. b. ussuriensis* are the next strongest. Neurotoxins were isolated from these venoms. A presynaptic neurotoxin, Agkistrodotoxin, has been purified from the venom of *A. b. brevicaudus* (Chen et al., 1981) and its amino acid sequence also has been determined (Kondo, 1989). Three presynaptic neurotoxins were purified from the venom of *A. intermedius*. Their  $LD_{50}$  are 38, 49 and 49  $\mu g/kg$  of mice respectively, higher than that of Agkistrodotoxin which has a  $LD_{50}$  of 55  $\mu g/kg$  (Zhang and Hsu, 1985a). A fraction from column chromatography of the venom of *A. b. ussuriensis* has been confirmed to be neurotoxic (Zhang and Hsu, 1985b). The venoms of *A. shedaoensis* and *D. acutus* are non-neurotoxic. Therefore the potency of toxicity appears to be related to the neurotoxin content.

TABLE 1. Comparison of toxicity and enzymatic activities of *Agkistrodon* and *Deinagkistrodon* venoms.

Snake venom	Toxicity (LD <sub>50</sub> )	Enzymatic Activities (Units/mg)		
		Arginine esterase	Proteolytic enzyme	Fibrinolytic enzyme
<i>A. b. brevicaudus</i>	0.525	180	29	1.0 x 10 <sup>3</sup>
<i>A. b. ussuriensis</i>	0.70	160	27	1.0 x 10 <sup>3</sup>
<i>A. shedaoensis</i>	0.735	190	16.5	0.82 x 10 <sup>3</sup>
<i>A. saxatilis</i>	2.064	220	18	0.82 x 10 <sup>3</sup>
<i>A. intermedius</i>	0.285	450	11.5	1.1 x 10 <sup>3</sup>
<i>A. strauchii</i>	1.75	250	24.5	0.65 x 10 <sup>3</sup>
<i>D. acutus</i>	2.94	78	62	1.1 x 10 <sup>3</sup>

### Discussion

There are many components in the venom of *Agkistrodon* which react with the blood circulation causing bleeding, such as; hemorrhagin, arginine esterase, proteolytic and fibrinolytic enzymes. Three hemorrhagins had been purified from the venom of *D. acutus* (Xu et al., 1981), which have proteolytic activity, reacting with the blood vessel wall causing the leakage of red cells. Arginine esterase containing three enzymes: thrombin-like, kallikrein and plasminogen activator, which cause the failure of coagulation of the blood, depression of blood pressure and activation of fibrinolytic system.

Enzymatic activity data shows no sharp differences in the venom of *A. shedaoensis* compared to other venoms studied. The fibrinolytic activities are very close to each other due to the inaccuracy of the diffusion method. We should point out that the quality of snake venoms are deeply affected by the conditions of milking venom, such as; seasons, temperature and lyophilizing equipment.

### Acknowledgments

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## Female Reproductive Cycle and Embryonic Development of the Chinese Mamushi (*Agkistrodon blomhoffii breviceaudus*)†

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**Abstract.** -*Agkistrodon blomhoffii breviceaudus* is a species of snake with seasonal reproduction. The female annual reproductive cycle is as follows: vitellogenesis begins in late March or early April; ovulation is in middle June and parturition is in middle or late August, or in early September. The gestation period lasts for about 65-75 days. By ovoviviparity, the Chinese Mamushi produces one clutch per year. In each clutch, there are 5 to 20 juveniles with a length of 154 to 203 mm and a weight of 2.0 to 5.3 g. The size of fat bodies is inversely proportional to that of the vitellogenesis. The fat bodies were larger in March and before hibernation (about November) than in the other months. The process of embryonic development is described by the external morphological investigation on 731 embryos from 82 females.

**Key words:** Reptilia, Serpentes, *Agkistrodon blomhoffii breviceaudus*, Chinese Mamushi, reproduction, embryonic development.

### Introduction

The Chinese Mamushi (*Agkistrodon blomhoffii breviceaudus*) is distributed mainly over southern Liaoning, Hebei, Jiangsu, Anhui, Zhejiang, Jiangxi, northern Fujian, Taiwan, Hubei, Shaanxi (southern part of the Qinling Mountains), southeastern Gansu, Sichuan and Guizhou provinces in China. It is also scattered over the Korean peninsula. It is a species of poisonous snake with a high medical value, so it attracts many scientists' attention. This paper reports the female reproductive cycle, embryonic development and reproduction of the Chinese Mamushi. It is hoped that this paper will serve as a reference material for research in reproductive biology and the artificial breeding of snakes.

### Methods

Mature female Chinese Mamushi (*A. blomhoffii breviceaudus*), 447-680 mm (mean 530 mm) in length and 31-120 g (mean 67 g) in weight, were collected from

Tiantai County, Zhejiang Province, and were bred in our snake garden. From March 1984 to December 1986, 178 females (about 5 females per month) were investigated. Each snake was measured in total length (SVL+TL) and total weight. The number and the size of follicles or embryos, as well as the weight of the ovaries and fat bodies, were examined by dissection. The pH value, whether sperms were stored up or not and the sperms' activity in the oviducts were determined too. All the above were done in order to understand seasonal variation of sex glands, ovulation and mating. From 1984 to 1987 in the gestation season (June, July and August) 82 mature female snakes were operated on and 731 embryos were obtained. The conditions of embryonic development were based on the studying of the external morphology of the embryos removed from the gravid females at regular intervals throughout the gestation period. Another 10 gravid females were bred apart to observe their rate of reproduction.

### Results

#### *The Female Reproductive Cycle*

*1. The seasonal variation of ovary weight.* The ovary weight is expressed by

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† This publication combines material previously published in Chinese by Huang et al. (1990) with additional discussion.

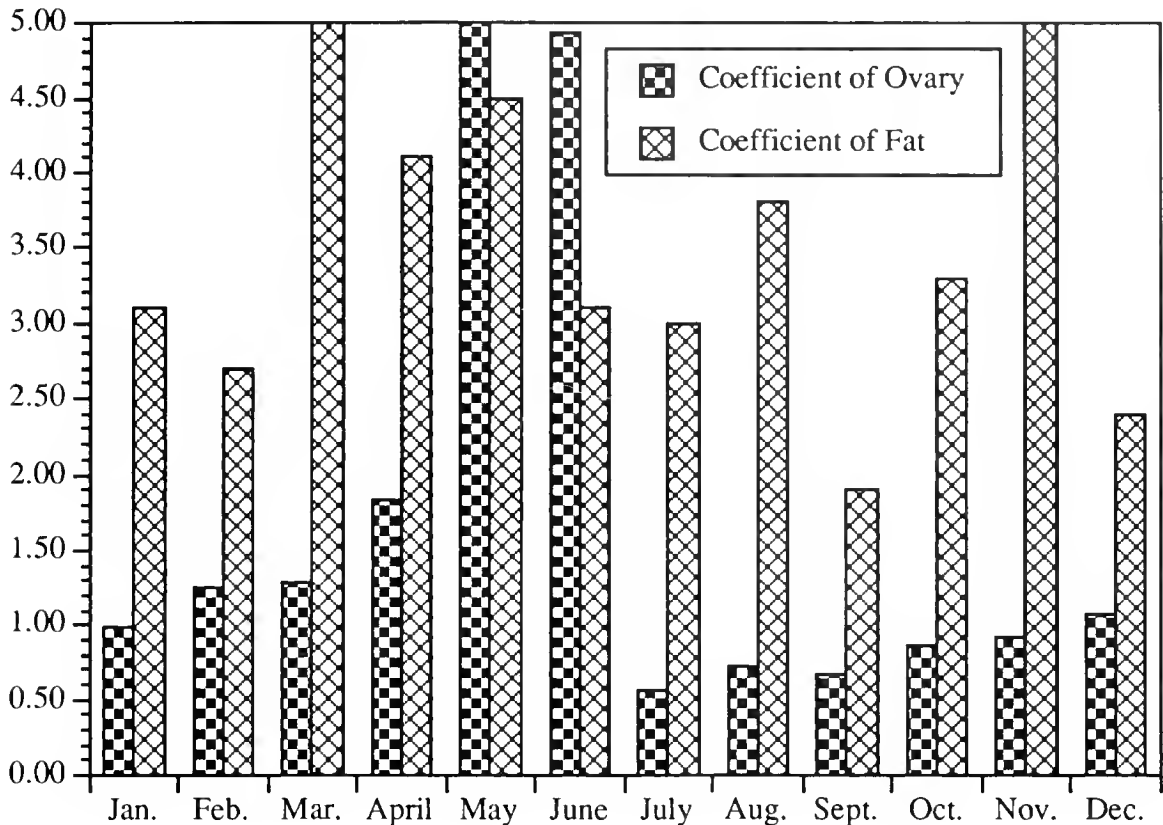


FIG. 1. Seasonal variation of ovary and fat body weight in *Agkistrodon blomhoffii brevicaudus*.

multiplying the coefficient of ovary (the ratio of wet weight of a pair of ovaries to that of total body weight of each individual) times 100 to take the form of a percentage. Figure 1 shows the seasonal variation. The eggs of the ovary were transferred to the oviduct in mid June. The coefficient of ovary reached the lowest point in July and then increased gradually. From late March to April in the next year, with vitellogenesis occurring, the coefficient of ovary rose obviously. It reached its top value in May or June.

### II. The seasonal variation of fat bodies.

The weight of fat bodies is expressed by multiplying the coefficient of fat (the ratio of the wet weight of fat body to that of the total body weight of each individual) times 100 to take the form of a percentage. Figure 2 shows its seasonal variation with two peaks in March and November. There was an inverse correlation between vitellogenesis and fat body size. Fat bodies enlarged in spring, reduced in September

(after parturition), and then increased gradually until November (before hibernation).

### III. The seasonal variation of follicle types.

Developing ovarian follicles were divided into three classes by their size and location. Previtellogenic follicles were designated as class 1, vitellogenic ovarian follicles as class 2, and oviductal eggs as class 3. The Chinese Mamushi (*A. blomhoffii brevicaudus*) is a species with annual snake reproduction. All the mature females have class 1 follicles with a diameter of 0.5 to 10.0 mm, with a transparent or white color and round or oval shape. In April class 1 follicles were at their maximum in number. On the average, there were 25 class 1 follicles per female. The larger the size of the female, the larger the number of class 1 follicles it had. The largest female was 680 mm in length and 120 g in weight, and had 69 previtellogenic follicles. In spring, vitellogenesis began and follicles grew rapidly. Some of the class 1 follicles

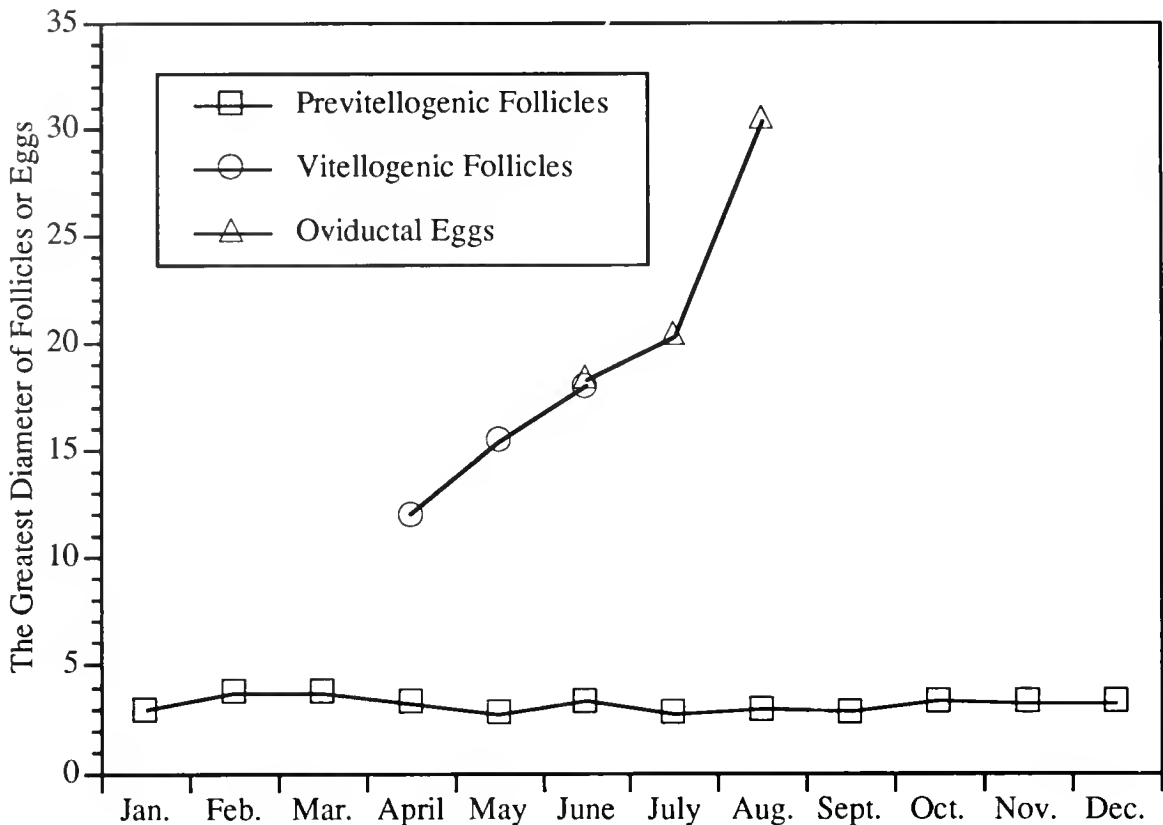


FIG. 2. Seasonal variation of follicle and egg size in *Agkistrodon blomhoffii brevicaudus*.

were transformed into class 2 follicles with yellow color, oval shape, and long diameters between 11.0-25.0 mm. They only existed from April to June. When follicles reached the largest value in about middle June, ovulation occurred. The date of the earliest ovulation took place on June 16. Class 3 eggs were present in the oviducts from middle June to late August. The maximum diameter of an egg was 28.0 mm. The pH in the oviducts was  $7.26 \pm 0.6$ .

#### *Embryonic Development*

The development of the external morphology is described as follows. In middle June ovulation occurred, and eggs transferred to the oviducts. Fertilization and development took place. A small oval blastodisk divided on the large ellipsoidal yolk mass to form the blastula. Then gastrulation proceeded to form a blastopore marking the posterior end of the embryonic shield (Huang et al., 1989, stages 1-3). In late June the neural plate raised and folded.

The blastopore was still visible. Then the neural groove appeared and expanded at the cephalic end. The amniotic fold was sharply raised anteriorly toward the head and covered more than half the embryo. After that the posterior amniotic fold was beginning to cover the tail bud. The neural tube was formed by the fusion of the neural folds. The amnion was closed. The allantois bulged slightly and was not inflated. The first rudiments of the heart and optic vesicles were formed (Huang et al., 1989, stages 4-9). In early July the allantois began to inflate. The heart took a "U" shape and began to beat. The caudal part of the embryo began to coil. Lateral placodes invaginated. The mandibular segment and the auditory pits were visible. Branchial clefts were formed with the appearance of the nasal pits. The eye was lightly pigmented. Furthermore, the heart was shaped like an "S". Then both the ventricle and auricle were distinguishable. The cloacal mound was visible and the rudiment of the hemipenes appeared. The

TABLE 1. Reproductive data on 10 adult female *Agkistrodon blomhoffii brevicaudus*.

Adult Females					Length (mm) of young at birth			Weight (g) of young at birth		
No.	Length (mm) Vent+ Tail	Weight (g)	Date of parturition	Clutch size	max.	min.	ave.	max.	min.	ave.
86-8091	570 (510+60)	83.0	86.9.9	5	147+26	133+21	140.8+23.0	3.9	2.6	2.74
86-8092	640 (575+65)	137.7	86.9.9	5	152+25	142+25	145.7+23.7	3.3	2.8	3.08
86-8093	680 (610+70)	176.7	86.8.23	12	159+24	151+24	155.8+24.6	4.1	3.8	3.86
86-8094	610 (545+65)	203.7	86.8.26	20	158+27	132+22	143.5+22.1	3.8	2.6	2.96
86-8095	630 (560+70)	193.7	86.8.20	14 <sup>1</sup>	145+25	119+18	132.9+20.7	4.1	1.6	2.61
86-8096	605 (540+65)	116.3	86.8.20	5 <sup>2</sup>	175+28	165+28	170.0+28.0	5.3	5.0	5.10
88-8097	537 (475+62)	97.6	86.9.6	10	138+23	132+25	134.6+22.4	2.6	2.0	2.24
86-8098-	645 (575+70)	157.0	86.9.9	8	144+21	136+21	140.6+21.5	3.0	2.8	2.84
86-8099	555 (500+55)	147.3	86.8.18	6	163+23	146+22	150.8+22.0	3.6	3.2	3.45
86-8100	602 (535+67)	114.0	86.8.28	7	145+22	130+24	135.8+22.7	3.0	2.2	2.61

1- Nine still born. 2- One still born.

trunk coiled 4.5 circles (Huang et al., 1989, stages 10-11). By middle July the hemipenes became vesicle-like projections. The upper and lower jaws were visible and the trunk loosened into four circles (Huang et al., 1989, stage 12). In late July the hemipenes were blunt fork-like projections. The tongue was visible. The mid-line of the ventral body was enclosed except in a small circular area. Scales appeared on the trunk but not on the head. The trunk loosened further and coiled only 3-3.5 circles (Huang et al., 1989, stage 13). During early August scales on the trunk appeared to be keeled and their pigment pattern was well developed. Scales and pigmentation on the head were visible but the pattern was not well developed. The whole mid-line of the ventral body was enclosed. The hemipenes were still everted. The trunk coiled 2-2.5 circles (Huang et al., 1989, stages 14-15). In middle August the pigment pattern fully developed. The hemipenes were inverted in all the male specimens. Just prior to parturition, the embryo showed all the morphological characteristics of its own

family. (Huang et al., 1989, stage 16).

### Reproduction

The gestation period lasted for about 65-75 days and parturition occurred in middle to late August or September. Table 1 shows the state of the reproduction of 10 gravid females. Ten gravid females produced 10 litters which included 97 juveniles. The mean number per litter was about 10. Among 10 litters of new babies, about 99% had survived except one litter which had 9 stillbirths. All the live babies were 154 to 203 mm in length and 2.0 to 5.3 g in weight.

### Discussion

I. According to Saint Girons (1982), the reproductive cycle of male snakes has four major types: 1) aestival (summer) or postnuptial type; 2) mixed type; 3) prenuptial type; and 4) continuous reproductive activity type. The reproductive cycle of the Chinese Mamushi (*A. blomhoffii brevicaudus*) belongs to the

first type (Lin et al., in press), which is found only in temperate and subtropical regions. Spermatogenesis begins in spring after hibernation and spermiogenesis begins in summer. The spermatozoa are stored throughout the winter in the epididymis and vas deferens of the male or in the oviducts of the female. According to Saint Girons (1966), the reproductive cycle of female snakes has annual types A-F-G and biennial types B-C-D. By our observation the Chinese Mamushi (*A. blomhoffii brevicaudus*) is thought to be the annual type F. Its mating season is spring (April or May) and ovulation occurs regularly in middle June, while spermatogenesis is the aestival type. Sperm are stored in winter in the vas deferens of the male or in the female oviducts if there is fall mating. Sperm of the Chinese Mamushi (*A. blomhoffii brevicaudus*) may be stored in the oviducts and kept available for about three years (Hu et al., 1966). This characteristic is of great benefit to the survivalship of the Chinese Mamushi (*A. blomhoffii brevicaudus*).

II. Several investigators have found an inverse correlation between reproduction (vitellogenesis) and fat body size in snakes (Seigel and Ford, 1987). In snakes with annual reproduction (e.g. *Opheodryx aestivalis*), fat bodies enlarge in spring, reach a low point in early to middle summer (egg-laying) and then increase gradually until hibernation. In species with biennial or triennial reproduction, e.g. *Vipera berus* and *Crotalus viridis*, fat body reserves are lowest at the time of parturition (Macartney and Gregory, 1988; Seigel and Ford, 1987). Seasonal variation of fat bodies of the Chinese Mamushi (*A. blomhoffii brevicaudus*) is similar to the above observation. There are two peaks in March (spring) and November (hibernation). The low point is in September (at the time of parturition).

III. The sexual maturity of the Chinese Mamushi (*A. blomhoffii brevicaudus*) is attained in 2-3 years. Jin et al. (1983) mentioned that vitellogenesis began in the second spring after birth (20 months old), 350-484 mm long and 20-60 g in weight. In the Lined Snake (*Tropidoclonion*

*lineatum*) from St. Louis, Missouri, USA, the same result was obtained by Krohmer and Aldridge (1985). All the females in our experiment were mature with a length of more than 447 mm and a weight of over 31 g each. There was a positive correlation between the number of yolking follicles or embryos and female length. The average number of embryos from 82 females was ten. Seventy one percent of the females 400-500 mm long contained less than ten embryos, while 75% of the females 500-600 mm long contained more than ten embryos.

IV. The Chinese Mamushi is ovoviviparous, which is evolved from oviparity. It is said to be an adaptation to variable environments where stochastic events jeopardize egg survivorship. But Seigel and Ford (1987) thought it also had some disadvantages, including lower clutch frequency, more mortality risks to the parent, less intake of food and higher metabolic cost of the parent. The clutch mass of ovoviviparous snakes is smaller than that of oviparous snakes. The physiological costs of reproduction (heart rate and oxygen consumption) significantly increased during pregnancy in ovoviviparous snakes. We found that pregnant snakes cease feeding during the last period of gestation, so they were thin and weak after parturition. If they did not gain enough food in time, they would be dead during hibernation or by the next spring. However we think that ovoviviparity is more favorable in protecting the filial generation because the survival rate is much higher in the Chinese Mamushi (*A. blomhoffii brevicaudus*). In our experiment the survival rate reached 90-99%.

#### Acknowledgments

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## Investigations on Ranid Larvae in Southern Sakhalin Island, Russia

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**Abstract.** -Using a special chemical technique, four breeding sites of two brown frog species, *Rana amurensis* and *Rana chensinensis*, were investigated on Sakhalin Island, Russia. They were living together with other amphibian species under very different conditions. A puddle with *Rana chensinensis* larvae was found adjacent to the Pacific coast with a salinity of 1.2%. The description of the mouth part morphology was completed by SCAN-investigations on the micromorphology of larval teeth, horny jaws and the warty epithelium.

**Key words:** Amphibia, Anura, Ranidae, *Rana amurensis*, *Rana chensinensis*, tadpoles, breeding sites, water chemistry, salinity, micromorphology, Russia, Sakhalin Island.

### Introduction

In July and August of 1989 the authors visited the southern part of the Russian Far East island, Sakhalin. We found in many places the only two ranid frog species inhabiting the island, *Rana amurensis* and *Rana chensinensis*. In most habitats they coexisted with the other amphibian species of Sakhalin Island, *Salamandrella keyserlingii*, *Bufo gargarizans* and *Hyla japonica*. The latter was only found near Kostromskoe. In other papers (Herrmann and Kabisch, 1990, 1991; Kabisch et al., 1990) the authors report on the herpetofauna of Sakhalin Island. The present paper is concerned with the life and environmental conditions of ranid frog larvae. Some micromorphological data for the species diagnosis are presented.

### Methods

Tadpoles of *Rana amurensis* and *Rana chensinensis* were observed in many breeding sites on the island. Some of them were caught and fixed in 70% ethanol. According to a technique of W. Pietsch (Dresden) one liter samples of water from four breeding sites were obtained from: (1) brook in the city park of Jushno-Sachalinsk (Fig. 1), (2) pools near Pjatyretske with *Lysichiton*

*camtschatcense* as the main botanical element, (3) pond near Kostromskoe with *Alisma orientale* as the dominant water plant, (4) puddle at the Pacific coast on the Krilon Peninsula (Fig. 2). The water samples were analyzed in the laboratory of W. Pietsch. The fixed larvae (24 specimens of each species, representing stages of the beginning of hind leg formation) were also prepared for investigation of their micromorphology (for technique see Herrmann, 1989). The preparations were investigated with a scanning electron microscope TESLA B 300 in the Technical College of Ilmenau (Thuringia).

### Results

#### 1. Characterization of the Breeding Sites

The water analysis data of the four investigated breeding sites are shown in table 1. From this information it can be concluded that the chemical nature of the water bodies is very different. In the first one, in a brook in the city park of Jushno-Sachalinsk, we found larvae of *Rana chensinensis* in addition to those of *Bufo gargarizans*. *Rana chensinensis* prefers running water as breeding sites on Sakhalin Island. The water can be characterized as follows: slightly acidic, oligotrophic, poor in humic material,



FIG. 1. Tadpoles of *Rana chensinensis* in a brook in the city park of Jushno-Sachalinsk.

nutrient poor, poor in electrolytes, rich in iron, and of a low total hardness. The only vegetation at the brook consisted of some grasses and rushes.

The second water body was a breeding pool of *Rana amurensis*. It is one of four permanent pools near the Naitsa River in the Pjatyretske River system. The four pools (area about 550 m<sup>2</sup>) are slightly acidic, very poor in humic material, nutrient poor and of a low total hardness.

In the third breeding site all amphibian species living on the island were found:

*Salamandrella keyserlingii*, *Rana amurensis*, *Rana chensinensis*, *Hyla japonica* and *Bufo gargarizans*. Typical species of the very rich vegetation of this small pond (area about 80 m<sup>2</sup>) were *Alisma orientale*, *Juncus bufonius*, *Epilobium palustre*, *Oenanthe decumbens*, *Phleum pratense*, and *Equisetum palustre*. The water was slightly acidic, oligomesohumic, rich in phosphates and carbonates, but of a low total hardness.

The fourth habitat was a very small puddle (area 1.5 m<sup>2</sup>) at the Pacific coast.



FIG. 2. Puddle with *Rana chensinensis* larvae adjacent to the Pacific coast on the Krilon Peninsula.

Splashing salt water contacted this puddle during the time of high tide. It was a breeding site of *Rana chensinensis*. The vegetation consisted of *Lemna* and *Juncus* only. We found many pieces of old wood in the water. The water can be characterized as follows: slightly alkaline, poor in humic material, nutrient poor, rich in electrolytes and of a medium total hardness. A typical feature of this breeding site is the NaCl content of 1.2%. Because of the high content of salt, the puddle can be classified as a  $\beta$ -mesohalobien water representing the upper limit of brackish water. The 24

larvae represented an earlier stage of development compared to tadpoles of the same species living in other breeding places at the same time.

## 2. Micromorphology Investigations

The schematic drawings of the larval mouth of *Rana amurensis* and *Rana chensinensis* show clear differences in their morphology (Fig. 3). With the SCAN, the small conical teeth on the upper and on the lower horny jaw could be visualized in both species. In the literature (Bannikov et al., 1977) only

teeth on the lower jaw were shown for *Rana amurensis*. We found 69-73 in the upper jaw of *Rana chensinensis* and 51-

55 in *Rana amurensis*. On the lower jaw 52-54 were counted in *Rana chensinensis* and 46-49 in *Rana amurensis* (Fig. 4-6). The labial teeth were identical in all rows in both species. Fan-like tips, 6-13 on each tooth, could be seen (Fig. 7). The warty epithelium around the mouth field of the larvae consisted of a fleshy skin. At the margin of this structure, labial teeth have been found (Fig. 8). The epithelium of the larvae was composed of hexaedric or octaedric plate cells.

### Discussion

Some papers on the effects of low pH and other chemical variables on amphibian larvae were published by Freda (1986) and Freda and Dunson (1985a, 1985b, 1986). A lot of data on acid tolerance in amphibians are summarized in the paper of Gebhardt et al. (1987). The lowest pH tolerated by a brown frog, as described for *Rana sylvatica*, was 3.0. Other conditions were observed by Freda and Dunson (1984) in experiments with *Rana catesbeiana*, *Rana clamitans* and *Rana pipiens* in the laboratory. An increasing of the external calcium concentration extended the survival time in acid water by slowing the loss of sodium. So it is possible to survive in salt water under special conditions. There was a regulatory principle for the magnitude of larvae populations in breeding sites with such special conditions obtained by Kovaltsyk (1981). The main factors were acidity and the contents of cat ions in the water. Another role was played by the temperature of the water in connection with the photo period (Dupre and Petranksa, 1985; Floyd, 1985).

The long days in spring and summer, as typical of Sakhalin Island, enable the amphibian larvae to develop under extreme conditions. These are characterized by extreme temperature differences, reaching minimum and

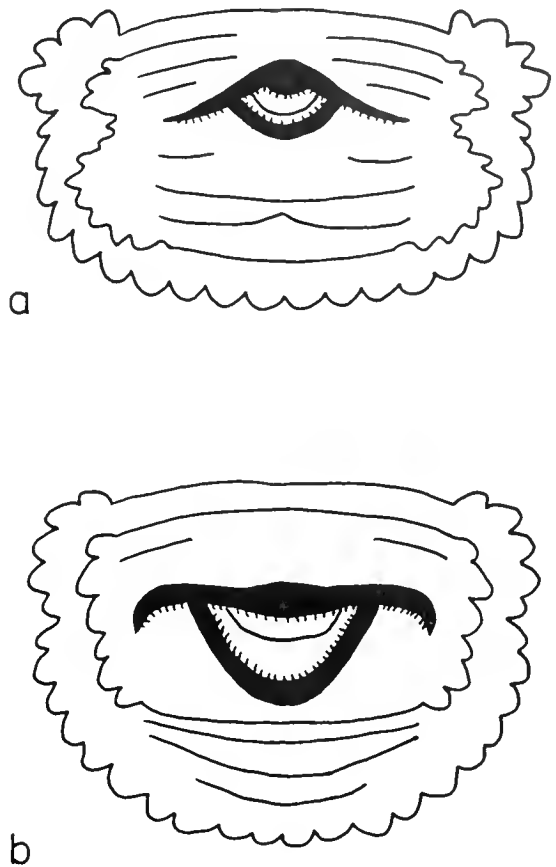


FIG. 3. Schematic drawings of the larval mouth parts of *Rana amurensis* (a) and *Rana chensinensis* (b).

maximum values in very short intervals, limiting the survival of larvae. The opportunity to survive in salt water was described for urodeles by Jones and Hillman (1978), (*Batrachoseps*), and Romspert and McClanahan (1981), (*Ambystoma tigrinum*). In the papers of Power (1937), Andren and Nilson (1979), Herrmann (1982), Dunson (1977), and Guix and Lopes (1989) some anuran species are listed as breeding and developing in brackish waters. Fljaks (1985) recorded some brackish breeding sites (1.5-9%) of *Bufo gargarizans* and *Rana amurensis* on the island of Sakhalin. Fljaks (1985, 1986) also reported on the mortality of the tadpoles of *Rana amurensis* and *Rana chensinensis* on this island. He observed the highest mortality in the first stages of larval development: 18-73% in



FIG. 4. Mouth parts of the tadpole of *Rana chensinensis* (x 120).



FIG. 7. Labial teeth of the tadpole of *Rana chensinensis* (x 2500).



FIG. 5. Teeth of the upper jaw of the tadpole of *Rana chensinensis* (x 1500).



FIG. 8. Warty epithelium of the tadpole of *Rana amurensis* (x 500).



FIG. 6. Teeth of the upper jaw of the tadpole of *Rana amurensis* (x 300).

*Rana amurensis* and 15-66% in *Rana chensinensis*. In a puddle with 9% salinity the *Rana amurensis* larvae had a mortality rate of 99.8%. An increased mortality was also found in acidic water. The slow development of ranid tadpoles in puddles at the ocean coast was also observed by Kopein (1973) in southern Sakhalin Island.

Micromorphological data on larvae of *Rana amurensis* and *Rana chensinensis* were found to be absent in the literature. Besides the macromorphology, form and topography of nostrils, spiracle, vent tube, lateral-line pores and buccal papillae according to Johnston and Altig (1986), the jaw sheaths and labial teeth can also

TABLE 1. Chemical/physical data of the breeding sites.

critterion	brook in Jushno-Sachalinks (1)	pool near Pjatyretske (2)	pond near Kostroms-koe (3)	puddle at the Pacific coast (4)
pH	6.8	6.6	6.9	7.2
pV (KMnO <sub>4</sub> mg l <sup>-1</sup> )	33.8	22.9	48.0	28.2
total hardness (°dH)	2.3	1.6	4.0	18.4
carbonate hardness (°KH)	2.1	1.5	4.0	11.9
nitrate (mg l <sup>-1</sup> )	3.2	2.4	4.0	3.8
sulfate (mg l <sup>-1</sup> )	0.9	1.6	7.6	32.5
ammonium (mg l <sup>-1</sup> )	0.12	0.06	6.40	0.08
iron (mg l <sup>-1</sup> )	1.52	0.08	0.56	0.02
calcium (mg l <sup>-1</sup> )	11.4	8.4	21.2	26.2
nitrite (mg l <sup>-1</sup> )	0.01	0.01	0.03	0.02
chloride (mg l <sup>-1</sup> )	7.6	9.5	34.8	76.5
magnesium (mg l <sup>-1</sup> )	3.1	1.8	4.3	7.8
CO <sub>2</sub> (mg l <sup>-1</sup> )	24.0	18.0	33.0	22.0
SiO <sub>2</sub> (mg l <sup>-1</sup> )	14.1	3.2	27.4	28.0
phosphate (mg l <sup>-1</sup> )	0.1	0.2	1.8	0.2
lime (mg l <sup>-1</sup> )	38.3	32.0	87.2	11.6
O <sub>2</sub> (mg l <sup>-1</sup> )	9.6	10.4	12.2	11.2
residue of evaporation (mg l <sup>-1</sup> )	94.0	94.0	230.0	864.0
residue of combustion (mg l <sup>-1</sup> )	50.0	49.0	104.0	376.0

be used for identification of anuran tadpoles. Wassersug (1980) and Viertel (1982) favored micromorphology for taxonomic classification. The present data support the necessity to add micromorphological data for species diagnosis in anuran larvae.

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## Historical Biogeography of the *Phrynocephalus* Species of the USSR

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**Abstract.** -There are 22 species and subspecies of *Phrynocephalus* in the USSR. Some species inhabit sandy deserts, while others occur in hard soil and gravel deserts. Speciation and present day distributions are a result of geologic events such as mountain building causing the isolation of valleys and basins and changes in the direction of river courses.

**Key words:** Reptilia, Sauria, Agamidae, *Phrynocephalus*, Armenia, Azerbaijan, Kazakhstan, Kirgizistan, Russia, Tadzhikistan, Turkmenistan, Uzbekistan, USSR, biogeography, distribution, evolution.

### Introduction

The reconstruction of the genesis of *Phrynocephalus* species can not be based on the paleontological evidence since data in this field are extremely poor. The only fossil locality is from the Pliocene of Turkey (Zerova and Chkhikvadze, 1984). However, a comparison of recent arealographic patterns of species studied with known ideas about the historical geography and paleogeography of the region where the species occur may be used as one method of research. The data about climate and the genesis of landscapes and vegetation are of great importance.

According to recent ideas, 22 species and subspecies of the genus *Phrynocephalus* live in the USSR (Bannikov et al., 1977; Borkin and Darevsky, 1987). We use here the last list and do not try to reflect more recent and often opposing ideas about *Phrynocephalus* taxonomy (Golubev, 1989a, 1989b; Mezherin and Golubev, 1989; Semenov, 1987; Semenov and Dunayev, 1989; Semenov and Shenbrot, 1982, 1990; Shenbrot and Semenov, 1987), and about the status of some populations, subspecies, and species. This paper does not consider problematic nomenclature problems that need special research. We try here to understand the present complicated distribution of *Phrynocephalus* in the USSR. This includes their disjunct populations. We also try to explain the

possible ways of the development and formation of the distributions of different forms independently from the disagreement on the opinion about their taxonomic status. We discuss here the information about the ranges of these lizards and although the status of some of them may be problematic, this does not so strongly influence our speculations about historical biogeography. Most *Phrynocephalus* species inhabit Middle Asia and Kazakhstan territories. Only a few species penetrate to the eastern part of the northern Caucasus and eastern Transcaucasia. *Phrynocephalus versicolor kulagini* extends to the southern regions of Tuva Autonomous Republic, Russia (Fig. 1).

### Discussion

As is well known, it is impossible to understand the history of the fauna without knowing the history of the flora and climatic and geological evolution. The history of the flora in the Caspian region is known from the Upper Cretaceous-Paleogene (Korovin, 1961) when the Tethys transgression flooded most of Middle Asia and central Kazakhstan. In this region a continental regime was retained only in the Tien Shan area and in the eastern part of the Kazakh hummock topography (Gvozdezky and Mikhailov, 1987), (Fig. 1). At that time the Central Asian land already had an arid regime (Agakhanyanz, 1981). The middle of the Gobi was probably real desert surrounded by steppe landscapes (Serebrovsky, 1936).

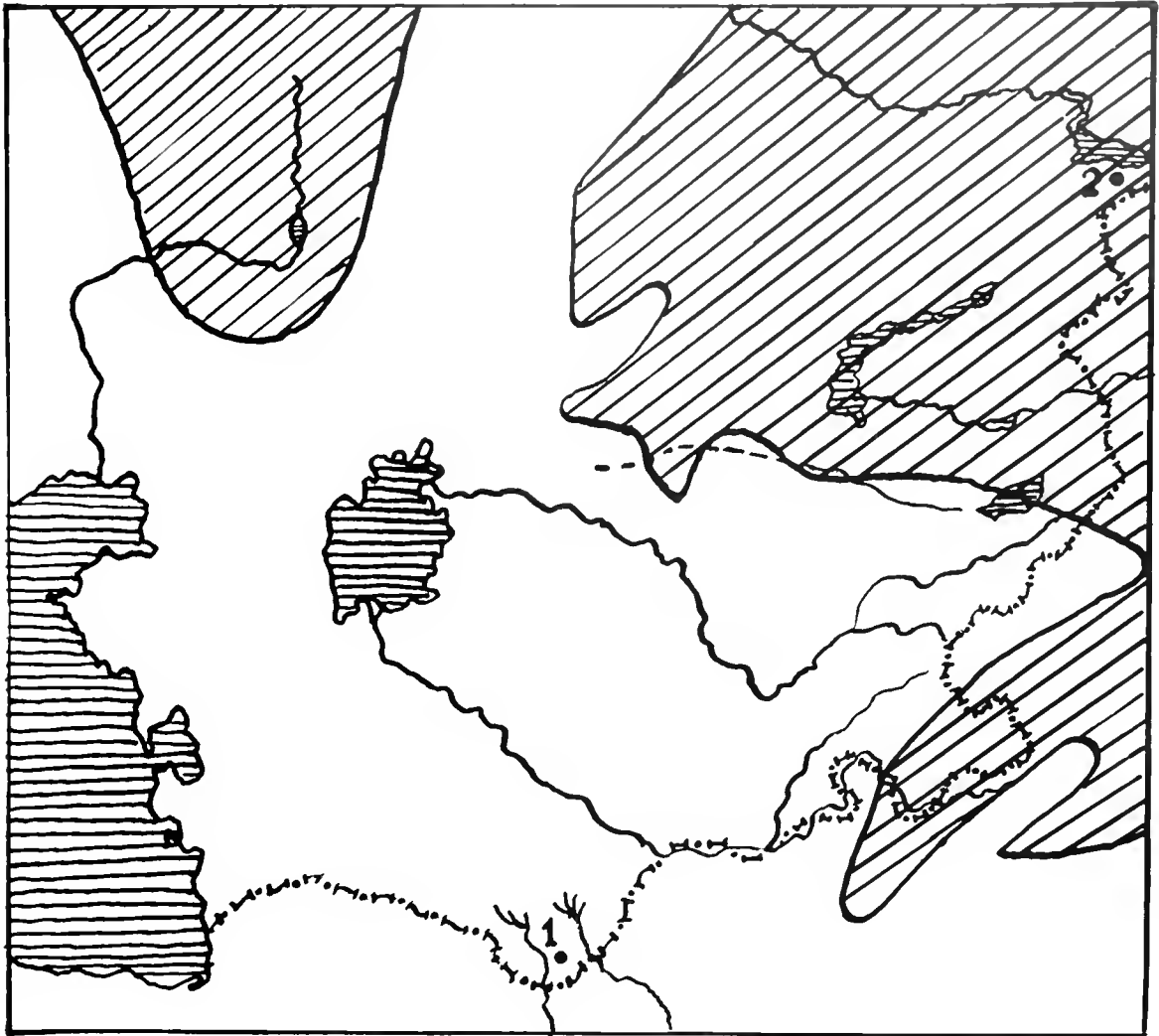


FIG. 1. Sea basin and land (hatched) in Middle Asia and Kazakhstan in Upper Eocene - beginning of the Oligocene. 1- the Lower Cretaceous records of plants in Er-Oliian-Duz Depression (Serebrovsky, 1936); 2- Eocene - Oligocene records of reptiles and amphibians in Zaissan Depression (Bakradze and Chkhikvadze, 1988).

A warm tropical and subtropical climate, humid, but from time to time with seasonal aridity and probably with seasonal falls of temperature, was dominant on the continental parts of Middle Asia (Gvozdezky and Mikhailov, 1987).

It may have promoted the growth of such species as *Taxodium distichum*, *Populus balsamifera*, *Juglans acuminata*, *Fagus antiposii*, *Liquidambar europaeum*, *Diospiros sp.*, *Gingko biloba*, and *Liriodendron tulipifera*. The analogous flora was distributed throughout all of the Siberian territory (Serebrovsky 1936).

Luxuriant thermophilous flora of Middle Asia was accompanied by a highly rich and diverse fauna of the Late Cretaceous such as salamanders and frogs from the families Scapherpetontidae, Batrachosauroidae, Prosirenidae and Pelobatidae (Bakradze and Chliikvadze, 1988). Lizards of the families Parasaniwidae, Teiidae, Anguidae, Agamidae, Saniwidae, Gekkonidae, and Varanidae were also present (Nesov, 1981a, 1981b).

From data about the Cretaceous flora in southern Middle Asia, we hypothesize the presence of a more dry and hot climate

(Korovin, 1961).

The Lower Tertiary findings in the Er-Oilan-Duz Depression in Badkhyz contains *Dryandra schrenkii*, *Celastrorhynchus turcomenicus* and other typical xerophilous plants which also indicates adaptation of these plants to the survival during the hot and dry periods during the vegetation period (Serebrovsky, 1936), (Fig. 1).

From the Eocene fossils of the family Agamidae were found in some localities in Kazakhstan including the Zaisan Basin (Bakradze and Chkhikvadze, 1988).

In the Oligocene the sea retreated and the formation of a continental landscape began. However, the development of relief took place in different ways. In the Kara-Kum and Kyzil-Kum deserts and the Ustyurt Plateau, anticlinal and synclinal structures were formed in the Neogene. In spite of their platformal type of structure, they are sufficiently sharp with an angle of declination of more than 10°. The Turgai Plateau and western Betpak-Dala were slightly touched by the most recent orogenic movements on these small territories. This not only resulted in the formation of different geomorphological structures which will be discussed below, but also in the difference of the amplitude of the raising and sinking of whole territorial divisions. These differences in the amplitude of movements have resulted in the isolation and formation of the specific relief in each of the plains in Middle Asia (Voskresensky, 1968).

In the middle Oligocene there was a sharp change in the composition of the herpetofauna of the Zaisan Depression. The early Oligocene giant salamanders (*Zaisanurus*), giant snakes (Boidae), Glyptosaurinae, etc. were replaced by amphibians of the families Pelobatidae, Ranidae, and Bufonidae and by boids of the genus *Bransateryx* (Bakradze and Chkhikvadze, 1988).

The formation of two centers of speciation of the genus *Phrynocephalus* probably began on the boundary of the

Paleogene-Neogene time in arid regions of Central Asia and in the southern part of Middle Asia (Fig. 2). Until middle or late Pliocene the herpetofauna of Central Asia and Turan represented, more or less, a single unit (Chkhikvadze et al., 1983). The independent formation of Central Asian and Middle Asian centers of different fauna began readily after their separation by mountain structures of Alpic orogenesis (Ananjeva, 1986; Chernov, 1959; Geptner, 1938; Peters, 1984).

In discussing the center of origin of the genus *Phrynocephalus*, Moody's (1980) opinion should be noted. He suggested that the most primitive *Phrynocephalus* species is *P. vlangalii* inhabiting north-eastern Tibet and Qinghai. The validity of this conclusion is problematic because he studied only two species of this genus in his phylogenetic and biogeographic study of agamids.

Of special interest for understanding the origin of *Phrynocephalus* is the finding of a new species, *Phrynocephalus langwalaensis* (Sharma, 1970), from the Radjastan Desert, in western India.

Whiteman (1978) suggested that *Phrynocephalus* probably originated in the early Miocene in Central Asia. On Whiteman's map (Whiteman, 1978: his figure 12) illustrating the hypothesized dispersal of *Phrynocephalus*, he showed this point in southern Middle Asia. The reason of such term confusion is connected with the absence of separating, in English, the terms Central Asia and Middle Asia traditionally used in German and Russian geographical and zoological literature.

Middle Asia is the part of Asian territory of the USSR from the Caspian Sea in the west to the Chinese border in the east, and also from the Aral-Irtysh drainage divide in the north to the border of Iran and Afghanistan in the south.

Central Asia is defined as the desert and semidesert plains, tableland and high plateaus which are limited to the east by the southern part of Great Khingan and



FIG. 2. Sea basin and land (hatched) during the Lower - middle Miocene. Hypothesized centers of *Phrynocephalus* speciation: A- Middle Asian center; B- western edge of the Central Asian center. Lower - middle Miocene records (Bakradze and Chkhikvadze, 1988): 1- northern Aral Sea region; 2- Turgai; 3- Zaisan Depression. The arrow shows the hypothesized direction of movement of ancestral forms of the *Phrynocephalus guttatus* complex.

Taikhanshan ridge and to the south by the longitudinal tectonic basin of the upper Indus River and Brahmaputra (Tsangpa). In the west and in the north the border of Central Asia corresponds to the mountain ridges of eastern Kazakhstan, Altai, western and eastern Sayan, approximately coinciding with the state border between the USSR on the one hand, and China and Mongolia on the other hand.

*Eremias* sp., *Varanus*, *Ophisaurus*, *Eryx*, and *Protestudo* were found in the late Miocene deposits in eastern Kazakhstan

(Bakradze and Chkhikvadze, 1988). The ancestor of *Phrynocephalus maculatus* may have already existed during the Neogene in Middle Asia in the condition of southern savannas and xerophytous vegetation of the southern and southeastern Transcaspian region. The ancestral form of *P. raddei* (Fig. 3) may have already been distributed along all the southern part of the Thetys geosyncline from the Caspian Sea to the Pamir. We can hypothesize this because fossil remains of giant land tortoises and monitors are known from the Pliocene in Tadzhikistan. Some lizards, *Trapelus*

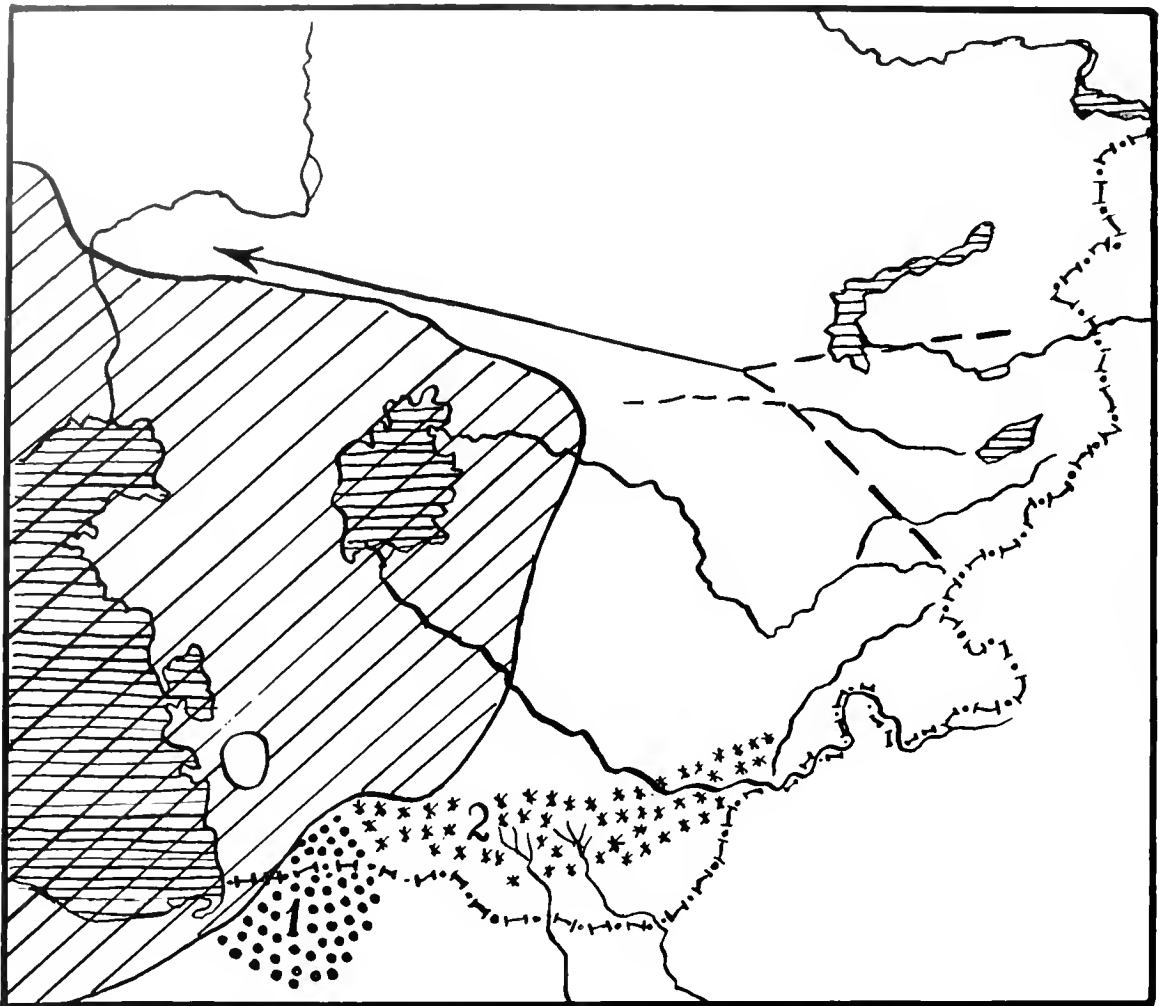


FIG. 3. Sea basin and land during the Upper Miocene (Sarmat Sea is hatched). 1- Hypothesized distribution of *Phrynocephalus maculatus* ancestor; 2- Hypothesized distribution of *Phrynocephalus raddei* ancestor. The arrow shows the direction of continuing dispersal of the forms of the *Phrynocephalus guttatus* complex.

*sanguinolentus*, *Eremias* sp., and *Varanus cf. griseus* are known from the Pliocene in Turkmenia (Ananjeva and Gorelov, 1981; Bakradze and Chkhikvadze, 1988)

In the Pliocene, the genus *Phrynocephalus* could have divided into species complexes or into the genera *Phrynocephalus* and *Megalochilus* (Ananjeva, 1986) on the territory of the southern Kara-Kum Desert. Federovitch (1946) assumes that one should look for the origin of typical recent sandy desert vegetation associations in the Neogene in the Kara-Kum (Fig. 4).

The Miocene may be considered as the time when the ancestral form of the *Phrynocephalus guttatus* complex (Figs. 5 and 6) from the Central Asian center penetrated as far as the eastern boundaries of the Tethys (recent regions of Pamir-Alai and Gissar-Darvaz mountains), (Fig. 2). This territory, now occupied by mountains and intermountain depressions, resembled low mountain relief now present northwest of Samarkand and Djizak (Voskresensky, 1968). The subsequent dispersion of this group to the west was along the northern shore of the Thetys (later the Sarmat Sea, Fig. 3). Further spreading to the north was

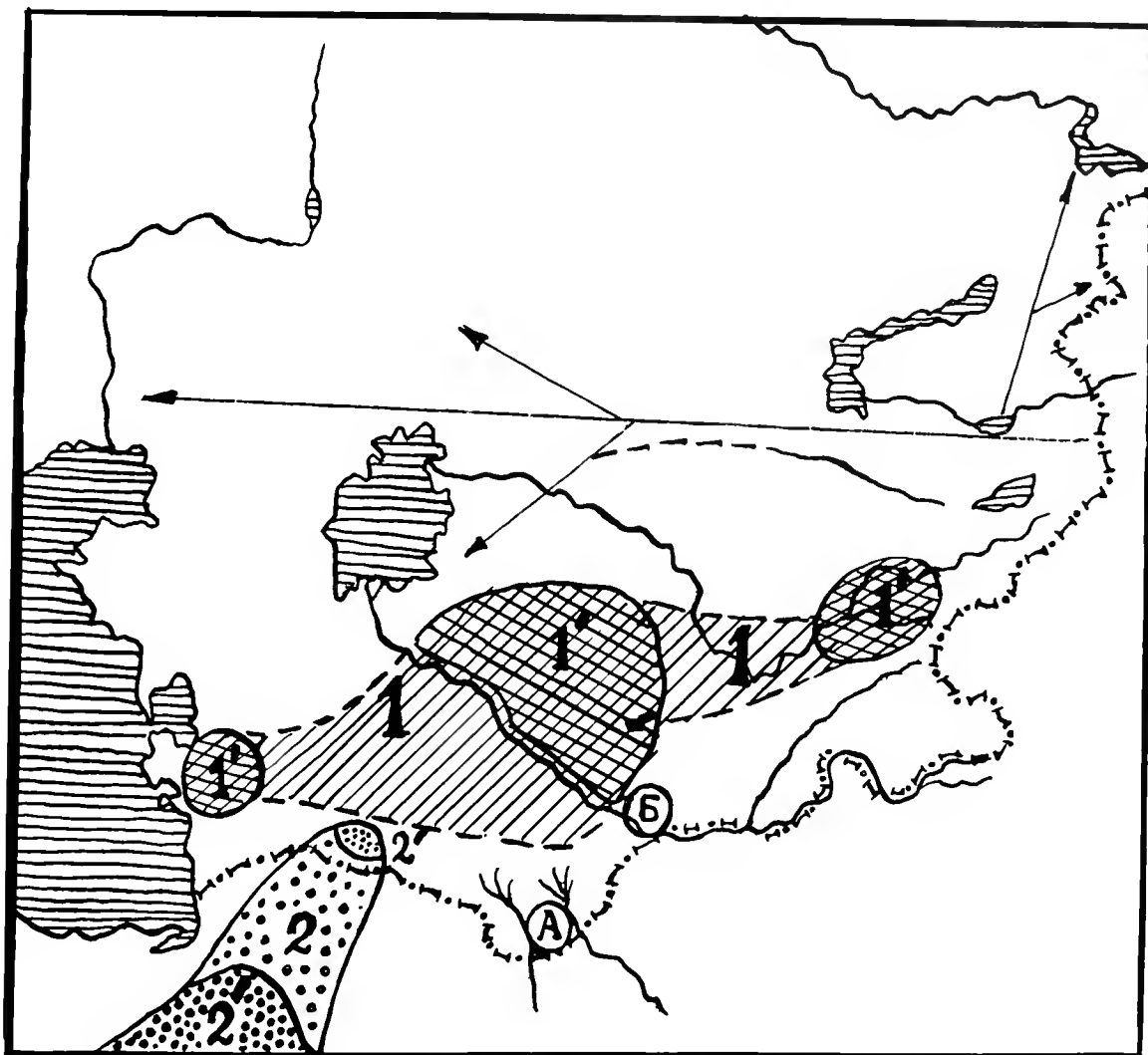


FIG. 4. The middle Pliocene changes of *Phrynocephalus*. 1- Lower Pliocene distribution of *Phrynocephalus reticulatus*; 1'- middle Pliocene populations of *Phrynocephalus reticulatus* on emerged land; 2- Lower Pliocene distribution of *Phrynocephalus maculatus*; 2'- middle Pliocene populations separated by alpic orogenesis of the Kopeth-Dag. The arrows show the direction of dispersal of the species of the *Phrynocephalus guttatus* complex. A- hypothesized place for divergence of *Phrynocephalus* and *Megalochilus*; B- hypothesized place of origin for *Phrynocephalus rossikowi*.

prevented by phytogeographical conditions since the plains of central Kazakhstan were covered by deciduous forests of *Populus sp.*, *Salix sp.*, *Alnus sp.*, *Zelkova sp.*, *Ulmus sp.*, *Acer sp.*, i.e. the vegetation was intermediate between the Turgai and recent types. The xerophilous formations were only beginning to develop in this territory (Gvozdezky and Mikhailov, 1987).

During the first half of the Neogene, a lake regime was predominate on the

elevated plains of Middle Asia such as the Turgai tableland and western Betpak-Dala. The southwestern branch of the *P. guttatus* complex dispersion could have penetrated this area. The process of uplifting took place across the entire plains of Middle Asia towards the end of Sarmatian time and to the beginning of the Pliocene. The sea basins disappeared and erosional division of the region took place (Voskresensky, 1968). During this period, *Phrynocephalus reticulatus* could have dispersed widely over the entire plain area from the Caspian



FIG. 5. *Phrynocephalus guttatus* from the west side of the Caspian Sea in Chechen-Ingush, Russia.

Sea in the west to the Fergan Depression in the east. This species apparently did not reach beyond the limits of the dry subtropic climatic belt. The same is observed at the present (Fig. 4). In such context, the opinion of Golubev (1989b) on the unity of the origin of *P. moltschanovi* and *P. reticulatus* from the forms penetrating here from the north in the middle Pleistocene seems to us doubtful.

The eastern branch of the *P. guttatus* complex, i. e. *Phrynocephalus versicolor* was widespread north and northeast of the Tien Shan (Mountains), (Fig. 4). Isolation of *Phrynocephalus rossikowi* (Fig. 4) could have taken place on the dense river sediments of the Amu Darya (River) which flowed into the Caspian Sea at that time. The Pliocene raising of Asia Minor and the Iranian Plateau had apparently already led to disjunction of the area inhabited by the

ancestor of *Phrynocephalus helioscopus* and also by some species of the genus *Trapelus* with similar ecological requirements. The diverged populations of *P. helioscopus*, *P. helioscopus persicus* (*P. persicus*, Meszzerin and Golubev, 1989; Nikolsky, 1915), could probably have separated in the Pliocene. In the middle of the Pliocene a sinking process occurred in the sand deserts of Middle Asia to the slightly elevated Zaunguz Plateau. However, on the Turgai Plateau in western Betpak-Dala and on the Ustyrt Plateau the raising of the Kysil-Kum and Mangyshlak was no longer restored by the regime of accumulation. The relief continued to develop slowly by an erosion and denudation process (Voskresensky, 1968). It was in the middle of the Pliocene that the disjunction of the continuous range of *Phrynocephalus reticulatus* took place. That led to isolation of three relict





FIG. 6. Habitat of *Phrynocephalus guttatus* on the west side of the Caspian Sea in Chechen-Ingush, Russia.

populations on the plateau islands not covered by sea: South Ustyurt Krasnovodsk, Kiysil-Kum and Fergana Depression (Fig. 4).

The formation of the *Phrynocephalus mystaceus* complex (or genus *Megalochilus*), (Figs. 7 and 8), and of the parallel sand inhabiting *P. interscapularis* complex, continued in the extreme southern portion of Middle Asia under conditions of sandy desert formation. The adaptive radiation of *Phrynocephalus* in sympatry, according to Peters (1984), could have been accompanied by increasing differences in the body size. This seems to have been important in the evolution of *P. mystaceus*. On quick moving sand dunes with steep slopes, the largest specimens could survive. They were able to dig uncrumpling deep holes protecting them from summer heat and low winter temperatures. They were also able to

release themselves from the captivity of the sand during movement of sand dunes. It should be noted that ridges formed from the stabilized aeolian landforms in the Pleistocene when mountain structures, which mainly determine the direction of the air streams, were formed. It is assumed that the direction of sand movement remained the same at least to the Upper Neogene (Voskresensky, 1968). The plains with newly formed meso- and microrelief created before the Quarternary drying and cooling by wind activity were alluvial plains with all the typical features (Voskresensky, 1968).

*P. mystaceus* evolved under the conditions of blowing sand. The decreasing of body size of *P. mystaceus mystaceus* in comparison with *P. mystaceus galli* may be indirect evidence in favour of this hypothesis. There may be correlations between this change of body



FIG. 7. *Phrynocephalus mystaceus* from Repetek (38° 34' N 63° 11' E), Turkmenistan.

size and the inhabiting of *P. mystaceus* in the comparatively stabilized Terek-Kuma rivers sands on the west side of the Caspian Sea in Russia. Smaller sizes of specimens of *P. mystaceus* are typical of the populations from the Sari-Kum Sand

Dune, Dagestan, Russia. This form developed under the conditions of a unique isolated sand dune with a special wind regime (Khonyakina, 1962).

The restricted distribution of *P.*



FIG. 8. Habiat of *Phrynocephalus mystaceus* (large sand dunes), *Phrynocephalus interscapularis* (sand dune edges), *Phrynocephalus raddei* (hard packed soil to the left) from the Kara Kum Desert 80 km north of Ashkabad (37° 57' N 58° 23' E), Turkmenistan.

*mystaceus* and relatively poor food availability of the sand dunes could have driven the small *P. interscapularis* back to the dune valleys. This species, sharing a common southern origin with *P. mystaceus*, could not spread beyond the limit of the subtropical climatic belt during the next geological epoch. Its present distribution almost completely lies in the climatic zone of the continental southern Turanian region with a small penetration to the extreme southern part of the continental north Turanian region (after Alisov, 1969). These species occur where the temperature during January  $-3^{\circ}\text{C}$  in the north, up to  $2^{\circ}\text{C}$  in the south and annual precipitation from 100 to 200 mm. According to Kashkarov and Korovin (1936) *P. interscapularis* inhabits Mediterranean deserts with a winter-spring period of precipitation and vegetation of the ephemeral type (Table 1). The relatively restricted range of *P.*

*interscapularis* may be explained by some ecological peculiarities. This lizard is very small. It is not capable of digging deep into the sand, and it also has a greater tolerance to high temperatures. The temperature preference of *P. interscapularis* may fluctuate only  $3^{\circ}\text{C}$ , whereas in *P. mystaceus* it may fluctuate  $4^{\circ}\text{C}$  and in *Eremias grammica* up to  $5^{\circ}\text{C}$  (Cherlin and Muzicenko, 1983).

The mode of preference of temperatures in *P. mystaceus* and *Eremias grammica* is  $39^{\circ}\text{C}$  which may be comparable with the very high level of tolerance known for *Dipsosaurus dorsalis*. However, for *P. interscapularis* this index is still higher ( $41.3^{\circ}\text{C}$ ). This may be considered an outstanding example of adaptation of a small lizard to extremely arid conditions.

In the north and northwestern deserts, *P.*

TABLE 1. Distributional characteristics of *Phrynocephalus* species in the USSR.

Name	Climatic Belt	Geo-morphology	Desert Type	Climatic Region	Ecological Type	Recent Area	Age of Recent Area	Center of Origin
<i>P. raddei raddei</i>	Subtropical	Accumulation plains with aeolian landforms	Mediterranean clay soil or sandy soil	Continental southern Turanian	Sclerobiont	Turkmenia	Pliocene-Pleistocene	Middle Asia
<i>P. raddei boettgeri</i>	Subtropical	Accumulation plains with aeolian landforms	Mediterranean clay soil or solonchaks desert	Continental southern Turanian	Sclerobiont	Kukhistan valleys	Miocene-Pleistocene	Middle Asia
<i>P. maculatus</i>	Subtropical	Accumulation plains with aeolian landforms	Mediterranean solonchaks desert	Continental southern Turanian	Sclerobiont	Turkmenia, Bami region	Neogene	Middle Asia
<i>P. rossikowi rossikowi</i>	Temperate	Plains of river valley origin	Mediterranean loess-clay soil	Continental northern Turanian	Sclerobiont	Lower course of Amu Darya (River) and southern coast of Aral Sea	Pleistocene	Middle Asia
<i>P. rossikowi schammakowi</i>	Temperate	Plains of river valley origin	Mediterranean loess-clay soil	Continental northern Turanian	Sclerobiont	Lower course of Amu Darya (River) and southern coast of Aral Sea	Pleistocene	Middle Asia
<i>P. reticulatus reticulatus</i>	Subtropical-temperate	Plateau with superimposed aeolian landforms	Mediterranean sand and gypsum desert	Border between continental northern Turanian and continental southern Turanian	Sclerobiont	Kysil Kum Plateau	Pliocene	Middle Asia
<i>P. reticulatus bannikowi</i>	Subtropical	Plains covered with superimposed aeolian landforms	Mediterranean sand and gypsum desert	Continental southern Turanian	Sclerobiont	Southern Ustyrt and Krasno-vodskoye Plateau	Pliocene	Middle Asia

TABLE 1. Continued.

Name	Climatic Belt	Geo-morphology	Desert Type	Climatic Region	Ecological Type	Recent Area	Age of Recent Area	Center of Origin
<i>P. strauchi</i>	Subtropical	Accumulative Aeolian landform on the synclorium	Mediterranean sand and gypsum desert	Continental southern Turanian	Sclerobiont	Fergan Valley	Pleistocene	Middle Asia
<i>P. helioscopus helioscopus</i>	Subtropical	Plains of different origins	Intrazonal takyrs	Continental southern Turanian	Sclerobiont	Plains of Middle Asia Kazakhstan Volga region	Pleistocene	Middle Asia
<i>P. helioscopus persicus</i>	Subtropical	Relief of the graben (trough) synclorium	Mediterranean clay soil and sand desert	Continental southern Turanian	Sclerobiont	Valley of the Middle Araks River	Pliocene	Middle Asia
<i>P. guttatus guttatus</i>	Temperate	Plains of different origins	Central Asian clay soil and sand desert	Continental northern Turanian	Psammobiont	Northern Caspian region and Aral region	Miocene-Pleistocene	Central Asia
<i>P. guttatus kuschakewitchi</i>	Temperate	Plains with accumulative aeolian relief	Central Asian sand desert	Continental northern Turanian	Psammobiont	Sary Ischik Otrau	Pleistocene	Central Asia
<i>P. moltshanowi</i>	Temperate	Plains of river and lake origin	Mediterranean loess-clay desert	Continental northern Turanian	Sclerobiont	Delta of Amu Darya (River)	Pleistocene	Central Asia
<i>P. versicolor kulagini</i>	Temperate	erosion accumulative relief on the bottoms of intermontane depressions	Central Asian clay and sand desert	Continental	Sclerobiont	Ubsu Nur Depression	Pleistocene	Central Asia
<i>P. versicolor paraskivi</i>	Temperate	Accumulative Aeolian relief on the synclorium	Central Asian clay and sand desert	Continental northern Turanian	Mesobiont	Ili River depression	Pliocene	Central Asia

TABLE 1. Continued.

<i>P. melanurus</i>	Temperate	Lake alluvial plain	Central Asian clay and sand desert	Continental northern Turanian	Psammobiont	Zaisan Depression	Pliocene	Central Asia
<i>P. interscapularis</i>	Subtropical	Accumulative plains with aeolian landform	Mediterranean sand desert	Continental southern Turanian	Psammobiont	Deserts of the south of Middle Asia	Pliocene	Middle Asia
<i>P. sogdianus</i>	Subtropical	Accumulative plains with aeolian landform	Mediterranean sand desert	Continental southern Turanian	Psammobiont	Kukhistan valleys	Pleistocene	Middle Asia
<i>P. mystaceus galli</i>	Subtropical-temperate	Plains of different genesis with aeolian landform	Mediterranean and Central Asian sand deserts	Continental southern Turanian	Psammobiont	Middle Asia and Kazakhstan	Pliocene-Pleistocene	Middle Asia
<i>P. mystaceus mystaceus</i>	Temperate	Plains of different genesis with aeolian landform	Central Asian sand desert	Continental southern Turanian	Psammobiont	Southeastern part of European USSR	Pleistocene	Middle Asia

*mystaceus* occurs on steep slopes of sand dunes were as the sympatric *P. guttatus* occurs in the valleys between sand dunes.

Large mountain ranges were formed in the place of residual plains and low mountain relief with a Paleozoic folded structure. The peneplain was subjected to folded deformations (Gvozdesky and Mikhailov, 1987). In this context it is difficult to share Golubev's (1989b) opinion that the conditions of the early Pleistocene were favorable for the penetration of *Phrynocephalus* from Central Asia to eastern Kazakhstan. However, Golubev (1989b) noted that owing to active alpic orogenetic processes in the Junggar Alatau and the Tian Shan, the contact of the reptiles between the Balkhash-Alakol and the Junggar Depression became gradually more difficult or was interrupted. This period was probably characterized by disjunction of continuous ranges and by the isolation in the intermountain depressions of the central branch of the *P. guttatus* complex. Further history of the speciation of each population seems to have resulted in the formation, during the Pleistocene, of more clearly isolated taxonomical forms in different depressions: Ili- (*P. alpherakii* according to Peters, 1984; Golubev, 1989b, or *P. versicolor paraskivi* according to Semenov, 1987); Alakol Depression- (*P. versicolor* ssp.), and Zaissan Depression- (*P. salenskyi* according to Peters, 1984; Golubev, 1989b, or *P. melanurus* according to Semenov, 1987). Definitive formation of eastern populations of the *P. reticulatus* complex, which subsequently led to the isolation of *P. strauchi*, may have taken place at the same time. Its speciation occurred because of the isolation of the Fergana Valley. Retaining of isolated populations in intermountain depressions was possible due to the absence of repeated leveling of the relief in Neotectonic time. This is supported by geological evidence such as the composition and thickness of sediments in the Ili and Fergana depressions (Voskresensky, 1968).

Most of the distribution of *P. mystaceus* seems to have been formed during the end of the Neogene when these lizards could

have occupied all of Middle Asia, from the Caspian Sea in the west to Balkhash Lake in the east, and from the plains near the slopes of Kopeth-Dagh and Hindu Kush in the south up to the Naryn Sands in the north. Its primary Aralo-Caspian (Turanian) origin and distribution is supported by all zoogeographers (Anderson, 1968; Chernov, 1954; Rustamov and Sczcerbak, 1985; Vereshagin, 1966). The penetration to the deserts north of the Caucasus Mountains probably took place around the northern Caspian Sea (Chernov, 1954; Darevsky, 1957).

In the Pleistocene, the Central Asian elements of the flora dispersed from the east to the north of Middle Asia and central Kazakhstan. The other important center which influenced the development of Middle Asian vegetation was the eastern Mediterranean center (Gvosdezky and Mikhailov, 1987). All the plains of this extensive region are classified by vegetation type into two kinds of deserts: Mediterranean (after Kashkarov and Korovin, 1936), and subtropical deserts of the northern zone (after Gvosdezky and Mikhailov, 1987), or accordingly, the deserts of the northern zone (after Gvosdezky and Mikhailov, 1987). The present boundary between the two zones approximately corresponds to the boundary distinguished by Alisov (1969) for the climatic regions of continental northern Turanian and continental southern Turanian.

In the Pleistocene, speciation of the *P. guttatus* complex occurred in the northern deserts of the Caspian and Aral Regions. During the Upper Pleistocene, river beds of the Amu-Darya and Syr-Darya rivers turned to the Aral Sea (Voskresensky, 1968). This resulted in a change from sand massive on the southern coast of the Aral Sea to loess and clay plains of river origin. Under these conditions of hard soils, the formation of the isolated southwestern population of the *P. guttatus* group, considered now as a separate species, *P. moltschanowi* (Semenov and Shenbrot, 1982) took place (Fig. 9). The taxonomic

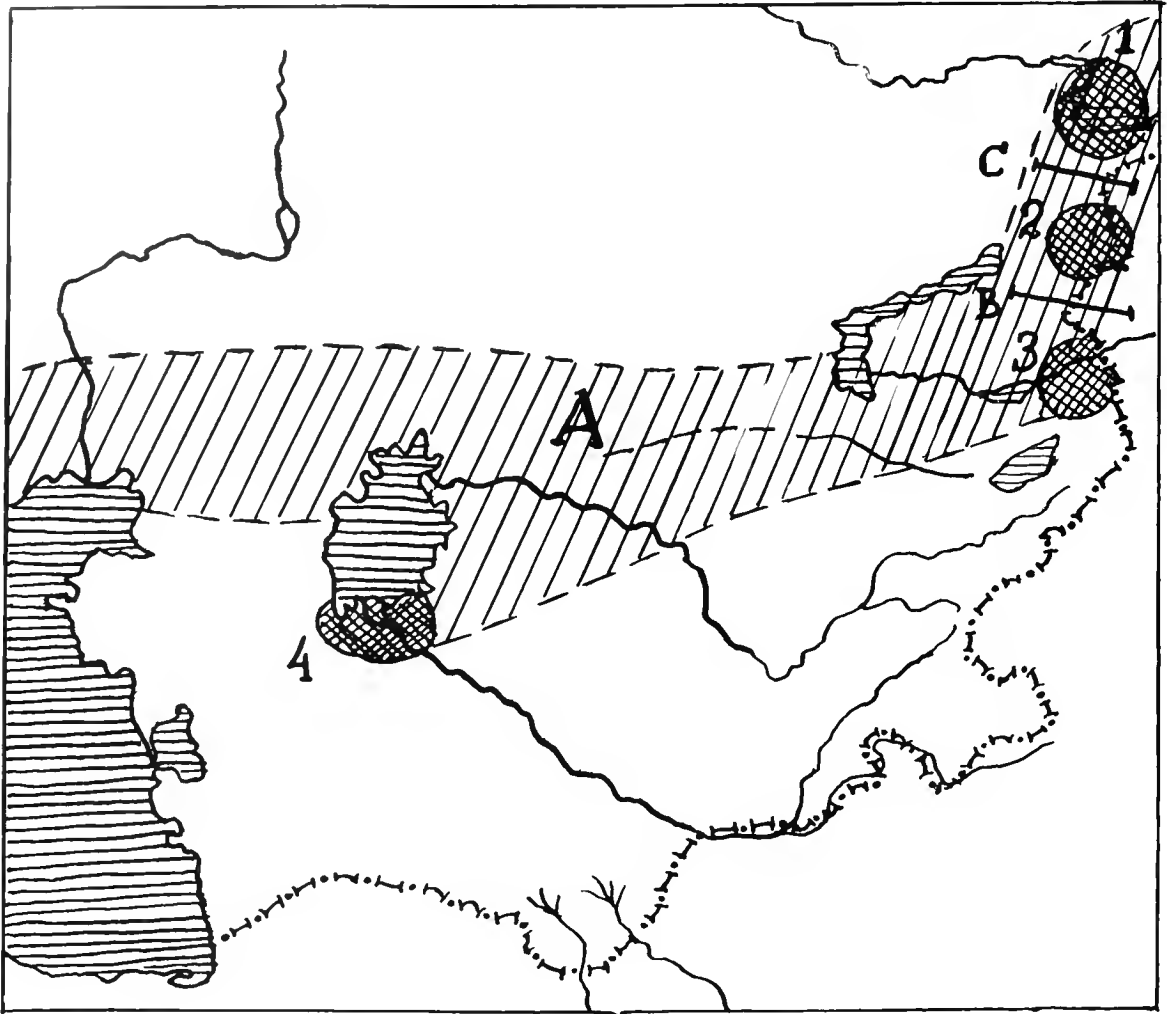


FIG. 9. Upper Pliocene changes of *Phrynocephalus*. A- middle Pliocene distribution of the species of the *Phrynocephalus guttatus* complex. The disjunction of the continuous distribution of this complex occurred in the Upper Pliocene by: B- Junggar Alatau (Altai mountains); C- Saur and Tarbagatai mountain ridges. 1- *Phrynocephalus melanurus*; 2- *Phrynocephalus versicolor* ssp.; 3- *Phrynocephalus versicolor paraskivi*; 4- the place of speciation of the southwestern branch of the *Phrynocephalus guttatus* complex and *Phrynocephalus moltschanovi*.

status of this species was discussed recently by Golubev (1989b).

It should be noted that the flow of Middle Asian rivers to the Caspian Sea changed to the Aral Sea, as a result of the downwarp of the region (Voskresensky, 1968). This was of crucial importance for the reconstruction of the ranges of most sclerobiont *Phrynocephalus* species. Probably before the Amu-Darya River (Uzboi), changed its course *P. raddei* was distributed on the clay and loess areas from the Caspian Sea to Kukhistan. Its range

decreased considerably from the north and from the south owing to orogenesis (Fig. 9). In the south this species remained on the incline plain of the Kopeth Dagh and in the loess regions in the estuaries of the Murgab and Tedjen rivers.

After the Amu Darya changed its flow to the Aral Sea, which coincided in time with the maximal development of the sand deserts, the area inhabited by *P. raddei* was divided into a number of isolated populations. These include the piedmont plains in Kukhistan and the Kopeth Dagh,



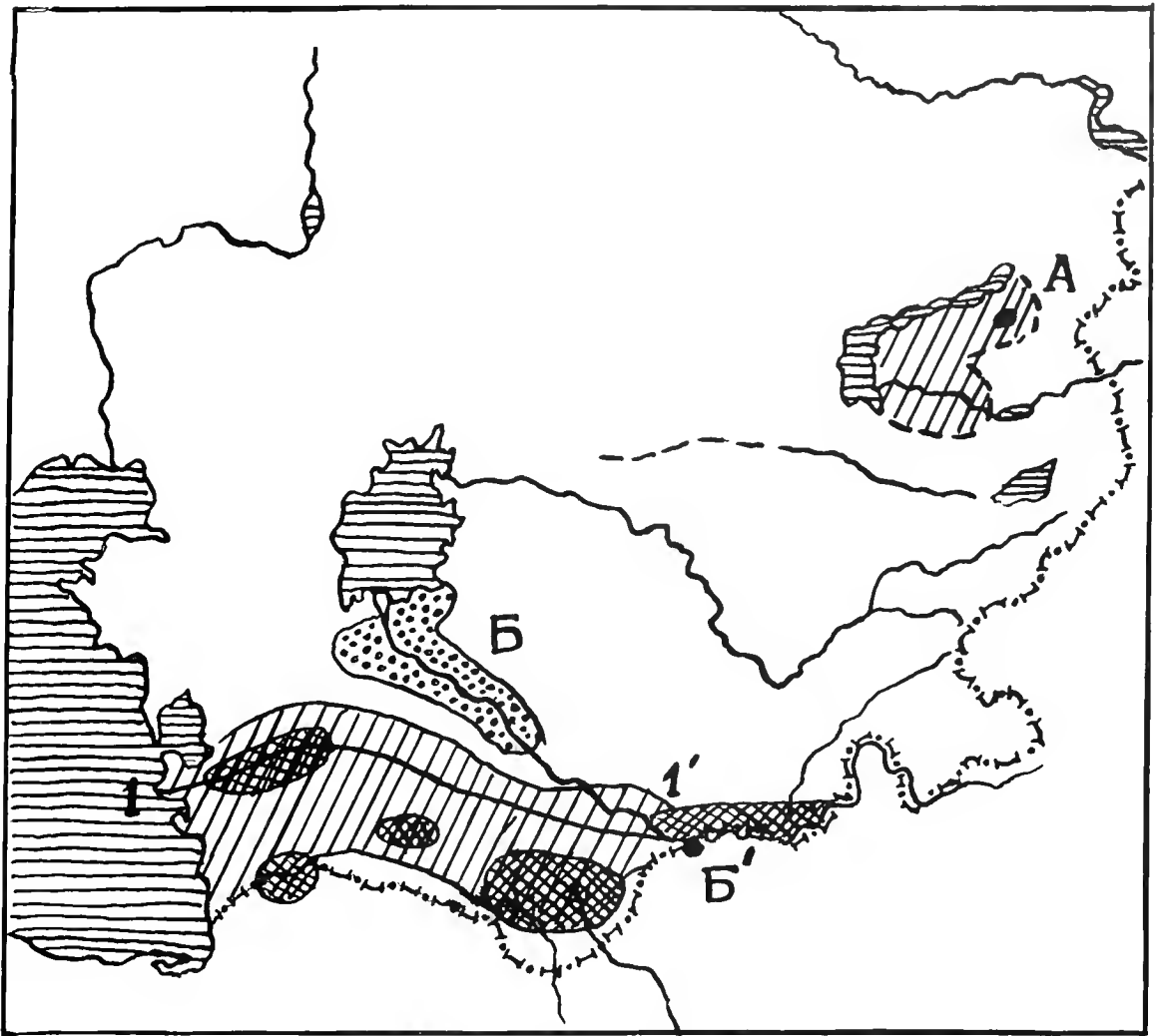


FIG. 10. Pleistocene changes of *Phrynocephalus*. 1 to 1'- the river course of the Amu Darya River (Kelif Uzboi and Uzboi) flowing in to the Caspian Sea before the Lower Pliocene. The distribution of *Phrynocephalus raddei* before the change of the Amu Darya River course to the Aral Sea is hatched. The relictual populations (Upper Pliocene to present) after the change of the Amu Darya River course to the Aral Sea are depicted by cross hatching. A- present distribution of *Phrynocephalus guttatus kushakewichi*; B- the transformed distribution of *Phrynocephalus rossikowi* during the Upper Pleistocene from pre-Pleistocene center of speciation (B').

remaining loess and other valley originated forms of the mouth of the Murgab and Tedjen rivers, and the dry bed of the Uzboi. *P. raddei boettgeri* was formed in the eastern isolated part and it is possible that the western populations also present combinations of different forms (now the nominative subspecies *P. raddei raddei*, (Fig. 10).

The genesis of the area inhabited by *P. rossikowi* (Figs. 11 and 12) is also

correlated with the change of course of the Amu Darya River. This area decreased in the south and reached the southern coast of the Aral Sea in the north (Fig. 10). Owing to the constant change of the configuration of the Amu Darya estuary also observed now (Voskresensky, 1968). The northern part of the range of *P. rossikowi* was also changing repeatedly, resulting in the isolation and long existence of this isolated western population. It was described recently as a distinct subspecies, *P.*



FIG. 11. *Phrynocephalus rossikowi* (size x 2) from along the Amu Darya River, 30 km WNW of Deynau (39° 15' N 63° 11' E), Turkmenistan.

*rossikowi shammakovi*. It is also possible that the extreme northeastern population has been isolated from the main distribution for a long time and represents a distinct taxonomical form.

After the formation of sand ridges and the deepening of the dune valleys slowed, the process of washing away the subtle material from the ridges to the valleys with the formation of the "takyr" landscapes began in the Pleistocene (Voskresensky, 1968). Under such new conditions *P. helioscopus* became widespread in the plains of Middle Asia.

The Pleistocene glaciation in Europe resulted in the sharp displacement of vegetation zones in the southern Russian plains and vegetation belts in the Caucasus Mountains. As a result, the distribution of *P. mystaceus* in the deserts north of the

Caucasus Mountains was separated into a number of isolated parts. Its range increased in the piedmont regions north of the Caucasus Mountains to the westward, probably in the postglacial xerothermic time of the Holocene. At this time *P. mystaceus* reached the present border of Dagestan and Stavropolsky Territory along the Terek-Kuma rivers sands.

During the Pleistocene, *P. mystaceus* and *P. interscapularis* dispersed into mountainous Kukhistan along the sands formed from the alluvial of the Amu Darya (River). *Phrynocephalus sogdianus* evolved as a result of the disjunction of the Kukhistan enclave during the Upper Quaternary from the continuous range of *P. interscapularis*. This species was described by Chernov (1959) as a subspecies, *P. interscapularis sogdianus*. This form was given the status of a distinct species after



FIG. 12. Habitat of *Phrynocephalus rossikowi* (size x 2) from along the Amu Darya River, 30 km WNW of Deynau (39° 15' N 63° 11' E), Turkmenistan.

Sokolowsky (1975) discovered considerable karyotypical differences between *P. sogdianus* and *P. interscapularis*. With the alternations of the Quaternary glacial and interglacial epochs, the pluvial and xero-thermic climatic periods were connected. However, during the whole Quaternary period, the climate was sharply continental. The desert or desert steppe (in pluvial epochs) regime was retained on the plains of Middle Asia (Gvozdezky and Mikhailov, 1987).

During the Quaternary, the last accumulation changing of the relief on the plains in Middle Asia took place. This may explain the present configuration of the ranges of desert animals. The last considerable accumulation (Khvalynskaya) included the Caspian and low land Kara Kum Desert, Muyn Kum and Sary Ishik Otrau. Toad headed agamids completely

disappeared in the middle Quaternary period from the Muyn Kum Desert. After which only *P. mystaceus* could inhabit it.

The Khvalynskaya transgression of the Caspian Sea defined the western part of the range of *P. raddei*. The flooding of the Sary Ishik Otrau sands near the southern coast of Balkhash Lake resulted in the almost total disappearance of *P. guttatus* and *P. mystaceus* in this region. They are retained probably only near the foot of isolated island mountains that have risen recently among the sands in the eastern part of Sary Ishik Otrau (Fig. 10). Subsequently, dispersal from these refugia and isolated areas could have led to the formation of *P. guttatus kuschakevitschi* in the Balkhash sands.

Thus, the history of the formation of *Phrynocephalus* distributions, which is the sclerobionts (hard soils) depressions and

the blooms of psammobionts, is correlated with step wise development of the sand deserts of the Middle Asian plains. It was influenced by geological processes. All this wide belt is correlated with the zone of most recent downwarp along the peripheral part of the mountain massives of Middle Asia with the accumulation in them. This was followed by transformation of river and estuary sediments under arid conditions.

In some *Phrynocephalus* groups, species secondarily inhabiting sands are known, (Semenov, 1987). For example this pattern is observed in the *P. guttatus* complex, apart from typical sclerobiont forms. Chernov (1948, 1959) noted that *P. guttatus* inhabits different types of sandy biotopes from *P. mystaceus* and *P. interscularis*.

In connection with the problems discussed, it is necessary to mention the problem of *Phrynocephalus* origin. As was already stated above, paleontological data are available for *Phrynocephalus* only from the Pliocene of Turkey. This is not enough significant data about fossil *Phrynocephalus*. The data of present distribution and life history allow us to speculate about the primary character of habitats typical of these lizards. Golubev (1989b) wrote, correctly in our opinion, about the development of the most primitive *Phrynocephalus* in gravel and sand-stone (Gobi) deserts. Most herpetologists (Chernov, 1948; Semenov, 1987; Whitman, 1978) suggest that the primary character is sand biotypes. Thus, Chernov (1948) assumed that *Phrynocephalus* originally adapted to sand habitats and then moved to hard soils. The same opinion is shared by Whitman (1978) and Semenov (1987). It is interesting that all these herpetologists use as the most serious argument, the number of morphological adaptations shared by all species of *Phrynocephalus* and are typical of many other lizards adapted to life in deserts. Whitman (1978), referring to Stebbins (1944), names the following morphological characters: 1) dorsoventral depressed body form; 2) protruding labial border; 3) nostrils closed

by special valves; 4) special "scaled" eyelids close the eyes; 5) tympanum absent or hidden under the skin; 6) granular smooth scales; 7) comparatively high speed of locomotion, sometimes bipedal; 8) increased finger surface, "sand ski"; 9) the capacity to bury into the sand; 10) short recurveable tail.

However a more detailed study of these characters refutes the simplified determination of their correlation with a habitat in the sand. It is doubtful that the dorsoventral depression of the body may be an indicator of inhabiting sand biotopes. This character is in the basis of the identification key in the Agamidae family (Boulenger, 1885), separating more specialized tree agamids from all terrestrial, rock and desert forms. It is well known that such form of the body of mountain agamids of the genus *Stellio* is not an indicator of their origin in sand deserts.

Such characters as closed upper lip covering the mouth, nostrils closed by special valves, and special "horny scaled" eyelids closing the eyes undoubtedly may be considered as defensive structures. However they can be developed in different kinds of deserts (not only sand deserts) with a typical windy regime.

Considering the ideas about the origin of *Phrynocephalus* and the so called "primary substratum" one may assume that the terms "desert" in general and sand desert are sometimes confused. Thus, Chernov (1948, p. 132) was absolutely right that *Phrynocephalus* "originated and developed in the conditions of rather sparse vegetation." This, however, does not permit these complexes of landscapes and sand desert to be considered as equal. The latter is only one type of desert and it is the youngest from a geological aspect.

The character, tympanum absent or hidden under the skin, is of special importance. Analysis of the distribution of this character and trends to the reduction of the middle ear among all the agamids, shows that it has arisen independently in some evolutionary lines. The loss of the

tympanum and tympanum cavity is typical of the Australian genus *Tympanocryptis*. Such reduction may arise even in primitive forms like *Ceratophora*, *Cophotis* and *Lyricephalus*. These convergent trends are noted in *Otocryptis*, *Phoxophrys*, *Phrynocephalus*, and *Ptyctolaemus* (Moody, 1980). The enumeration of these genera shows that side by side with the desert lizards (but not psammophilous) there are even forest species. Thus *Otocryptis* is a terrestrial lizard which prefers to inhabit the vicinity of rivers shaded by vegetation in India and Sri Lanka. With this consideration, further examination of the new form, *Phrynocephalus laungwalaensis* from the Radjastan Desert of India may be important.

The granular smooth scales also may be observed not only in psammophilous agamids but also in *Leirolepis*, *Uromastyx*, and *Physignathus* (Moody, 1980). Besides, an examination of the correlation of *Phrynocephalus* morphological characters and the type of substrate (Galayeva, 1974) shows that psammophilous species have granular smooth scales. Where as lizards inhabiting hard soil (rock debris desert or arid desert with clay soil) usually have somewhat enlarged, imbricate scales and small protuberances. These data show that there are gradations of morphological characters among *Phrynocephalus* from sclerobionts to psammobionts, and not indisputable psammophilous morphological adaptations of the whole genus. The possible functional importance of small granular scales in the capillary collection and transport of the water in many desert lizards should be noted (Schwenk and Greene, 1987).

The comparatively high speed of locomotion, sometimes bipedal although the limbs may be weak, are typical of many agamids inhabiting open areas (Sukhanov, 1968; Cogger, 1975) and can not be restricted to psammophilous species only.

The increased toe fringes are widely discussed but there are no good

explanations of their function (Chernov, 1948; Fausek, 1906, 1959; Luke, 1986; Werner, 1987). These structures are really typical of many sand lizards, but simple character environment correlation may be misleading (Luke, 1986; Smith, 1935). Toe fringes have arisen independently at least 26 times in seven families of lizards (Luke, 1986) and can be used for locomotion on shifting sand, across water, and for digging in some kinds of soil such as sand and loess (Chernov, 1948; 1959; Luke, 1986).

The original capability of burying into the sand with horizontal movements of the whole body is very well expressed in psammophilous *P. mystaceus* and *P. interscapularis*. There exists an opinion that such behavior may evolve only on large areas of moving sand (Fausek, 1906). But one should not excluded the development of such interesting defensive behavior on the loose sand from the elements of cryptic and or sit and wait behavior with similar patterns observed in *P. helioscopus* on hard soil. This species presses the depressed widening body to the ground with several horizontal movements before standing still.

In general, the idea of Geptner (1933) seems to be fruitful for such considerations. He thought that the animal world of the sand deserts and that of the deserts with hard soils are two formations different in many aspects with their own, to a considerable extent independent, ways of development. The purpose of the adaptations in the two kinds of landscapes is considerably different.

To summarize the review of the recent chorology of *Phrynocephalus* in the USSR fauna, it should be noted that the differences in the outlines of the distributions in general correspond to two main centers of origin. The species of Central Asian origin have the northern most distribution, inhabiting totally a moderate climatic zone and the species of Middle Asian origin mainly did not go beyond the limits of the subtropical climatic zone. The relatively young species (*Phrynocephalus*

*helioscopus*, and *P. mystaceus*) have the widest distribution. A large portion of their distributions were formed in the Pleistocene in immediate connection with the development of the sand deserts and accompanied takyr.

We can distinguish several types of the present ranges of *Phrynocephalus*:

1. Miocene-Pleistocene range of a northern Thetys origin (*P. guttatus guttatus*).

2. Miocene-Pleistocene disjunct range of a southern Thetys origin (*P. raddei raddei*, and *P. raddei boettgeri*).

3. Pliocene relict range: a) connected with marine transgressions (*P. reticulatus reticulatus*, and *P. reticulatus bannikowi*); b) connected with alpine orogenesis (*P. maculatus*, *P. melanurus*, *P. versicolor parasskiwii*, *P. versicolor ssp.*, *P. helioscopus persicus*, and *P. strauchi*).

4. The Pliocene-Pleistocene ranges: a) wide (*P. helioscopus helioscopus*, and *P. mystaceus*); b) subtropical (*P. interscapularis*, and *P. sogdianus*).

5. Pleistocene transformed area (*P. moltschanowi*, *P. rossikowi rossikowi*, *P. rossikowi shammakowi*, and *P. guttatus kuschakewichi*).

Since the process of continuing aridization of Middle Asia is undoubted, it may be predicted that a reduction in the ranges of the stenotopic sclerobiont *Phrynocephalus* is occurring.

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## On the Ecology of Przewalsky's Gecko (*Teratoscincus przewalskii*) in the Transaltai Gobi, Mongolia

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**Abstract.** -Przewalsky's Gecko (*Teratoscincus przewalskii*) is one of the least studied representatives of the herpetofauna of Central Asia. We present the results of a study of the habitat, demography, spatial distribution, activity, and diet of this lizard. Our observations indicate that individuals of *T. przewalskii* are active foragers that feed primarily on beetles, and are strictly nocturnal. Individuals of this species do not protect territories, but do exhibit aggressive behavior. We present a detailed analysis of home ranges over a five year period.

**Key words:** Reptilia, Lacertilia, Gekkonidae, *Teratoscincus przewalskii*, Gobi Desert, Mongolia, ecology.



FIG. 1. An adult *Teratoscincus przewalskii*.



FIG. 2. A juvenile *Teratoscincus przewalskii*.

### Introduction

From the time it was first described, Przewalsky's Gecko (*Teratoscincus przewalskii* Strauch, 1887) has remained one of the least studied representatives of the herpetofauna of Central Asia. As distinguished from its close Central Asian relative, the Turkestan Plate-Tailed Gecko (*T. scincus* Schlegel), this species has been very rarely studied in nature, and it was only in 1961 that it was recorded in the fauna of Mongolia (Figs. 1, 2 and Plate 1). Occasional data on its biology are available (Borkin et al., 1983a, 1983b; Munkhbayar, 1976; Obst, 1962; Semenov and Borkin, 1986; Szczerbak and Golubev, 1986;

Zhao, 1985).

In the summers of 1981, 1982, and 1985, observations of this species were performed at the Ekhiyn-Gol (Ehiin-Gol) Desert Station of the Joint Soviet-Mongolian Complex Biological Expedition. In addition, material on this species was collected in other regions of the Transaltai Gobi in the course of faunal surveys. The Ekhiyn-Gol (Ehiin-Gol) Oasis is situated in the subzone of extremely arid deserts (average annual precipitation is 20-50 mm) in the south of the Bayanhongor Aymag (Province), (Fig. 3). Frosty winters with air temperatures of as low as -34°C, hot summers (air temperatures of up to 42°C

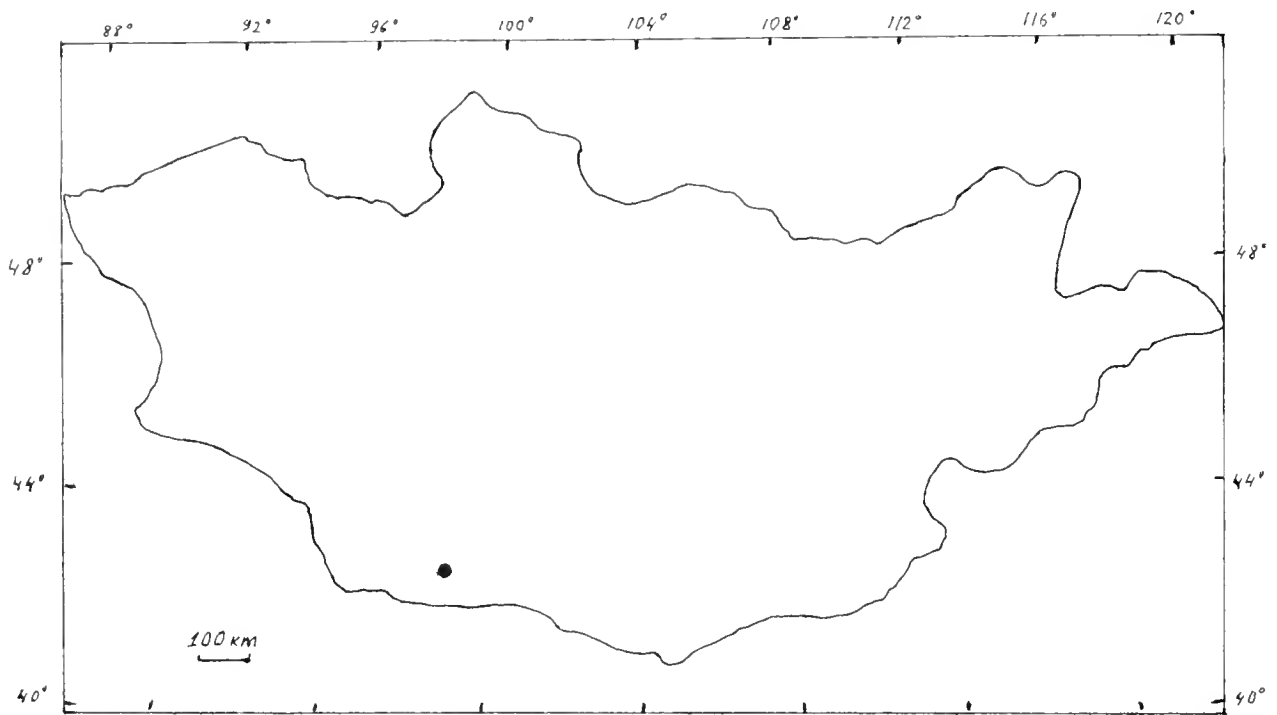


FIG. 3. The geographic position (dot) of Ekhiya-Gol Oasis, Transaltai Desert, Bayanhongor Aymag (Province), Mongolia.

and ground surface temperatures of up to 70°C), abrupt daily temperature fluctuations (up to 42°C), strong winds, and sand storms are the main features of the local climate (Figs. 4 and 5).

The most typical landscape of the Transaltai Gobi is broken stone desert plains or depressions surrounded by mountains. Vegetation in the vicinity of the Ekhiyn-Gol Oasis consists of Saxaul (*Haloxylon ammodendron*) with some *Nitraria sphaerocarpa*, *Zygophyllum xanthoxylon*, *Ephedra przewalskii*, *Calligonum mongolicum*, *Reaumuria soongorica*, and others. On the edge of the oasis there are two small sand sites with tall Saxaul trees. On one of these sites a plot was established for observation of geckos (Fig. 6). Here Przewalsky's Gecko coexists with a lacertid lizard, *Eremias vermiculata*, a colubrid snake, *Psammophis lineolatus*, and a boid snake, *Eryx tataricus*. Another lizard species, the agamid *Phrynocephalus versicolor*, was occasionally recorded in peripheral parts of the sands, near broken stone desert habitat

where this species is more common. More detailed information on the nature of the Transaltai Gobi and on the Ekhiyn-Gol Desert Station is available from the book "Deserts," edited by Sokolov and Gunin (1986).

### Methods

At night, geckos are easily discernible due to a characteristic ruby reflection of their eyes in the light of an electric torch. Thus, lizards may be located from a distance of a few dozen meters. To characterize their spatial distribution, individuals were marked by paint and by toe-clipping on the first capture. On subsequent captures, the lizards were remarked with paint if necessary. White numbers painted on the back of the animals make them easily recognizable (until molting) at night in the light of a torch without much disturbance to them. This double marking scheme allows an estimate of the time interval between molts. Marking and observation were performed on a 100 by 100 m plot established on a

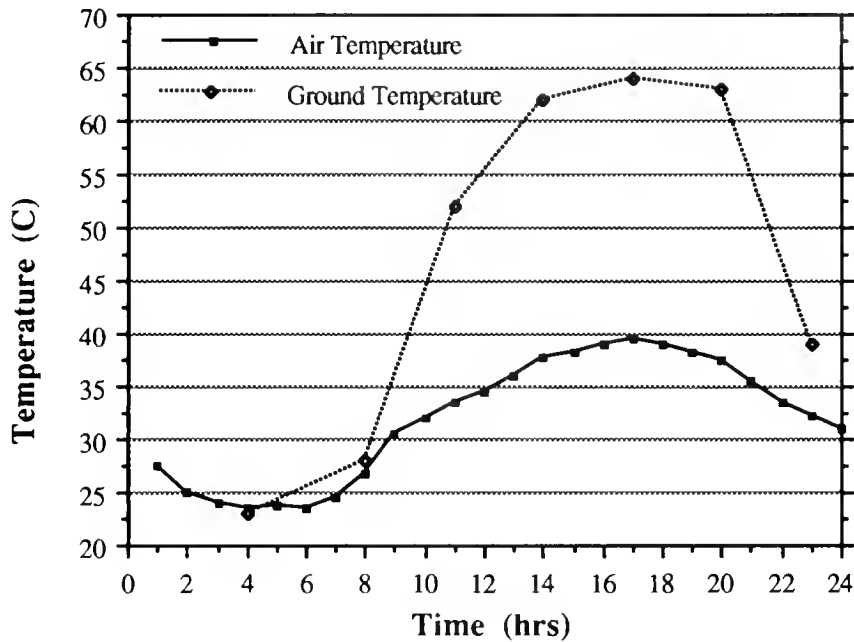


FIG. 4. Daily variation in air and ground surface temperature at Ekhiya-Gol Oasis, Transaltai Desert, Bayanhongor Aymag (Province), Mongolia, June 15, 1981, warmest day of the Summer.

sandy site with some Saxaul. Marked stakes were placed at 10 m intervals. The plot was inspected daily at various times from June 26 to August 17, 1981, from July 5 to August 13, 1982, and July 7-8, 1985. Gecko observations were recorded in relation to the stakes. In 1981 and 1982, a total of 83 geckos were marked, and 365 recaptures were recorded on the plot and near its boundaries. In fact, all individuals inhabiting the plot during this period were marked. Occasional non-marked animals appeared due to irregular invasions. The data were processed according to Semenov and Kulikova (1983) and Semenov and Borkin (1985). For each individual, the size of the home range, average and maximum movement, average radius of sightings, extent of reciprocal overlapping, and changes in range position were determined depending on the completeness of the data. Body length, tail length, and sex of captured animals were also recorded. Along with observations on this permanent plot, the population density of this species in Ekhiyn-Gol was determined by a complete removal study on August 16-23,

1981 on another plot of the same size, located on the other sand site. The absolute density with consideration of the marginal effect was estimated according to Semenov and Shenbrot (1985).

To characterize the daily and temperature dependent activities of Przewalsky's Gecko, the time of observation and air and ground temperatures were recorded. Cloacal temperatures were recorded from 45 geckos in three localities.

The stomach contents of 29 individuals caught in the vicinity of the Ekhiyn-Gol Oasis were studied. The weight of the stomach and its contents and the taxonomic identity, size, and dimensions of food items were determined, and the parameters of diet diversity were calculated according to Semenov (1986).

The behavior of geckos in their natural environment was observed in a corral 2 by 2 m, by 25 cm in height, constructed of polyethylene film. Observations were performed day and night with a red torch.

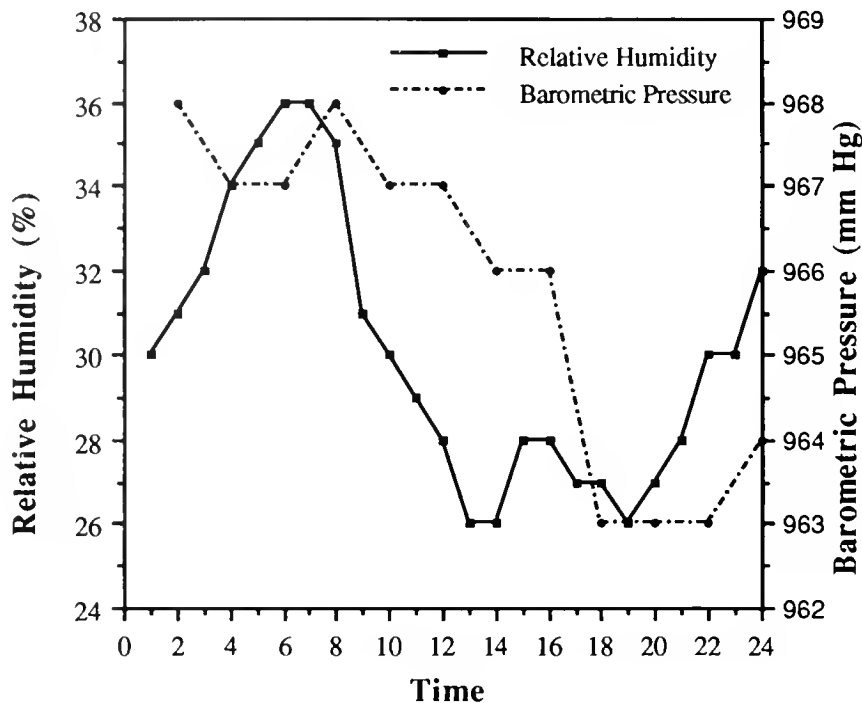


FIG. 5. Daily variation in relative humidity and barometric pressure at Ekhiya-Gol Oasis, Transaltai Desert, Bayanhongor Aymag (Province), Mongolia, June 15, 1981, warmest day of the Summer.

## Results and Discussion

### Habitat Preference

Unlike the stenotopic psammophilous *T. scincus* (Szczerbak and Golubev, 1986), Przewalsky's Gecko (also a predominantly psammophilous species) regularly occurs in other biotopes. It seems to depend on the relative rarity and patchiness of sandy sites in the Transaltai Gobi where broken stone deserts prevail. The commonest habitat of *T. przewalskii* in this region is semistabilized sands overgrown with Saxaul (Fig. 6). Stationary observations are performed at precisely such a place. The marking plot in 1981 was permanently inhabited by 18 individuals. A similar result was obtained on the other census plot where 19 geckos were caught. With consideration of the marginal effect, the last figure yields an estimated density of 11.5 individuals per hectare. In 1982, 12 permanent residents were recorded on the plot.

In gecko habitats, *Tamarix* sp. and *Calligonum mongolicum* may be present in

addition to Saxaul on sand, and sometimes replace it. On margins of oases, geckos occur on small sandy hills with low shrubs (*Reaumuria soongorica*, *Zygophyllum xanthoxylon*, *Ephedra przewalskii*, and rarely, *Nitraria sphaerocarpa*). It should be noted that Przewalsky's gecko was found in only part of all seemingly suitable sandy biotopes (habitats) in the Transaltai Gobi. They definitely avoid clear nonstabilized sand without vegetation.

Sometimes geckos also settle on small hills with fine soil covered by a dense surface crust, or on takyr-like sites, such as at Toli-Bulag in the vicinity of Ekhiyn-Gol or at Dzamiin-Huren-Els [southernmost Mongolia, Ömnögovii Aymag (Province)]. At the latter site, geckos were numerous under *Tamarix* sp. bushes and under *Nitraria sphaerocarpa*. Thus, on August 31, 1982, in spite of rain, 22 individuals were caught in a 1.5 hour period.

As well as on sandy biotopes, this species may be found on broken stone desert sites adjacent to sand, including hammada absolutely devoid of vegetation.



FIG. 6. A small sand hill with Saxaul Trees (*Haloxylon ammodendron*). This was a plot used for observation of *T. przewalskii*, June 22, 1981.

According to our data, *T. przewalskii* may live in areas up to 200 m distant from sand. Obviously, this enables geckos to populate isolated sandy areas scattered in the Transaltai as islands in stony regions of the desert. We note a particularly interesting situation in Bayan-Gol [Ömnögovi Aymag (Province)] where in the middle of July, geckos were found only on slopes (sometimes steep) of stony hills, and were completely absent from adjacent sands (Semenov and Shenbrot, 1986b).

#### *Demographic Parameters*

In the Ekhiyn-Gol population, adults with body lengths exceeding 70 mm are prevalent. The maximum body length of a mature gecko is 94 mm for males, and 96 mm for females. Body weight reaches 25 g. The minimum body length of individuals that have overwintered once is

51 mm. After hatching, juveniles have a minimum body length of 40 mm and a body weight of about 2 g (Fig. 7).

On the plot in 1981, 16 males, 11 females, 22 subadults, and 15 juveniles were marked. On the same plot in 1982, 13 males (12 marked the previous year), 8 females (6 marked the previous year), 15 subadults (7 marked the previous year), and 3 juveniles were recorded. Of the 12 geckos caught on the plot in 1985, 6 were marked in 1981-1982, including a male and a female marked as adults in 1981, a female marked as an adult in 1982, a male marked as a subadult in 1981, and a male and a female marked as subadults in 1982.

All subadults marked in 1981 reached the adult size by the summer of 1982, though some of them were provisionally left in the subadult group. Thus, maturity

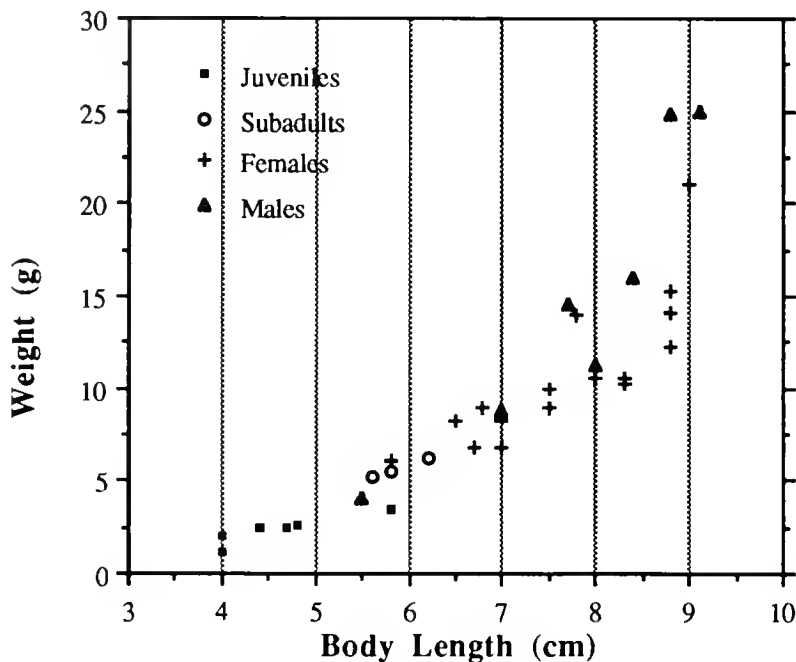


FIG. 7. The relation between body weight and body length (snout to vent) in *T. przewalskii*.

is reached after two winters. The life span of these geckos reaches 6 years in the wild. It is to be taken into consideration that the body length on a female caught in 1985 was the same as in 1981, while lizards which had overwintered twice had a body length of 78 mm. Thus, the life span may exceed 6 years.

According to our measurements of marked and recaptured geckos, juveniles grow 15-18 mm in length by the beginning of the next season. The annual growth of immature individuals fluctuates between 4 to 18 mm. Adult males grow 0-8 mm; adult females grow 0-4 mm. It should be noted that errors of measurement of body length of live lizards in the field are quite high (2-4 mm). Thus, these geckos grow rapidly during the first two years of life before maturity, then their growth slows down. The female mentioned above whose length was 90 mm in 1981 remained the same over 4 years, while a male marked in 1981, having a body length of 77 mm, was 84 mm long in 1982 and 92 mm in 1985.

Some of the prevalence of males among recorded geckos is obviously related to their larger home ranges (see below). The

approximate sex ratio in nature is close to 1:1.

Unfortunately there are no collections made in the spring and the beginning of summer, which is obviously the time of reproduction and egg laying. Spring begins in the Transaltai Gobi in March and terminates in May, and is commonly dry. Snow melts in the first half of April. The summer months last from June to the beginning of September. Commonly up to 80% of the annual precipitation (mainly rainstorms) falls during three summer months, mainly between the second half of July and the middle of August. In this region, *T. przewalskii* begin their reproduction not earlier than the second half of April, and probably later. Females caught in various places from July to August had no eggs ( $N = 21$ ), and only small follicles up to 3 mm in diameter were present. In a female caught in May 27, 1982, 80 km southeast of Nomgon settlement [the Ömnögovi Aymag (Province)], follicles reached 5 mm in diameter. On August 26, 1982, N. L. Orlov found two eggs about 16 mm in diameter with developed embryos (see Szczerbak and Golubev, 1986). Juvenile

TABLE. 1. Spatial distribution in a population of *T. przewalskii*.

Sex/age groups, year of observations	Home range area, m <sup>2</sup>	Average movement, m	Radius of recurrent sightings, m	Maximal movement, m
Males (1981)	1434.4±623.7	31.7±6.0	16.8±2.5	48.3±6.8
N	7	13	7	8
Males (1982)	1267.3±510.2	35.5±12.5	16.3±2.2	47.3±8.8
N	8	10	8	8
Males (1981+82)	1345.3±384.3	33.3±6.2	16.5±1.6	47.8±5.4
N	15	23	15	16
Females (1981+82)	1004.4±403.3	20.6±2.2	15.0±1.1	38.3±3.2
N	4	9	6	6
Subadults (1981-82)	312.0±61.4	19.5±3.5	10.1±1.3	35.8±5.4
N	11	21	13	12
Juveniles (1981-82)	-	14.3±4.2	-	-
N	-	4	-	-

*T. przewalskii* appear later than other lizard species in the same region. In 1982, the first juveniles were found in July, 1985 [July 10 in the Örgöstiyn-Us Oasis of the Gobi-Altai Aymag (Province), and July 13 in the Ekhiyn-Gol Oasis]. In 1985, the first juvenile was caught on July 18 at the Bayan-Gol area, south of the Ömnögovii Aymag (Province). However, in 1981, the first juvenile in the Ekhiyn-Gol Oasis was not found until August 4.

This leads us to believe that the period of egg laying is shorter in *T. przewalskii* than in the Middle Asian *T. scincus*, which mates in April and lays between June and July (rarely in the beginning of August) (see Szczerbak and Golubev, 1986). It is possible that Przewalsky's Gecko lays only one clutch of 1-2 eggs, as related species due. Demographic parameters characterize Przewalsky's Gecko as having a K-selection strategy (Pianka, 1981).

#### Spatial Distribution

*Teratoscincus przewalskii* do not migrate. Most individuals possess clearly delineated home ranges. Some geckos seem to be nomadic, partly explaining the disappearance of some individuals from the plot, and the appearance of new geckos. However, such translocations are rare; in spite of regular surveys in the vicinity of the plot, no marked geckos were found at distances much exceeding their normal

range of movements. The maximum recorded movement during one season is 140 m for an adult male in 1982 (it is interesting that in 1981, the same lizard moved 19.5 m, also the maximal movement of the year). On the average, movements were much lower (Table 1).

Home ranges do not differ much from year to year. The seven geckos for which home ranges were determined in 1981 had nearly identical ranges in 1982 (Figs. 8 and 9). The mean distance between the centroids of the 1981 and 1982 home ranges was 19.4 m (range: 3-36 m). Other geckos recorded in both years were found either within their 1981 home ranges in 1982, or between 1 to 58 m from the nearest point of observation in 1981. The greatest distance between points of observation in 1981 and 1982 is 180 m, by a subadult male (first marked as a juvenile after hatching in 1981). In 1985, six geckos were found from 30 to 130 m from the nearest point of observation in 1982. Thus, Przewalsky's Gecko, like the agamid lizard, *Phrynocephalus versicolor*, studied by the same method, a gradual shift of home ranges takes place (Semenov and Borkin, 1985; Smirina and Semenov, 1985).

Individual movements of geckos did not vary significantly among age/sex classes between 1981 and 1982 ( $t = 0.27$ ,  $N = 23$ ,  $P > 0.05$ ). The size of home ranges and

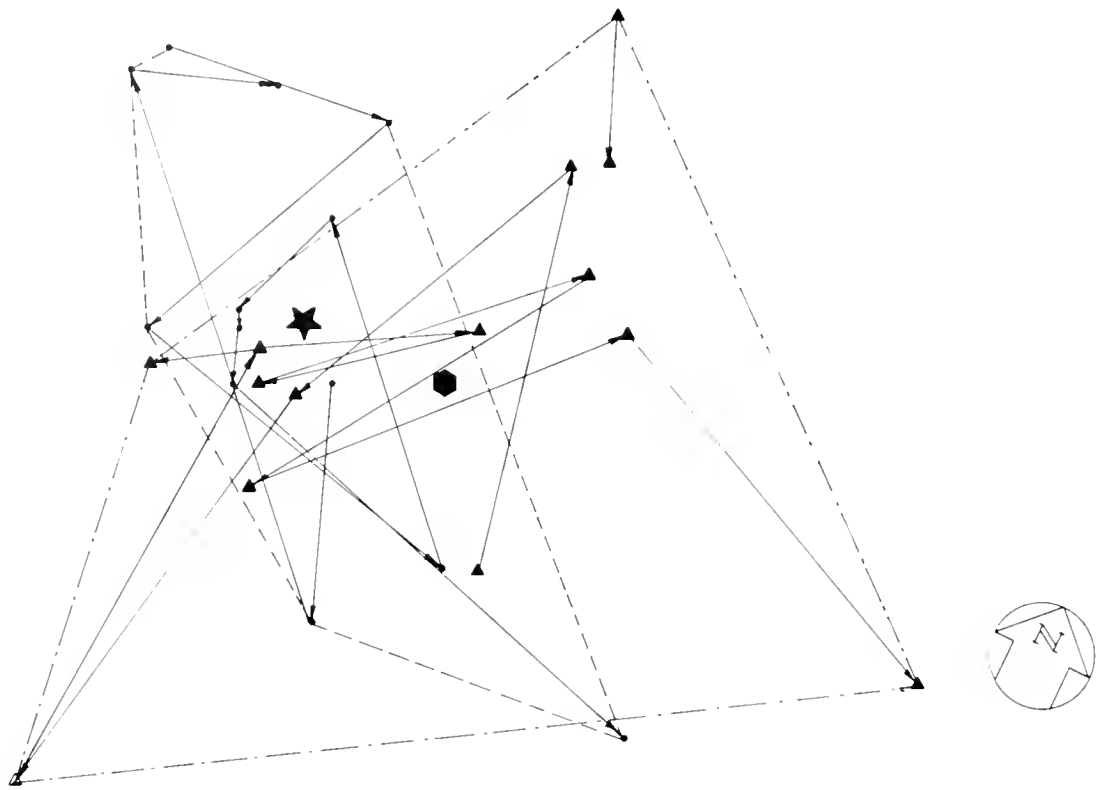


FIG 8. The movements of an adult female *T. przewalskii*. Dot: records of the lizard in 1981. Triangle: records of the lizard in 1982. Star: centroid of the 1981 records. Hexagon: centroid of the 1982 records. Solid arrow: denotes the next closest sighting in time. Dashed line: arbitrary boundary of the 1981 individual range. Dot-dash line: arbitrary boundary of the 1982 individual range.

other parameters (the combined data for both seasons) are higher in males than in females (Table 1), but in no case is the difference at a significant level (home range:  $t = 0.61$ ,  $N = 19$ ,  $P > 0.05$ ; individual movements:  $t = 1.92$ ,  $N = 32$ ,  $P > 0.05$ ; radius of recurrent sightings:  $t = 0.77$ ,  $N = 21$ ,  $P > 0.05$ ; maximum movements:  $t = 1.51$ ,  $N = 22$ ,  $P > 0.05$ ). However, the home range area and the radius of recurrent sightings is significantly greater in males than in subadults (home range:  $t = 2.66$ ,  $N = 26$ ,  $P < 0.05$ ; recurrent sightings:  $t = 3.12$ ,  $N = 28$ ,  $P < 0.01$ ).

The home ranges of these geckos overlap greatly (Fig. 7), irrespective of sex. Obviously Przewalsky's Geckos are not territorial. Their spatial distribution corresponds to the scheme typical lizards actively looking for their prey, living in

conditions of relatively poor visibility, and widely exploiting nonvisual orientation methods (Stamps, 1977).

Special attention should be given to the movement of marked juveniles. Unlike adults (see above), only 2 of 15 juveniles marked in 1981 were recorded in the next year (one of them was at a distance of 180 m; another had formed a home range 23 m from the marking point). Altogether, 18 juveniles were marked, of which 14 were not encountered during the same year, and 4 occurred twice each. It may be assumed that in Przewalsky's Gecko, juveniles are in the dispersal mode, similar to the agamid, *Phrynocephalus versicolor* (Semenov and Borkin, 1985). Having hatched, juveniles do not form home ranges, but disperse and only settle after the first overwintering. Movements of juveniles may exceed the maximum





FIG. 9. Individual ranges of the gecko, *T. przewalskii* in 1981. Open triangle: records of lizards captured only once. Solid line: arbitrary boundary of individual ranges.

movements of adults (see above).

### *Shelter*

Przewalsky's Geckos use their own burrows and those of rodents as shelters. Gecko burrows are, as a rule, made at the base of bushes, with a semicircular opening. The length of the burrow is a few dozen centimeters.

### *Activity and Temperature*

Przewalsky's Gecko is exclusively nocturnal. This is its distinction from many other "nocturnal" representatives of the Gekkonidae, which are characterized by mixed or crepuscular activities (Szczerbak and Golubev, 1986). According to Obst (1963), in the Galbyn-Gobi, in the first 10 days of September, geckos were active between 20:00 and 24:00 hours. We observed active individuals from 21:50 to 04:00 hours, at air temperatures of 16-29.5 °C and ground temperatures of 18-29 °C.

Strong wind and drizzling rain do not decrease the activity of geckos noticeably. Distinct periods of increased and decreased activity are evident at different times not clearly related to any weather conditions. Such periods are not restricted to post-sunset hours, as in some other gecko species (Pianka and Pianka, 1976; Cooper et al., 1985). This ecological aspect of this species requires special study.

The cloacal temperature in 45 geckos measured from 22:00 to 23:30 hours at three different localities ranged from 17.5 to 28.5 °C. Figure 10 demonstrates the relationship of cloacal temperature to air temperature in 25 individuals of different age and sex [in the vicinity of Ekhiyn-Gol and Shara-Hulsny-Bulag oasis in the south of Bayanhongor Aymag (Province)]. As a rule, cloacal temperature is slightly lower than air temperature by about 1°C. In only six individuals was cloacal temperature higher than air temperature. This may have been the result of stress since these lizards

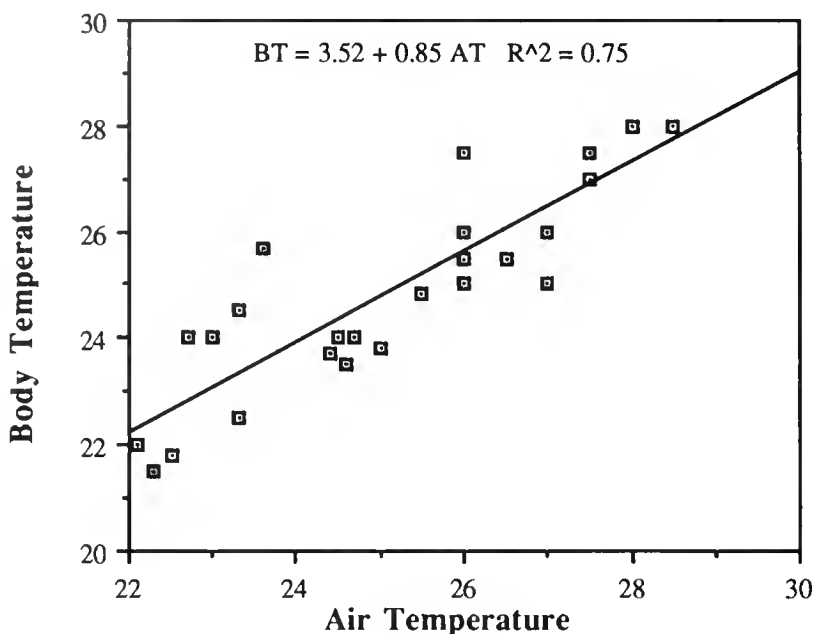


FIG. 10. The relation between air and cloacal temperatures in *T. przewalskii*.

were either being pursued or handled for a long time. During a few minutes of handling, the cloacal temperature in a gecko may increase by 3-4°C. Figure 11 shows the temperatures of 11 geckos from the vicinity of the Shara-Hulsny-Bulak Oasis. Measurements were made on July 5, 1982, during a strong wind. The sand temperature was slightly higher than the air temperature. The temperature of the back of the lizards slightly exceeded the cloacal temperature. In 20 individuals caught in the Dzamiin-Huren-Els area in late summer (August 31, 1982), the cloacal temperature was 17.5-19.8°C, averaging 18.3°C, with an air temperature of 18.0-18.2°C. The temperature of the sand surface was 18°C, and the temperature of the ground air layer dropped from 17.5 to 16.2°C during the 22:00-23:20 hour measurement period. It should be noted that lizards were caught and measurements made during a weak rain.

On the whole, the above data are too scanty and diverse to make any final conclusions on the thermobiology of Przewalsky's Gecko.

The strictly nocturnal activities of this species seem to be controlled by a light

factor of by the combined action of light and temperature, rather than by temperature alone. In any case, suitable temperatures occur not only at night, but also in the evening and morning (Fig. 4), but geckos were never met during the light of day.

#### Diet

Analysis of the stomach contents of Przewalsky's Gecko (Table 2) demonstrates that, like the Middle Asian *T. scincus*, (Bannikov et al., 1977) this species feeds mainly on beetles. Specialization in feeding on beetles manifests itself in the development of a robust jaw apparatus. Relatively low diversity parameters of feeding are the consequence of this specialization (Table 3). Similar values are only known for some populations of the agamid lizard, *Phrynocephalus versicolor* feeding mainly on ants. They are much higher in other lizards of the Transaltai Gobi (Semenov, 1986). The largest food items are the tenebrionid darkling beetles (18x6 mm), and their larvae (24x4 mm) [these are so large that only one beetle or one larva is consumed at a time]; the smallest are ants (1x3 mm). Sometimes geckos may devour larger objects. A gecko consumed an adult

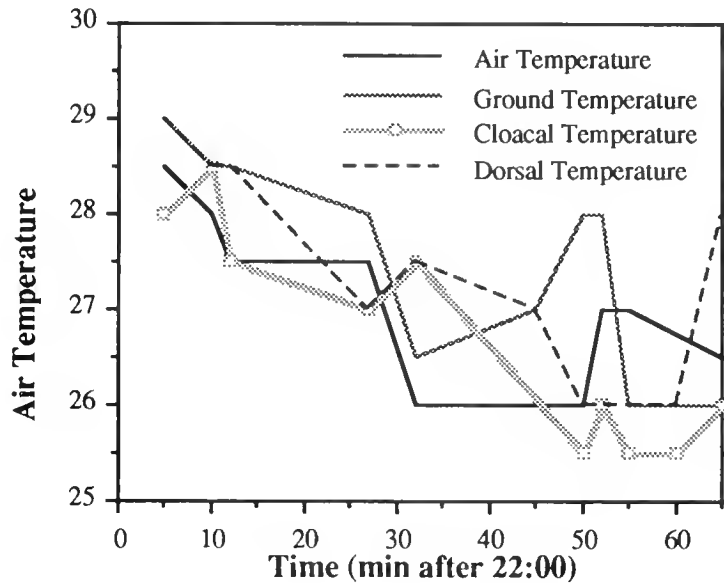


FIG. 11. Environmental and body temperatures in *T. przewalskii* versus time.

lizard, *Phrynocephalus versicolor* (about 80 mm in length, including the tail, and 10 mm in width) placed in the same bag with it. According to the observations of Szczerbak and Golubev (1986), these geckos will attack small lizards in a terrarium. The average weight of a full stomach reaches 7.8% of body weight.

#### Molting

Prolonged observations of marked lizards helps to record the frequency of molting (Semenov and Shenbrot, 1986a). Approximately half of the geckos observed in 1981 and 1982 molted during the period of observation. Only one individual (a subadult male) made two molts during one season: one in the middle of July and one in the middle of August, 1981. As all molted geckos were supplied with dorsal numbers again, and since in the next year these individuals were once again without numbers, it may be stated that molting takes place more than once a year. According to our data, there are no special molting periods, since molting individuals were observed throughout our observation period. Like other geckos, Przewalsky's Gecko devours the shed skin layers (found in two stomachs). According to observations in a terrarium, molting occurs

quite rapidly over the period of several hours (Obst, 1963).

*Teratoscincus scincus* molts not less than three times during the season. According to observations in captivity, molting takes 5-6 days (Szczerbak and Golubev, 1986).

#### Behavior

As was noted above, Przewalsky's Geckos do not protect territories. Nevertheless, in the corral, distinct aggressive behavior was observed: an adult darted at an approaching young gecko and inflicted a powerful blow to its head (perhaps having bitten it); one of them emitted a short acoustic signal. Przewalsky's Geckos have no permanent "observation posts" on the home range, and seemingly do not protect either the range or their shelters. Such protection is known for most of the Gekkonidae (Stamps, 1977). The aggressive behavior must be related to the support of the individual distance (Carpenter, 1965).

Judging by its movements, Przewalsky's Gecko is a typical predator that actively forages for its prey, in contrast to most other geckos that mainly wait for prey (Stamps, 1977). It is interesting to

TABLE. 2. Stomach contents of *T. przewalskii* (N=14).

Food items	Portion of total amount of food items (%)	Portion of total volume of food items (%)	Portion of stomachs with given food items (%)
Aranei	1.2	2.2	14.3
Solifugae	0.6	1.3	7.1
Hemiptera	8.1	3.1	57.1
Cydniidae	7.0	2.8	57.1
indet.	1.2	0.3	14.3
Neuroptera	2.9	7.4	28.6
Myrmeleonidae	2.3	3.9	28.6
larvae	0.6	3.5	7.1
Coleoptera	83.1	84.6	100.0
Tenebrionidae	80.2	80.5	100.0
larvae	0.6	2.6	7.1
Curculionidae	0.6	0.3	7.1
Chrysomelidae larvae	0.6	0.3	7.1
indet.	1.2	0.9	7.1
Hymenoptera	4.1	1.4	28.6
Formicidae	1.2	1.1	14.3
Mutillidae	0.6	0.1	7.1
Parasitica	0.6	0.3	7.1
indet.	1.7	0.2	14.3

TABLE. 3. Diet diversity of *T. przewalskii*.

Diversity parameters (width of the feeding niche-B)	Food groups (families)	Food groups (orders)
Volume of food items	1.295	0.923
Amount of food items	1.329	0.968

B is calculated according to Colwell and Futuyma (1971).

note that according to our observations in the corral, geckos often touch the ground surface with their tongue. Such chemoreceptive behavior is common in the Lacertidae and the Scincidae (Stamps, 1977), and is noted in some agamids (Panov and Zykova, 1986; Semenov, 1985). In contrast to *T. scincus*, Przewalsky's Geckos can swiftly and easily climb bushes, and do it rather often in escaping the pursuit. Geckos may climb bushes up to the height of 80 cm. In the corral, burrowing of a gecko was observed. Only its forelegs participated. Acoustic signaling is not noted in natural conditions, but handled geckos sometimes emit a brief squeak. Similar to the Middle Asian *T. scincus*, the autotomized tail emits a rather loud rustling, and wriggles for a long time (up to 19 minutes). The skin of these geckos is fragile, thus helping them to "slip out" if taken in hand. When handled, they desperately twist and try to bite.

The alarmed gecko rises in its straightened legs and lifts up its short, fleshy tail. In this posture, the gecko is somewhat similar to a dog. Evidently for this reason it is called in Mongolia, "Nokhoy-Gurvel," meaning, "a dog lizard."

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## Intrapopulation and Geographic Variation of *Eremias przewalskii* Strauch in Mongolia

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**Abstract.** -Body size and proportions, characters of pholidosis, coloration and pattern of *Eremias przewalskii* from western, southern and eastern Mongolia were studied. Sexual dimorphism is displayed in the relative sizes of the tail, head, legs, number of scales around 9-10th tail ring and ventralia. Some characters of pholidosis, as number of scales around the mid-body, number of femoral pores on the right side of the thigh and others displayed clear geographic variability. Live specimens from western Mongolia have blue ocelli on the body flanks. The lizards from southern Mongolia significantly differ from the specimens from other parts of the range by a larger number of scales around the mid-body, number of femoral pores on the right side of the thigh and other features. The intraspecific structure of *E. przewalskii* is discussed.

**Key words:** Reptilia, Squamata, Lacertidae, *Eremias przewalskii*, Mongolia, geographic variation, morphometrics, pholidosis, population variation.

### Introduction

*Eremias przewalskii* Strauch is a common species of western and southern Mongolia (Bannikov, 1958; Dely, 1979, 1980; Munkhbayar, 1973, 1976; Obst, 1963; Orlova, 1984, 1989; Orlova and Semenov, 1986; Szczerbak, 1970, 1974; Terbish, 1989). Earlier it was thought that it only occurred along the boundaries of southeastern Mongolia (Bannikov, 1958; Szczerbak, 1974). Now it is known to be the most widely distributed lizard in this region (Semenov and Shenbrot, 1986). Outside of Mongolia this lizard is distributed in northern China and Russia, in the southern portion of Tuva Autonomous Republic (Bedriaga, 1909; Flint, 1960; Pope, 1935; Schmidt, 1927; Strauch, 1876; Szczerbak, 1974).

All researchers who have observed *E. przewalskii* in the wild have noted its preference for soft soils. This species inhabits sands overgrown with *Nitraria* sp., sand dunes with *Haloxylon* sp. and *Tamarix* sp. In the Transaltai Gobi, *E. przewalskii* rarely occurs in gravel areas adjacent to sandy habitats (Borkin et al., 1983). In Uws-Nuur hollow and on the right bank of the river Khowd-gol it occurs on semi-anchored sands with *Caragana*.

Rarely, *E. przewalskii* lives on saline soil, in the dry gullies with almond-bush. In Bayan-Drag it is found among the stones of Cretaceous red sandstone precipices (Borkin, 1986; our observations). As compared to *Eremias multiocellata*, this species does not extend into high mountains, inhabiting either hollows and foothills with elevations 760-1800 m above sea level (Szczerbak, 1974) or in a narrower range of elevation, 1030-1650 m above sea level (Borkin, 1986).

Within its range, *E. przewalskii* is syntopic with *E. multiocellata* (e.g., near the well Buiesengijn-khuduk, 35-40 km northeast of Ba-Tsagan, in Bayan-Dzag).

High variability of external morphological features of *E. przewalskii* has been noted repeatedly in the literature. Such investigations were started by Strauch in his description of three *Eremias* species from China in 1876. Later (Boulenger, 1921; Nikolsky, 1915; Szczerbak, 1969, 1974) these forms (*E. brachydactyla*, *E. przewalskii* and *E. kessleri*) were synonymized with *E. przewalskii*.

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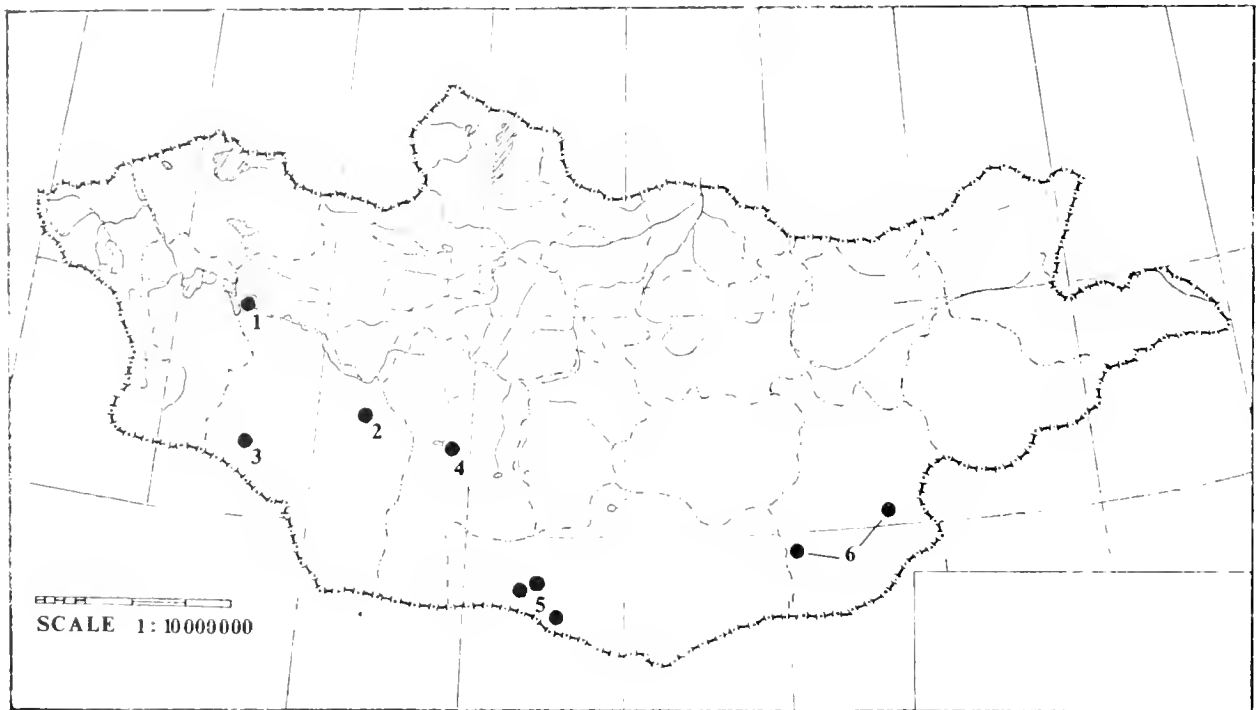


FIG. 1. Localities of the samples studied. See **Methods** below for a reference to the numbers.

Expedition of the Academies of Sciences of the USSR and MPR allow us to report more detailed information on intrapopulational and geographic variability of the species within the territory of Mongolia. The results are later to be used for comparative analysis of the variability of *E. przewalskii* and *E. multicellata*, in discussion of the relationships of these and other Mongolian species.

### Methods

Our material originates from western, southern and southeastern Mongolia. Localities of *E. przewalskii* are noted on figure 1. Samples collected are combined in to groups as follows:

1. Northern coast of Char-Us-Nuur Lake, Somon Urdgol (=Chandman), 19.06.1986, coll. Kh. Terbish, n=30.

2. Gobi-Altai Aymag: Lake Beger-Nuur, 20.07.1982, coll. Herpetological Department, n=17 (N 5034).

3. Gobi-Altai Aymag: Lake Alag-Nuur,

15.07.1982, coll. Herpetological Department, n=25 (N 5030).

4. Bayan-Chongor Aymag: 35-40 km NE of Ba-Tsagaan, 30.07.1984, coll. Herpetological Department, n=20 (N 5402).

5. South-Gobi Aymag: Shavgijn-Us, southern Chovuun (=Noen), 19.08.1982.; Sain Khuduk Well, 02.09.1982.; 6 km East of Obot-Khural, 17.08.1982, coll. Herpetological Department, n=54 (NN 5023, 5029, 5031).

6. East-Gobi Aymag: 43° 53' N 108° 05' E, 28.-30.07.1987, coll. G. I. Schenbrot et al.; 60 km SSE of Dzuun-Bayan, 06.1986, coll. G. I. Schenbrot, n=21 (NN 5614, 5802).

In all specimens investigated (162 specimens in total) the snout-vent length (L); tail length (L. cd.); foreleg and hindleg length ( $P_a$  and  $P_p$ ); head length, width and height ( $L_p$ ,  $C_p$ ,  $H_p$ ) were measured. The indices:  $L/L. cd.$ ,  $P_a/L$ ,  $P_p/L$ ,  $L_p/L$ ,  $C_p/L_p$  and  $H_p/L_p$  were calculated. The following



characters of pholidosis were taken into consideration: 1 - number of scales around the midbody (Sq.); 2 - number of scales along mid-line of throat (G.); 3 - number of femoral pores on the right side of the thigh (P. fm.); 4 - distance between the internal sides of the rows of femoral pores; 5 - number of transversal rows of pectoral and ventral scales (ventrale); 6 - number of scales around the 9-10th tail ring (Sq. c. cd.); 7 - number of subdigital lamellae on the 4th toe of right hindleg; 8 - number supralabial scales (labialia); 9 - number of infralabial scales (infralabialia); 10 - number of dorsal scales between parietals and level of anus; 11 - number of frontonasal scales.

In addition to characters mentioned above, pattern and body coloration were recorded, including the presence or absence of blue spots on the body sides.

For the treatment of material standard statistical methods were used (Lakin, 1980) with the calculation  $\bar{X}$ ,  $m_x$  and t-criterion for revealing sexual dimorphism and geographic differences.

## Results

*Sexual dimorphism.*—*Eremias przewalskii* males and females in Mongolia differ from each other by their snout-vent length in all samples, except those from South-Gobi Aymag (5) and East-Gobi Aymag (6). Males are slightly larger than females. The maximum difference in linear size between the sexes was in South-Gobi Aymag sample (5) from southern Mongolia, but statistically significant differences were not revealed, as in all other samples (Tables 1 and 2). The tail in the males is longer than in the females [except the samples from Gobi-Altai Aymag (2) and Gobi-Altai Aymag (3)]; as is length of the hind legs [except the sample from East-Gobi Aymag (6)]. As to the head proportions, there is a stable difference in relative head length ( $P < 0.01$ ,  $P < 0.001$ ). At the same time, other proportions, mainly  $H_p/L_p$ , slightly differed from each other in both sexes.

Some characters of pholidosis also displayed sex differences, although Szczerbak (1970, 1974) considered such sexual dimorphism to be absent in *E. przewalskii*. In all the samples we investigated the number of scales around the 9-10th tail ring is larger in males than in females (Fig. 2). In the samples from Gobi-Altai Aymag (3), South-Gobi Aymag (5) and East-Gobi Aymag (6) such tendency is displayed in the number of transversal rows of the pectoral and ventral scales. In specimens from western Mongolia (samples 1-4) the number of scales around the middle of the body differed between the sexes, but these differences are statistically insignificant.

*Coloration and pattern.*—We did not find clear differences in coloration and pattern between males and females. The ventral surface of the body, legs and tail is always entirely white in both sexes. In the western part of its range, *E. przewalskii* has blue spots on the flanks which is less bright in old females.

Thus, sexual dimorphism in *E. przewalskii* is displayed in relatively long tail, head, both pairs of legs, number of scales around the 9-10th tail ring and ventrals in males as compared to females.

## Geographic Variability

*Body size and proportions.*—The largest (maximum length 84.5 mm) lizards inhabit the southern and southeastern parts of the country, and the smallest lizards in the northern and northwestern regions. Moreover, animals of minimum size have been found near lake Alag-Nuur, Gobi-Altai Aymag (3). Slender specimens with relatively long tail and hind legs are seen in the samples from Gobi-Altai Aymag (3) and South-Gobi Aymag (5). Lizards from the southeast of Mongolia [East-Gobi Aymag (6) sample] are similar to those from the south [South-Gobi Aymag (5)] in the relative tail length, but they have a more robust habitus and shorter hind legs. Thus, within the range of *E. przewalskii*, its body size, relative tail and hind leg length

TABLE 1. Geographic variation of size and proportions in *Eremias przewalskii* (males).

Loc.	n	$\frac{L}{\text{lim, } \bar{x} \pm m\bar{x}}$	n	$\frac{L/L, \text{cd.}}{\text{lim, } \bar{x} \pm m\bar{x}}$	n	$\frac{P_2/L}{\text{lim, } \bar{x} \pm m\bar{x}}$	n	$\frac{P_p/L}{\text{lim, } \bar{x} \pm m\bar{x}}$
1	22	52.6-78.4	15	0.68-0.79	21	0.32-0.38	21	0.49-0.55
		66.42±1.43		0.73±0.008		0.34±0.003		0.51±0.004
2	10	51.1-68.5	7	0.68-0.87	10	0.31-0.35	10	0.49-0.56
		63.55±1.64		0.75±0.02		0.33±0.003		0.52±0.006
3	13	50.1-78.6	7	0.58-0.68	13	0.32-0.38	13	0.48-0.57
		63.23±2.45		0.64±0.02		0.36±0.006		0.54±0.008
4	15	52.6-77.9	11	0.67-0.78	15	0.33-0.38	15	0.50-0.58
		71.63±2.08		0.71±0.01		0.35±0.004		0.52±0.005
5	18	52.1-83.3	12	0.62-0.75	18	0.32-0.38	19	0.48-0.58
		67.12±2.47		0.68±0.01		0.35±0.005		0.54±0.007
6	11	53.8-79.0	11	0.64-0.76	14	0.31-0.38	14	0.47-0.56
		71.45±2.27		0.69±0.009		0.35±0.005		0.52±0.008

TABLE 2. Geographical variation of size and proportions in *Eremias przewalskii* (females).

Loc.	n	$\frac{L}{\text{lim, } \bar{x} \pm m\bar{x}}$	n	$\frac{L/L, \text{cd.}}{\text{lim, } \bar{x} \pm m\bar{x}}$	n	$\frac{P_2/L}{\text{lim, } \bar{x} \pm m\bar{x}}$	n	$\frac{P_p/L}{\text{lim, } \bar{x} \pm m\bar{x}}$
1	14	51.9-74.8	7	0.75-0.85	13	0.29-0.35	14	0.44-0.52
		64.52±2.03		0.81±0.01		0.32±0.006		0.47±0.008
2	7	54.0-69.4	3	0.75-0.84	7	0.29-0.35	6	0.45-0.53
		63.04±1.86		0.81±0.03		0.31±0.008		0.49±0.01
3	8	50.0-67.2	6	0.61-0.86	10	0.33-0.36	10	0.51-0.54
		59.29±1.92		0.70±0.04		0.34±0.003		0.52±0.003
4	6	63.33-75.5	4	0.77-0.87	6	0.30-0.34	6	0.47-0.51
		71.28±1.91		0.82±0.03		0.32±0.004		0.49±0.004
5	25	55.0-84.5	10	0.70-0.83	25	0.30-0.39	25	0.43-0.55
		72.67±1.51		0.74±0.01		0.33±0.004		0.50±0.008
6	3	67.0-78.3	4	0.72-0.76	4	0.32-0.37	4	0.48-0.55
		73.23±3.32		0.75±0.01		0.34±0.01		0.51±0.02

increases from north to south. This tendency is more clear in males. As to the relative head size, index  $L_p/L$  is stable in all samples ( $X=0.22$  in females and  $X=0.24$  in males) except the sample from Bayan-Chongor Aymag (4), where males and females have lower values of the index mentioned. Relative head width and height do not allow us to differentiate between lizards from different parts of the range.

*Pholidosis*.—The characters of pholidosis demonstrate clear geographic variation in some cases. As shown in table 3, lizards from southern Mongolia, are sharply distinguished from others by a markedly higher scale number around the middle of the body (and wider variation limits), femoral pores, scales around the 9-

10th tail ring, infradigital lamellae on the fourth finger of the hind leg and, to a lesser degree, by the number of transversal rows of pectoral and ventral scales. The distance between the rows of femoral pores is less in lizards from the south and southeast [South-Gobi Aymag (5) and East-Gobi Aymag (6) samples] as compared with the northern and northwestern ones. The tendency of reduced mean values of some characters of pholidosis is more pronounced in the western part of the range. These characters are: the number of scales around the midbody (Sq.), (Fig. 3), number of scales along mid-line of throat (G.), number of femoral pores on the right side of the thigh (P. fm.), (Fig. 4), ventrale and number of scales around the 9-10th tail ring (Sq. c. cd.)

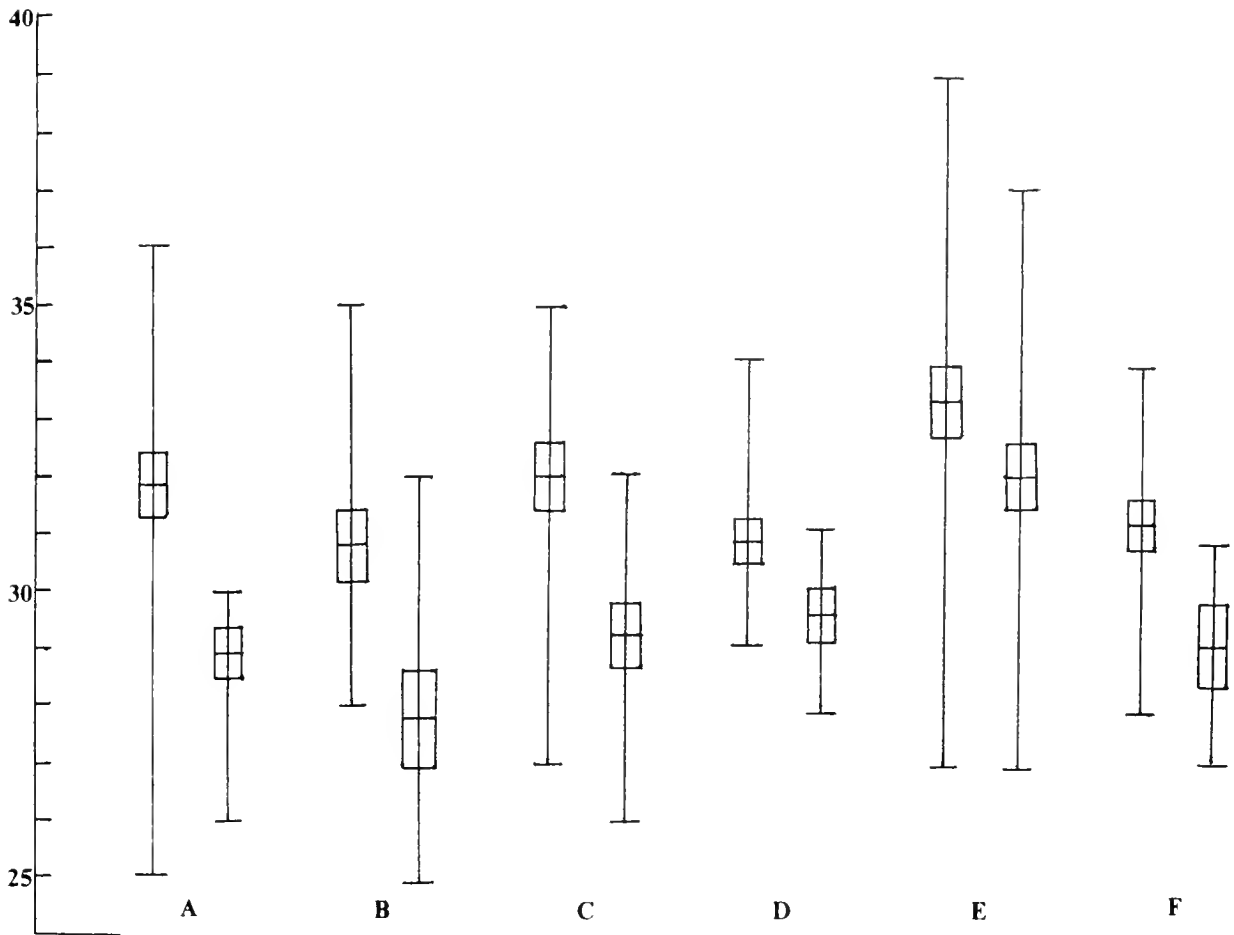


FIG. 2. Sexual dimorphism and geographic variation in the number of scales around 9-10th tail ring (Sq. c.cd.)

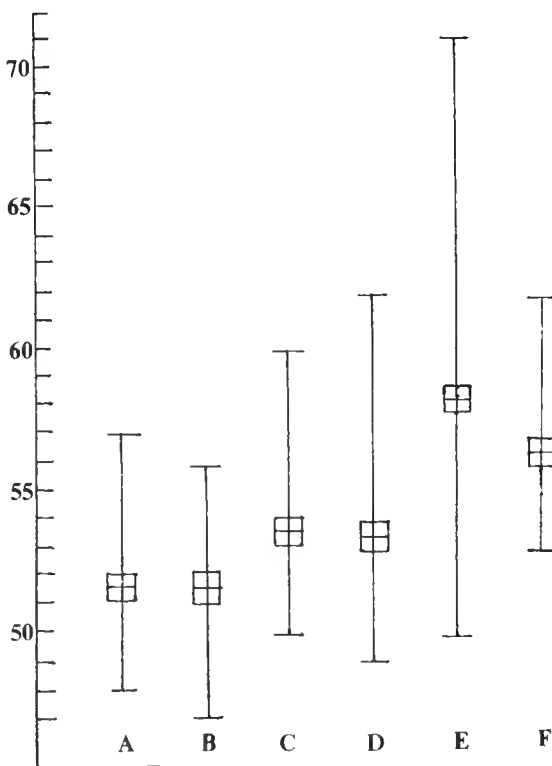
The characteristics of external morphological features includes, along with others, the number of scales along the spine (from parietals to posterior border of hind leg). For the lizards from the South-Gobi Aymag (5) sample this feature shows a similar situation as in many others, i.e. their number is markedly higher than in lizards from the western part of the range. Other features, such as the number of supra- and infralabials, are less variable.

*Coloration and pattern.*—The coloration varies from sandy or grey to dark-brown and black. The pattern may be made up either of relatively thin lines, or of rather wide, interwoven, wavy stripes and spots. The dorsal pattern of specimens from the Great Lakes Hollow (Fig. 5) is formed by sandy or light-coffee wavy lines or spots.

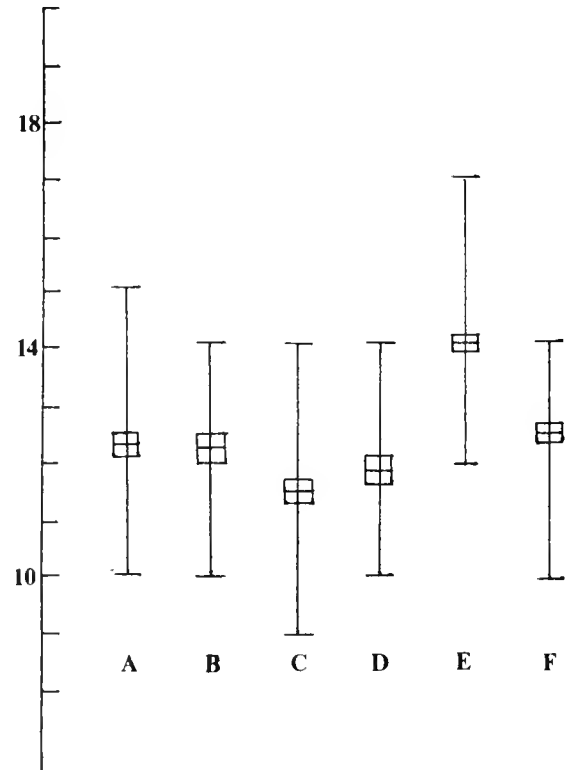
Between these colored areas there are 4 longitudinal rows of white ocelli or larger eroded light spots. The legs (especially hindlegs) are covered by a pattern of light spots surrounded by brown. The upper tail surface (about one third of the tail length) has a similar pattern, caudally it is divided into single dark spots, and the tip of the tail is light. The upper surface of the head is olive-grey in immature specimens without spots, or with a few spots in the parietal and supraocular scales. There is a dark and light striped pattern on the side of the parital scales which sometimes reaches the supraorbitalia. In individual specimens the entire head surface is covered by dark spots, which are more or less apparent. Temporalia are covered by a pattern of dark spots or stripes alternating with light spots or ocelli. The ventral surface of the body

TABLE 3. Geographic variation in characters of pholidosis.

Character	Population 1	Population 2	Population 3	Population 4	Population 5	Population 6
Sq	48-57 51.67±0.49	47-56 51.58±0.64	50-60 53.72±0.37	49-62 53.24±0.62	50-71 58.20±0.48	53-62 56.32±0.50
G	25-34 29.80±0.41	24-34 28.65±0.71	24-35 27.44±0.52	25-34 30.28±0.47	25-41 31.54±0.46	29-25 31.84±0.40
P. fm.	10-15 12.33±0.21	10-14 12.24±0.28	9-14 11.52±0.27	10-14 11.90±0.29	12-17 14.05±0.16	10-14 12.63±0.19
Ventrals	31-36 33.80±0.21	30-34 32.88±0.25	31-34 32.92±0.18	33-37 34.67±0.23	32-38 34.39±0.22	32-35 33.74±0.20
Sqmc. cd.	25-36 31.07±0.47	25-35 29.64±0.62	26-35 30.80±0.49	29-34 30.57±0.31	27-39 32.88±0.41	27-34 30.79±0.45
Labials	9-12 10.93±0.18	10-12 10.94±0.14	10-15 11.72±0.23	9-12 11.14±0.19	10-14 11.94±0.13	10-13 11.68±0.20
Infralabials	6-9 7.37±0.14	7-9 7.65±0.15	7-9 7.54±0.13	7-11 7.86±0.20	7-10 7.81±0.11	7-9 7.47±0.16
Dorsal scales along spine	117-137 129.00±0.89	112-134 124.47±1.37	120-139 129.96±0.98	118-138 127.62±1.12	140-162 148.29±1.09	- -

FIG. 3. Geographic variability of scale number around mid-body (Sq.) in *Eremias przewalskii*.

and tail are white. Each body flank has one row of blue ocelli, not clearly visible in all fixed specimens. The general pattern is preserved in lizards from the lakes Alag-Nuur (sample 3) and Bon-Tsagan-Nuur

FIG. 4. Geographic variability of the porac femorales (P. fm.) in *Eremias przewalskii*.

(sample 4). However, those from Alag-Nuur have black color, while those from Bon-Tsagan-Nuur range from light to dark brown. The blue spots are bright. In the south [South-Gobi Aymag (5) sample]

lizards have the most bright and contrasting dorsal pattern (Figs. 5, 6 and 7). It is black and white, with the pileus pattern as bright. The ventral surface is white, but a slightly yellowish tint may be present. Regarding the blue spots on the body flanks, one could not make a definite conclusion. Fixed specimens may have blue spots, but these, as a rule, are positioned on the parts not characteristic for their usual occurrence. This could be a consequence of preservation in alcohol. Intrapopulation pattern polymorphism is characteristic of sample 2 from the Beger-Nuur Lake environs (Fig. 6), where the following specimens occur: 1- with black wavy spots (combined with white ones) on the body flanks, with a brown tint in the mid-dorsum; 2- with an unclear dorsal pattern and three rows of white spots (surrounded by black) on the body flanks; under these rows is a row of blue ocelli on each side; 3- with a pattern of thinner transversally elongated, black, wavy stripes, connected with each other or isolated, and with single white ocelli. The same pattern covers also the anterior one third of the tail, and is then divided into single small spots of dark color. The head in most cases is light-gray or beige, with a pattern on the parietal and temporal parts (mainly in specimens with a fine pattern - type 3). These blue spots are more or less visible in almost all the specimens.

### Discussion

Analysis of *Eremias przewalskii* intrapopulation size and proportions variability in Mongolia reveal clear sexual differences. They are expressed to different degrees in populations studied from the western, southern and southeastern parts of Mongolia. These differences do not concern, as a rule, the absolute sizes of the body (L) but relatively, length of the head, limbs and tail are larger in males than in females. We have also shown dimorphism of some characters of pholidosis in our material, including samples of adult specimens from each locality. Such sexual dimorphism had not been shown by Szczerbak (1974) during his researches of Tuva (Russia),



FIG. 5. The dorsal surface pattern in *Eremias przewalskii* from the northern coast of Char-Us-Nuur Lake, Somon Urdgol (=Chandman) sample 1.



FIG. 6. The dorsal surface pattern in *Eremias przewalskii*: from Gobi-Altai Aymag, Lake Beger-Nuur, sample 2.



FIG. 7. The dorsal surface pattern in *Eremias przewalskii*: from South-Gobi Aymag, sample 5.

northwestern Mongolia, China and single specimens of *Eremias* from southern Mongolia. The number of scales around the 9-10th rings of the tail differs in all the samples and the number of ventrals differs in the samples from Gobi-Altai Aymag (3) and East-Gobi Aymag (6). The coloration and the pattern of adult specimens have no significant sexual differences.

The wide range of pholidosis variability is clearly expressed to various degrees in all the samples from Mongolia. Dely (1979, 1980) speculated that an explanation of the high variability may be ecological isolation and interbreeding, connected with relatively low population density and low fecundity of the females. It was interesting to find 2 frontonasals in 25% of investigated lizards from southern Mongolia (Orlova, 1989) together with other characters (larger size, contrasting coloration, larger number of scales around the midbody, number of dorsal scales between parietals and level of anus, etc.). It is curious not only as a trait reflecting the isolation of these populations that the presence of 2 frontonasals is normal for *E. argus* and occurs in *E. multiocellata* as an exception. It may suggest a close relationship of these species, noted by previous authors (Bedriaga, 1912; Szczerbak, 1974). Szczerbak has not mentioned specimens of *E. przewalskii* with 2 frontonasals in Mongolia and did not report this in the description of the species and nominative subspecies, while Strauch (1876) indicated it in the description of his new species.

Strauch's descriptions of 3 species from China were based on the variability of coloration and pattern of *E. przewalskii*. Specimens with a "rough-spotted" pattern consisting of black or dark-brown stripes or spots drawn in transverse direction were described as *E. przewalskii*. Specimens with a "netted" pattern consisting of fine, fused, wavy, interwoven lines were described as *E. brachydactyla*. The third type of pattern was designated by Szczerbak (1970) as "transitional", intermediate between the first and the second characteristics of *E. kessleri*. Within Mongolia, these lizards' coloration

and pattern are also variable, but among specimens studied we have not found "rough-spotted" ones. In China, where the dorsal pattern of the lizards is known to be variable, nobody has mentioned the blue spots on the body flanks, which are characteristic of *E. przewalskii* in the western part of Mongolia. Strauch (1876) gave detailed descriptions of single specimens of the new species, but not in one case did he note blue spots. Possibly, southern Mongolian specimens also do not have these spots. In this connection the specimen of *E. kessleri* (ZIN 5145: collection of Zoological Institute, Russian Academy of Sciences, St. Petersburg) from the lower Tarim, collected by N. M. Przewalskii, is interesting. Bedriaga (1912:577) wrote about this specimen: "Das Originalstück der *E. kessleri* stammt aus Gansu; ein anderes soll von Przewalski am unteren Tarim erbeutet worden sein (N 5145). Diese weit westlich vorgerückte Fundstelle und die Tatsache, dass nur ein einziges, an den Seiten sonderbarerweise blau geaugtes Individuum von dort mitgebracht worden ist, hat in mir Anfangs einige Zweifel hinsichtlich der Herkunft desselben erweckt; dock überzeugte ich mich nachtraglich, das es im Jahre 1878 dem akademischen Museum übergeben worden ist, und dass der General vorher, nämlich in den Jahren 1876 und 1877, aus seiner Reise nach dem Lob-nor in Wirklichkeit am Unterlauf des Tarim-Flusses gewesen ist."

In no samples from the enormous Mongolian territory were such drastic pattern differences recorded, as in specimens from China, where lizards with 2 pattern types coexist (collections of the Zoological Institute, Academy of Science, St. Petersburg; T. J. Papenfuss and J. R. Macey, pers. comm.).

At present, *E. przewalskii* is considered a species with two subspecies: nominative *E. p. przewalskii* (Strauch) (southern Mongolia and northern China) and *E. p. tuvensis* Szczerbak (Tuva, Russia, and western Mongolia) (Szczerbak, 1970, 1974). Dely (1979, 1980), analyzing the variation of external morphological

characters of lizards from Mongolia, noted the population from the southern Gobi as most clearly distinct. While the author did not have the possibility of studying the materials from Tuva, Russia he suggested the existence of two subspecies of *E. przewalskii*. At the same time, each of the populations investigated by him was referred to the nominative subspecies.

Determination of the structure of the species as a whole will depend upon future research on *E. przewalskii* from China (with detailed analysis of intrapopulational and geographic variability, including biochemical analysis).

### Acknowledgments

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## Feeding Ecology of the Caucasian Salamander (*Mertensiella caucasica*), with Comments on Life History

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**Abstract.** -The feeding and developmental ecology of the Caucasian Salamander (*Mertensiella caucasica*) were studied in western Georgia. Age changes of larval feeding rate are weak. The main food of larvae consists of gammarids and insects. Larval prey size spectrum widens and displaces to more large objects during ontogenesis. However age, diurnal, seasonal and habitat differences in diet are weak. The majority of preys are consumed with negative electivity. During metamorphosis feeding does not cease. A review of literature on adult Caucasian Salamander feeding is presented. A comparison of larval development data with skeletochronology suggests that metamorphosis takes place after the second wintering. Three to five annual rings were counted in tubular bone diaphyses of mature specimens.

**Key words:** Amphibia, Caudata, Salamandridae *Mertensiella caucasica*; Caucasus Mountains, Georgia, feeding, larvae, electivity.



FIG. 1. Stream habitat of *Mertensiella caucasica* in Akhaldaba Region, Georgia.

### Introduction

The Caucasian Salamander, *Mertensiella*

*caucasica* (Waga, 1876) is a stenobiont species which lives near rocky streams in mountain forests of western Georgia and adjacent areas of Turkey (Figs. 1, 2, and Plate 1). Members of this relict genus were widely distributed in Europe in the Pliocene (Borja and Mlynarski, 1979). Data on Caucasian Salamander ecology are very poor, especially on feeding ecology. The latter are limited to food composition and feeding behaviour in captivity (Knoblauch, 1905; Lantz, 1911; Mertens, 1942; Obst and Rotter, 1962; Rotter, 1958; Wolterstorff, 1942), speculations on diet based on invertebrate fauna in the environment (Cyren, 1911; Hemmerling and Obst, 1968; Lantz, 1911; Mertens, 1942), and observations and dissections of single specimens (Basoglu and Özeti, 1973; Ekvimishvili, 1940; Knoblauch, 1905; Nikolsky, 1913; Sikmashvili, 1970; Wolterstorff et al., 1936). Quantitative data on adult diet are presented only in papers by Bozhansky and D.V.Semenov (1982) and Ekvimishvili (1948).

### Methods

From June to August, 1985 the ecology of the Caucasian Salamander was studied in the Akhaldaba environs, Borzhomi (41° 51' N 43° 23' E) region, Georgia. In the same



FIG. 2. Mountain forest habitat of *Mertensiella caucasica* in Akhaldaba Region, Georgia.

months of 1986 additional material on newly metamorphosed salamanders was collected. Adults were measured (snout-vent length- L., tail length- L. cd.), marked by toe-clipping and released. Besides that, we have captured larvae and newly metamorphosed specimens. Animals of these two age groups as well as adult clipped toes were fixed immediately in 5% neutral formaldehyde solution.

Before treatment, fixed larvae were immersed in water for several hours. I measured them by ocular-micrometer under a stereoscopic microscope or (larger specimens) by vernier calliper with a precision of 0.1 mm. Then I dried them with filter paper and weighed them with a precision of 1 mg. To determine the salamander age, numbers of annual rings in femoral (larvae) or finger (adults) bone sections were counted (according to

Smirina and Sofianidu, 1985). For the sake of species' conservation I didn't make dissections of mature salamanders. I have obtained information on their feeding from the literature cited above.

To study larval and newly metamorphosed salamander feeding, entire digestive tracts were obtained. Their contents were studied under a microscope. The bulk of food was dried with filter paper and weighed with a precision of 0.1 mg. Food objects were identified and measured under the microscope. From their linear dimensions, reconstructed weights were determined (for details see Kuzmin, 1984 a, 1984b).

I have determined percentages of each prey category by its weight and number. Because of uncertainty of prey length and mass as measures of its size availability for

Caudata, ratio  $d_{\max}/L_t$  or. (see Kuzmin, 1985) was used, where  $d_{\max}$ =maximum prey diameter (width or height),  $L_t$  or.=width of amphibian mouth (between hind angles of lip folds). It must be noted that some later identical parameter was successfully used in *Onychodactylus japonicus* feeding behaviour investigations (Kusano and Hayashi, 1985).

Feeding rate in different groups of salamanders was compared by digestive tract-fill indices:

$$Y = \frac{m \cdot 1000\%}{M \cdot m}$$

where  $m$ =food mass,  $M$ =total consumer mass. Caloric content of different preys was determined using the methods of Cummins and Wuysheck (1971). After this, the mean caloric content of food was counted.

Trophic niche overlap was determined using Morishita similarity index in the form:

$$I_{\lambda} = \frac{2 \sum_i p_{ij} p_{ik}}{\sum_i (p_{ij}^2 + p_{ik}^2)}$$

where  $p_{ij}$ =percent of  $i$ -th component in the diet of  $j$ -th predator,  $p_{ik}$ =percent of  $i$ -th component in the diet of  $k$ -th predator, and  $0 \leq I_{\lambda} \leq 1$ .

To estimate feeding electivity the contents of larval digestive tracts were compared with the invertebrate fauna of the stream. Invertebrates were counted after their total sampling from stream pools where salamanders were collected. The feeding electivity is estimated using Ivlev's formula:

$$E = \frac{r_i - p_i}{r_i + p_i}$$

Where  $r_i$ =percent of  $i$ -th component in the diet,  $p_i$ =its percent in environmental complex, and  $-1 \leq E \leq +1$ . Observations on the feeding behavior in captivity were also conducted (for methods see Kuzmin,

1986).

## Results

### Body Size and Skeletochronology

All larvae sampled are clearly divided into 3 groups by their  $L_t$ : 15.4-19.5 mm (106-108 mg), 23.7-27.5 mm (330-644 mg) and 29.0-35.4 mm (632-1400 mg). These three groups morphologically differ from each other (Fig. 3). Size groups 1 and 2 contained mainly specimens that were born in the given year. Annual rings in their femoral bone sections are as a rule absent (Fig. 4). Larger larvae (size group 3) had one annual ring, commonly only vaguely expressed. On the femoral bone sections of two newly metamorphosed animals (captured in June and August 1985) one annual ring is also recognized. From 10 marked adults captured 13 June, 1985 ( $L_t = 66.7 \pm 1.6$  mm;  $L_{cd} = 171.5 \pm 4.3$  mm) annual rings were successfully counted in 7. Each specimen had on the average  $3.57 \pm 0.30$  (3-5) rings.

### Diet and Feeding Behaviour

*Quantity of food consumed.*—In laboratory conditions Caucasian Salamanders lived some time on endogenous yolk and transfer to active feeding takes place at larval size group 1 (I. A. Serbinova, pers. comm.). It must be noted that all the smallest larvae found in nature belong to group 1. The latter already feed upon exogenous prey with high intensity. Yolk is not recognized in their digestive tracts. Furthermore, digestive tract-fill index ( $J$ ) changes slightly with age. Its values are similar in different months and in different size groups (July: group 1-  $40.1 \pm 5.4\%$ ; 2-  $34.1 \pm 4.2\%$ ; 3-  $41.5 \pm 15.2\%$ . August: group 2-  $41.8 \pm 7.2\%$ ; 3-  $34.8 \pm 3.0\%$ ). Just after metamorphosis  $J$  remains almost on the same level ( $34.8 \pm 5.5\%$ ). There are little differences in  $J$  values between the larvae from medium and lower stream currents ( $39.5 \pm 4.3\%$  and  $35.4 \pm 7.0\%$  respectively). Salamander larvae are more active at night than in the daytime. The values of  $J$  are influenced by this ( $L_t = 16-$

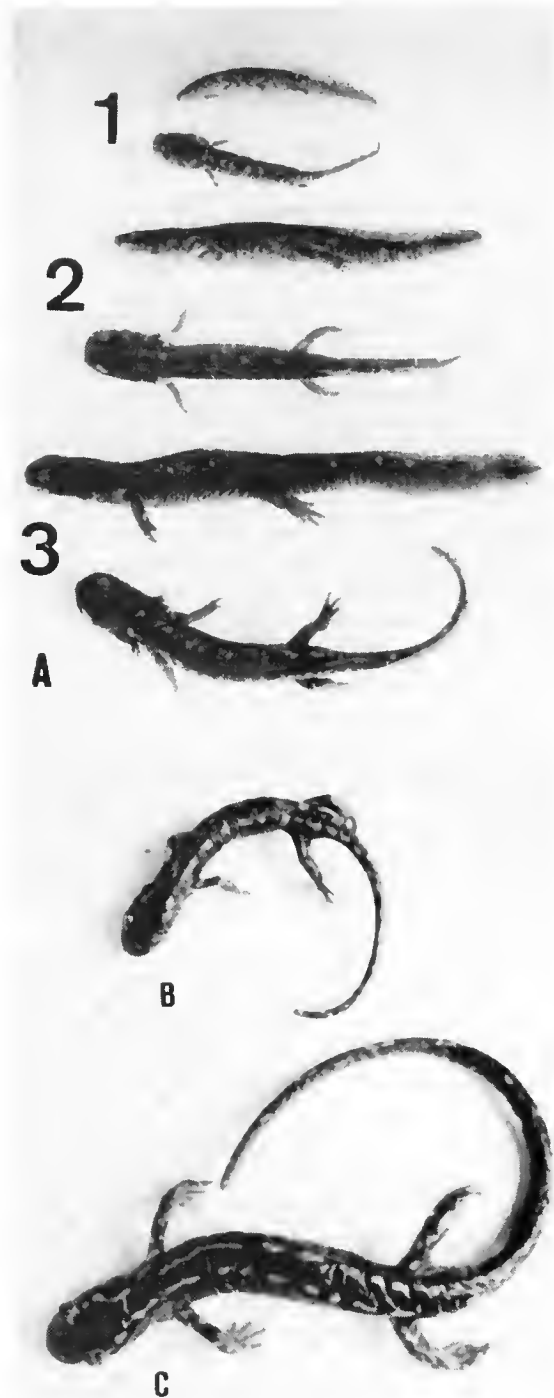


FIG. 3. Caucasian Salamanders of different ages. A- larvae of three size groups (1-3); B- newly metamorphosed specimen; C- adult specimen.

17 mm: 01 h - 53%; 12-13 h - 40%).

Mean caloric content of food of different

groups has a weak monthly variation (1.01-1.24 cal/mg).

Average number of preys per digestive tract increases with larval size from  $3.00 \pm 0.43$  (group 1) to  $4.88 \pm 1.43$  (group 3).

Food spectrum of larvae widens in ontogenesis. Along with widening, there is a marked displacement of prey size spectrum to larger and larger objects (Table 1, A, B). Maximum values of  $d_{\max}/L_{t.or}$  reached 62.6%.

The main food of salamander larvae are gammarids and larval insects (Table 2). The smallest invertebrates, *Ostracoda* and *Hydracarina*, occur in the diet of smallest salamanders. Generally, age changes of diet are weak (see Table 2). Food similarity ( $I_k'$ ) by prey numbers are: for groups 1 and 2 - 0.73; 1 and 3 - 0.82; 2 and 3 - 0.61. For weight proportions they are 0.80, 0.73, and 0.52, respectively. Likewise in summer (group 2 - June and August:  $I_k' = 0.97$  by prey number and 0.50 by weight) and day (group 1: 12-13h and 01 h:  $I_k' = 0.82$  and 0.75) larval diets changed very slowly. Larval food differences are slightly more apparent in medium and lower stream currents ( $I_k' = 0.59$  and 0.42).

Metamorphosed salamander food composition changes sharply due to habitat change (see Table 2). Terrestrial insects become dominant. Food becomes more and more diverse with age. Crustaceans, arachnids and insects are the main adult salamander's prey (see Table 2). At the same time interpopulational differences in their feeding are insufficient: for Akhaldaba (Bozhansky and Semenov, 1982) and Baniskhevi (Ekvtimishvili, 1948) samples  $I_k' = 0.87$  by numeric percents. Sexual differences in diets are absent (Bozhansky and Semenov, 1982).

Apart from food items, plant remains, parasitic nematods (in newly metamorphosed salamanders) soil and sand were found in the digestive tracts of

different stages.

**Feeding electivity.**—This has been studied in June larvae. *Limoniidae* are positively elected by the larvae of group 3 ( $E=+0.52$ ), whereas in the diet of younger ones, these insects are not found. Electivity to a close family, Chironomidae, decreases during ontogenesis (group 1:  $E=-0.13$ ; 2:  $-0.42$ ; 3:  $-1$ ). The larvae of group 3 ignored the smallest object - *Ostracoda* ( $E=-1$ ). This prey is consumed almost unselectively by smaller larvae (group 1:  $E=+0.03$ ; 2:  $-0.05$ ). Gammaridae are utilized with weak electivity (1:  $+0.06$ ; 2:  $-0.32$ ; 3:  $+0.23$ ). Salamanders of all three groups negatively selected *Trichoptera* (1:  $-0.73$ ; 2:  $-0.42$ ; 3:  $-0.43$ ).

**Feeding behaviour.** In captivity, larvae ( $L.=30-35$  mm) noticed the large prey (Gammaridae 3-10 mm long, *Planaria* about 10 mm) from distances of 10-16 mm, approached up to 2-3 mm and attacked. *Planaria* orientation in the mouth takes 10-20 seconds; larger gammarids, about 40 seconds. In natural conditions salamander larvae exhibit diurnal foraging more frequently than adults. Among the latter this is observed mainly in wet and dark places. During the winter salamander feeding ceases. In the summer they forage in shallow water more frequently than in early spring and autumn (Ekvtimishvili, 1948). Under the water adults waited for moving invertebrates (Knoblauch, 1905). This may be an adaptation to foraging in a lotic environment. According to Knoblauch (1905), salamander feeding requirements do not decrease even at  $9^{\circ}\text{C}$ . My observations reveal the upper thermal limit of adult foraging activity as  $23-25^{\circ}\text{C}$  range. At these temperatures animals respond to approaching invertebrates, but don't make attempts to catch them.

### Discussion

From spring to autumn larvae of different size groups are found in streams (Berg, 1910; Cyren, 1911; 1968; Hemmerling and Obst, 1968; Koroljov, 1986; Mertens, 1942; my data). Evidently

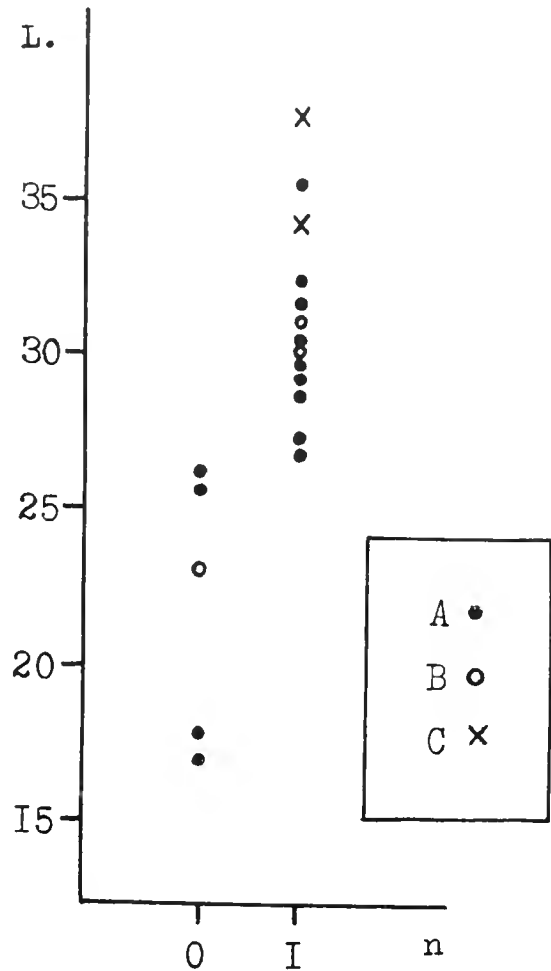


FIG. 4. The number of annual rings (n) in the sections of femoral bone diaphyses of young Caucasian Salamanders of different body length (L.). A- larvae, June; B- Larvae, August; C- newly metamorphosed specimens.

group 1 consists of recently hatched larvae that have begun their active feeding. Group 3 is metamorphic. Their share in larval samples markedly decreased to August due to entering land by metamorphs. Thus, the lack of annual rings in the bones of most of the specimens from groups 1 and 2 indicates their birth was mainly in the given year. Animals larger than 27 mm and newly metamorphosed specimens had one annual ring, so they had survived one wintering. The largest specimens of a given birth year only slightly differ from the smallest that had wintered. This could be explained by a prolonged salamander breeding period.

TABLE 1. Prey size composition of Caucasian Salamander larvae (June, 1985).

A. Proportions  $d_{\max}/L.t. or., \%$ 

$d_{\max}$ , mm	Larval size groups		
	1 (n=13)	2 (n=9)	3 (n=9)
0.1-0.5 (0.3)	8.2	5.5	4.5
0.6-1.0 (0.8)	21.8	14.7	11.9
1.1-1.5 (1.3)	35.3	23.9	19.4
1.6-2.0 (1.8)	49.0	33.1	26.9
2.1-2.5 (2.3)	62.6	42.3	34.3
2.6-3.0 (2.8)	-	51.5	41.8

B. Proportions by numbers of prey with different  $d_{\max}$ , %

$d_{\max}$ , mm	Larval size groups		
	1	2	3
0.1-0.5 (0.3)	41.0	12.9	10.7
0.6-1.0 (0.8)	41.0	41.9	14.3
1.1-1.5 (1.3)	10.3	16.1	10.7
1.6-2.0 (1.8)	5.1	12.9	39.3
2.1-2.5 (2.3)	2.6	12.9	17.9
2.6-3.0 (2.8)	-	3.2	7.1

Thus, Caucasian Salamander larvae completed their metamorphosis during the next year after hatching. So the opinions of a 3 year (Koroljov, 1986) or less than 1 year (Zhordaniya, 1975) larval period of the Caucasian Salamander are not confirmed.†

According to some authors (Bozhanski

† If the first wintering occurs in larvae just before the start of their hind limb skeleton ossification, the annual ring of this wintering will be absent. If so, the first annual ring must reflect the second wintering. If this is confirmed, Tarkhnishvili and Servinove's (in Press) proposal of a two-year larval period for *M. caucasica* is true.

and Semenov, 1982), Caucasian Salamanders reach their maturity after the second wintering. The secondary sex character, male dorsal spine on the tail base, appears when the total length ( $L.+L.cd.$ ) reaches about 130 mm (Hemmerling and Obst, 1968; Obst and Rotter, 1962). My skeletochronological data do not allow me to make a perfect determination of adult salamanders age, because of the lack of data on the inner annual ring resorption rate. Therefore, we must consider their age to be not less than the number of annual rings (after Smirina and Sofianidu, 1985), i.e. 3-5 years.

The main changes of salamander trophic niche during ontogenesis take place under

TABLE 2. Prey taxonomic spectrum of *Mertensiella caucasica* in ontogenesis. 1-3 - larval size groups; juv. - newly metamorphosed specimens; by horizontal: 1-% by prey number; 2-% by prey weight. For adults from Baniskhevi (n=67) data of Ekvümlshvili (1948); from Akhaldaba (n=21) data of Bozhansky and Semenov (1982).

Prey taxa	June						August		June		June-Sept.	Sum-mer
	1 (n=13)		2 (n=9)		3 (n=9)		2 (n=11)		juveniles n=7		adult n=67	adult n=23
	1	2	1	2	1	2	1	2	1	2	1	1
OLIGOCHAETA	-	-	3.6	0.59	-	-	-	-	-	-	2.3	1.7
GASTROPODA	-	-	-	-	-	-	6.4	13.2	-	-	7.6	6.7
Crustacea												
Ostracoda	13.9	0.10	14.2	0.74	-	-	17.0	0.62	-	-	-	-
Gammaridae	38.9	36.3	17.9	25.1	55.2	77.2	29.8	48.5	-	-	2.0	5.9
Asellidae	2.8	2.7	-	-	3.7	7.8	-	-	20.0	28.9	-	-
Oniscidae	-	-	-	-	-	-	-	-	-	-	23.9	16.9
MYRIAPODA												
Diplopoda et Chilopoda	-	-	-	-	-	-	-	-	4.0	4.3	5.1	4.2
ARACHNIDA												
Acarina	2.8	0.14	-	-	-	-	-	-	12.0	0.97	1.5	0.80
Aranei	-	-	-	-	-	-	-	-	4.0	0.32	2.5	0.80
Opiliones	-	-	-	-	-	-	-	-	-	-	2.5	0.80
Pseudo-scorpiones	-	-	-	-	-	-	-	4.0	0.32	0.32	2.5	0.80
INSECTA												
Collembola	-	-	-	-	-	-	-	-	40.0	11.4	4.6	-
Blattoidea	-	-	-	-	-	-	-	-	-	-	-	0.80
Ephemeroptera l.	13.9	18.0	39.3	45.7	20.7	8.5	36.2	12.6	-	-	0.50	-
Plecoptera l.	-	-	-	-	-	-	-	-	-	-	4.6	-
Lepidoptera l.	-	-	-	-	-	-	-	-	4.0	21.5	-	-
Lepidoptera i.	-	-	-	-	-	-	-	-	-	-	-	0.80
Coleoptera i.	8.3	16.8	10.7	9.7	-	-	4.3	8.8	-	-	14.5	3.3
Tricoptera l.	2.8	13.7	7.1	16.8	6.9	4.7	-	-	-	-	1.3	17.8
Orthoptera	-	-	-	-	-	-	-	-	-	-	1.3	17.8
Dermaptera	-	-	-	-	-	-	-	-	-	-	-	0.80
Hemiptera	-	-	-	-	-	-	-	-	-	-	1.3	-
Hymenoptera	-	-	-	-	-	-	-	-	-	-	1.3	-
Chironomidae l.	16.7	12.2	7.1	1.4	-	-	2.1	0.11	4.0	4.3	-	-
Limoniidae l.	-	-	-	-	13.8	1.9	2.1	0.77	-	-	-	-
Tipulidae l.	-	-	-	-	-	-	2.1	15.4	-	-	-	-

l.-larvae; i.-imago

the transfer from endogenous to exogenous feeding and, to a smaller degree, at metamorphosis. The rest of the time food changes are insignificant. This weak feeding variability is in accordance with the results of single specimen dissections from different parts of the species range (Basoglu and Ozeti, 1973; Knoblauch, 1905; Nikolsky, 1913; Wolterstorff et al., 1936).

Some authors (Hemmerling and Obst, 1968; Mertens, 1942) considered larval size variability to be a result of their different food provisions. But the data on larval age presented above together with weak age and spatial variability of digestive tract-fill index and diet confirms the opposite. A shortage of small invertebrates in streams, however, could be a factor influencing the comparatively large sizes Caucasian

Salamander larvae feed on, as compared with larvae of limnophilous tailed amphibians (Cyren, 1911). Narrow trophic spectrum consisting of relatively large invertebrates as far as low occurrence of small forms in stream samples served as its indirect confirmation.

Positive electivity in larval feeding is weakly expressed. Evidently, their diet reflects mainly the available invertebrate composition in the environment. A low percentage of larval *Trichoptera* in salamander diets may be connected with their low electivity. Probably the latter is due to the difficulty of swallowing this energetically unprofitable prey (sand case mass could be of 5-6 times heavier than the food object).

The environmental conditions of the Caucasian Salamander are very uniform and almost unchanged since Pleistocene (Wolterstorff et al., 1936). Indirect confirmation of an endemic ecological pattern is the parasitological data. The Caucasian Salamander is the host of four parasitic nematod species. Three of them are specific for this amphibian (Lomakin, 1982; Sharpilo, 1976, 1978; Timofeeva and Sharpilo, 1979). Thus, the high Caucasian Salamander trophic niche stability at each step of its life history reflects the stenobiont state of this species in the western Transcaucasian relict ecosystems.

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## Preliminary Research on the Function of the Eggshell in the Chinese Alligator (*Alligator sinensis*)<sup>†</sup>

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**Abstract.** -There is a layer of mucous material on the eggshell of freshly laid Chinese Alligator eggs. Alligator eggshells have different functions in different periods of embryonic development. Over 95% of the eggshell consists of calcite and calcium carbonate. The freshly laid egg is strong and rigid to withstand the weight of the adult female alligator crawling over the closed and compacted nest. As incubation proceeds, erosion craters and cracks appear on the surface of an eggshell. This change of the eggshell is adapted to more efficient oxygen requirements and prevents the egg from dehydration or from too much water flowing into the egg, as the embryo rapidly develops. The eggshell does not provide calcium to supply embryonic developmental demands. The eggshell membrane plays an important role in the antimicrobial defence of the egg.

**Key words:** Reptilia, Crocodylia, Alligatoridae, *Alligator sinensis*, China, eggshell function

### Introduction

Ecological examination in the field and long term artificial culture has revealed that a series of changes appear in the Chinese Alligator's (*Alligator sinensis*) eggshell as the egg develops. These changes seem to relate closely with the alligators' embryonic development and climatic conditions. In order to study this relationship, in 1976 we made some observations and experiments on the change of the Chinese Alligator's eggshell in the course of incubation. In 1987 and 1988, we made some additional experiments.

### Methods

Experiments concerning the mucous material covering freshly laid eggs investigate its influence on egg incubation. Four clutches laid by a field alligator were marked as A, B, C, and D respectively. There were 21 eggs in clutch A (with 1 broken and 1 infertile), 17 eggs in clutch B, 20 eggs in clutch C and 18 eggs in clutch D (with 1 infertile). The eggs of clutches A and B were laid in the same day. Eleven

eggs from clutch A were selected randomly for the experiment, with 10 eggs for the control. Eight eggs of clutch B were selected randomly for the experiment, with 9 eggs for the control. The experimental eggs of clutches A and B were put together into group I. Control eggs were put together into group II. The eggs were laid one day earlier in clutch C than in clutch D. Each half of the eggs of clutch C and D used were put together in group III, the other half of the eggs were used for a control and were put together into group IV. Each egg of group I and III was washed slightly with gauze in 26°C distilled water, had its mucous material cleaned and was wiped dry. The eggs of group III and IV were submerged in oxygenated distilled water (27-28°C) for 8 hours. Then the four groups were set in an environmental chamber in the same condition and incubated at 30-32°C.

The next experiment investigated the influence of humidity on egg incubation. Eighty-seven eggs, which were laid by an artificially cultured alligator in the Anhui Research Center of Chinese Alligator Reproduction (ARCCAR), were selected randomly and divided into three groups. In group 1, humidity was maintained at 95% from 0 to 21 days after laying, at 80-85%

<sup>†</sup> This publication was previously published in Chinese by Chen and Liang (1990).

TABLE 1. The influence of the mucous material surrounding Chinese Alligator (*A. sinensis*) eggshells during incubation.

Groups	Eggs	Preparative treatment	Hatchlings	Average hatching (days)	Average time from puncture to emergence (hours)
I	19	Mucous material cleaned	16	62	10.5
II	19	None	18	58	4.6
III	19	Mucous material cleaned, submerged in distilled water 8 hours	3	64	31
IV	19	Not cleaned, directly submerged in distilled water for 8 hours	8	63	32

humidity from 22-40 days, and at about 90% humidity from 41 days to hatching. In group 2, the humidity of incubation was maintained at 95-100% humidity from the beginning to the end. In group 3, humidity was maintained at 85-95% and increased to nearly 100% all day respectively on the 10th, 30th, and 40th days of incubation. Generally, the embryonic developmental state was examined with lamp light at 20 day intervals. After group 3 was treated with high humidity, examinations were increased. Except for humidity, the rest of the incubation conditions of the three groups were similar, and temperature was maintained at 31-32°C. The method of determining the calcium and magnesium contents in the alligator's eggshell used by Gu et al. (1987) was adopted. The observations on morphological change of the alligator's eggshell in the course of incubation was primarily in ARCCAR.

### Results

The influence of mucous material around the alligator's eggshell on incubation is shown in table 1.

The Joanen and McNease (1977) experiment regarding the influence of washed and unwashed eggs in *Alligator mississippiensis* on egg incubation suggested that washed eggs had no influence on hatching rate, but their

emergent duration was extended. Our results on Chinese Alligator eggs show that washed eggs have an 84.2% hatching rate, while unwashed eggs have a 94.7% hatching rate (with the exception of infertile eggs). Incubation periods of washed eggs is delayed an average of 4 days and emergent duration is delayed an average of 5.9 hours. The experiments of groups III and IV indicated that after the eggs were submerged in distilled water for 8 hours, their hatching rates, hatching time and hatchling's emergent duration are very much influenced. Simultaneously, such hatchlings after emergence are weaker and grow slower.

Eggs in group III, in which mucous material was cleaned, have far lower hatching rates (15.8%) than unwashed eggs (42%) in group IV. We consider that this phenomenon probably is related to the mucous material around the eggshell. The mucous material possesses functions that protect the egg from both dehydration and too much environmental water flowing in. This may protect the early embryo from being effected by bad weather.

Clearly, this is of ecologically important significance, because female alligator's lay their eggs in an egg cavity piled with grasses. The initial constructed nest is loose, with free air circulation. When it is a fine day and temperatures are higher, water

rapidly evaporates easily leading to dehydration. Conversely, during continuous cloudy and rainy days, the rain easily permeates loose nests into the egg cavity and influences normal egg development. A small opaque white patch was observed on the top surface of the eggshell of a freshly laid Chinese Alligator egg. As incubation progressed, the patch expanded in width around the shell center and in length towards the ends of the shell. About one day after egg laying, it expands approximately 2/5 around the shell, 3/4 around in two days, and completely around the shell after three days. This band slowly extends in length, completely reaching the ends of the shell after about one month.

Ferguson (1982) has reported a similar change for *A. mississippiensis* eggshells and suggested a variety of explanations. One of these explanations is the development of erosion craters that rendered the calcite opaque, altering the optical properties of the shell. Another is a drying out of the eggshell due to polarization of the watery albumin towards the ends of the egg and an increase in porosity of the shell. We quite agree with his explanations. Erosion craters on the Chinese Alligator eggshell increased with the advance of incubation and then progressively became cracks. Some longitudinal cracks were observed on the eggshell around the third week of incubation. They became progressively more extensive in number and diagonal cracks appeared around the fifth week. Eventually these cracks became more and more extensive in size, number, and distribution up until hatching.

In chemical analysis of the Chinese Alligator's eggshell, calcium carbonate in calcite form reached above 95% (Gu et al., 1987). This is similar to *A. mississippiensis* eggshells (Ferguson, 1982). During examination of Chinese Alligator nests in the field, broken eggs were observed in nest cavities less than 1% of the time. Apparently, the freshly laid egg is strong and rigid to withstand the weight of the adult female crawling over the closed and compacted nest. In the initial

stage of incubation, due to nest material decay, the resulting acidic effect produces erosion craters on the eggshell surface. The eggshell's strength decreases, but at that time, the frequency of the female alligator crawling over nest tops decreases, so the eggshell isn't damaged. Moreover, there is better air circulation to allow more efficient oxygen requirements during rapid embryonic development. In addition, there is an increase of exchange between interior and exterior water of the egg. At that time, the average atmospheric temperature remains at approximately 29-30°C. It is uncertain whether water loss from the egg should be present or not. In order to explore the relations between incubative humidity and eggshell change, we made some experiments on the hatching rate of alligator eggs versus humidity.

As shown in table 2, group 1 had the best efficiency, and the hatching rate was 100%. Group 2 was hatched under high humidity throughout the incubative period. After the inter-period of incubation, there were 9 eggs which took in water, the eggshell swelling, and cracking. Four eggs were particularly swollen, and the eggshells membrane was cracked. Nine swollen eggs were approximately  $6.13 \pm 0.29$  cm in diameter, and  $4.46 \pm 0.21$  cm in width. Fifteen normal eggs, from the same incubative period, were randomly selected and measured  $6.14 \pm 0.27$  cm in diameter, and  $3.48 \pm 0.12$  cm in width. Both were similar in diameter, but the width of the former is about one centimeter larger than the latter.

Packard et al. (1979) reported that the water conductance of alligator eggs is five times higher than that of birds eggs, which is in keeping with the porous nature of the late alligator eggshell. Our experimental results agree with their report. The humidity of group 3 was 85-95% throughout the incubation period, and only on 10th day increased to nearly 100%. There were no unusual phenomenon to be observed. On the 30th and 40th day there was one and three dead embryos respectively. The above experiments indicate that high humidity in the inter-

TABLE 2. The effect of humidity on *A. sinensis* egg development.

Groups	Eggs	Humidity (%)			Hatchlings	Hatching rate (%)	Comments
		Ante-period	Inter-period	Post-period			
1	29	95	80-85	90	29	100	Normal hatching
2	27	over 95	Over 95	Over 95	23		9 swollen eggs eggshells cracking
3	31	85-95	85-95	85-95	27	87.1	One dead embryo after humidity increase on 30th day, three more dead after increase on 40th day

Note: Ante-period- from the beginning of incubation to 21st day; Inter-period- 22nd day of incubation to 40th day; Post-period- 41st day of incubation to hatching.

TABLE 3. The calcium and magnesium contents of Chinese Alligator (*A. sinensis*) eggshells.

Number	Sample	Mg content		Ca content	
		Number of tests	Means (%)	Number of tests	Means (%)
1	After hatch	4	0.04±0.02	4	38.6±0.1
2	After hatch	4	0.06±0.05	4	38.0±0.0
3	Infertile	4	0.18±0.05	4	38.7±0.1
4	Infertile	4	0.21±0.06	4	38.7±0.01
5	Infertile	4	0.22±0.04	4	38.4±0.0

period is adverse to embryonic development. In ARCCAR, incubative humidity was maintained at over 95% (hatching rate about 90%) throughout the incubation period before 1986. In 1987 and 1988, humidity remained at about 95% in the ante-period and was decreased to 80-90% during the inter- and post-period. The hatching rate was over 95%, and hatchlings were strong. Both survival rate and growth state were better. In addition, according to observations in the field which happened to be during the rainy season in the ante-incubation period, nest humidity remained at more than 95%. High humidity within the nest can prevent water loss in the embryo.

Weather in the wild changed, with clear days and decreasing rainfall after the third week of incubation (inter- and post-period). Humidity within nest cavities measured in the field averaged about 80-85%, and the atmospheric temperature averaged 30-31°C. At that time, some longitudinal cracks appeared on the eggshells. As incubation

proceeded, the cracks became progressively more extensive in size and number. Then the exchange between interior and exterior water of eggs increased as humidity within the nest cavity decreased. But at that time, the corneous layer within the skin of the alligator embryo was well developed allowing it to depend less on the surrounding humidity. Clearly, such incubative humidity is adapted to the change of the eggshell. In addition, the cracks progressively increased in size and number to let more and more air through during the growth and development of the alligator embryo. Thus, these changes of the eggshell are not only to satisfy developmental needs, but also to adapt to environmental climatic conditions. The eggshell has different functions at different periods of embryonic development.

Jenkins (1975) estimated that embryos of *Crocodylus novaeguinae* obtains between 1.7 and 2.4 times as much calcium from the shell as from the egg contents. Ferguson (1982) has reported the fact that

embryos of *A. mississippiensis* obtains much less calcium from the eggshell than either birds or turtles, indicating that it should be possible to grow normal alligators using shell-less culture techniques.

Gu et al. (1987) have analyzed the calcium and magnesium contents of Chinese Alligator eggshells (Table 3). As shown in table 3, calcium contents in eggshells after hatching are similar to infertile eggs not incubated. This indicated that the calcium content in eggshells which underwent incubation for about two months did not decrease. This is greatly different from bird embryos which obtain a large amount of calcium from eggshells. The experiment proved that alligator eggshells provide very little or no calcium for embryonic developmental. Thus, the eggshell does not store calcium. A lot of experiments of artificial incubation made in ARCCAR indicate that if Chinese Alligator eggs are damaged due to various causes, so long as the eggshell membrane is not breached, and temperature and humidity is well controlled, the eggs will develop normally; their hatching rate still reached over 80%. But if the membrane is punctured, microbes easily invade and the eggs rot and stink. This suggests that the eggshell plays an important role in antimicrobial defense of the egg.

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## Electrocardiogram Research on the Chinese Alligator (*Alligator sinensis*)

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**Abstract.** -This paper is a report on the determination and analysis of the electrocardiogram of the Chinese Alligator (*Alligator sinensis*) under conditions of different air temperatures all year round. From the determination and analysis mentioned above, we discovered that the electrocardiogram of the Chinese Alligator consists of a P wave, QRS waves and a T wave.

**Key words:** Reptilia, Crocodylia, Alligatoridae, *Alligator sinensis*, China, electrocardiogram.

### Introduction

The Chinese Alligator (*Alligator sinensis*) is a species of crocodylian endemic to China. In 1987, we began to collect data about the electrocardiogram of Chinese Alligators under conditions of different air temperatures throughout the year at the Anhui Research Center of Chinese Alligator Reproduction. We hope that these data may be applied to studies on growth, reproduction, ecology, and physiology of Chinese Alligators. Here is the detailed report of the results.

### Methods

The Anhui Research Center for Chinese Alligator Reproduction supplied nine 6 year-old adult female Chinese Alligators weighing 7.3 to 14.6 kg for the experiments. Using a XDH-3 hot-pen electrocardiograph made in China, we recorded I, II, and III standard limb leads with the standard voltage of 1 mv=10 mm at the paper passing speed of 25 mm per second. Laying on its back with four legs fixed to the operating table, the unanesthetized Chinese Alligator's electrocardiogram was determined by having four needle-like electrodes made by ourselves being placed at the four points beneath the skin which are relevant to standard limb leads after it calmed down.

### Results

1). The amplitudes of Chinese

Alligators' electrocardiogram waves are small. Electrocardiogram waves of I standard limb lead are so low, even the components of it can hardly be distinguished. Therefore the data used in this paper are all from the determination from the II standard limb lead.

2). The electrocardiogram of a Chinese Alligator basically consists of a P wave, QRS waves and a T wave (Fig. 1). Both the P wave and the R wave are positive, the T wave is reverse, and the QS waves are not clear.

3). The amplitude of the Q wave, which is made up of Pr and Pl is the smallest. The time continued, which is at an average of about 0.18 seconds, is short. The time difference between Pr and Pl is about 0.09 seconds. The crests of the P wave are round and the rate of appearance is moderate (Table 1). Data show that the P wave does not appear during the hibernating period (from the last-ten-day period of November to the last-ten-day period of April of the next year). The rate of appearance is the highest from May to June.

4). QRS waves are the main waves. The amplitude of the R wave is the greatest and the crests of it are pointed. The time continued, which is at on average about 0.14 seconds, is quite short. The rate of appearance is the highest (Table 1).

5). The amplitude of the reverse T

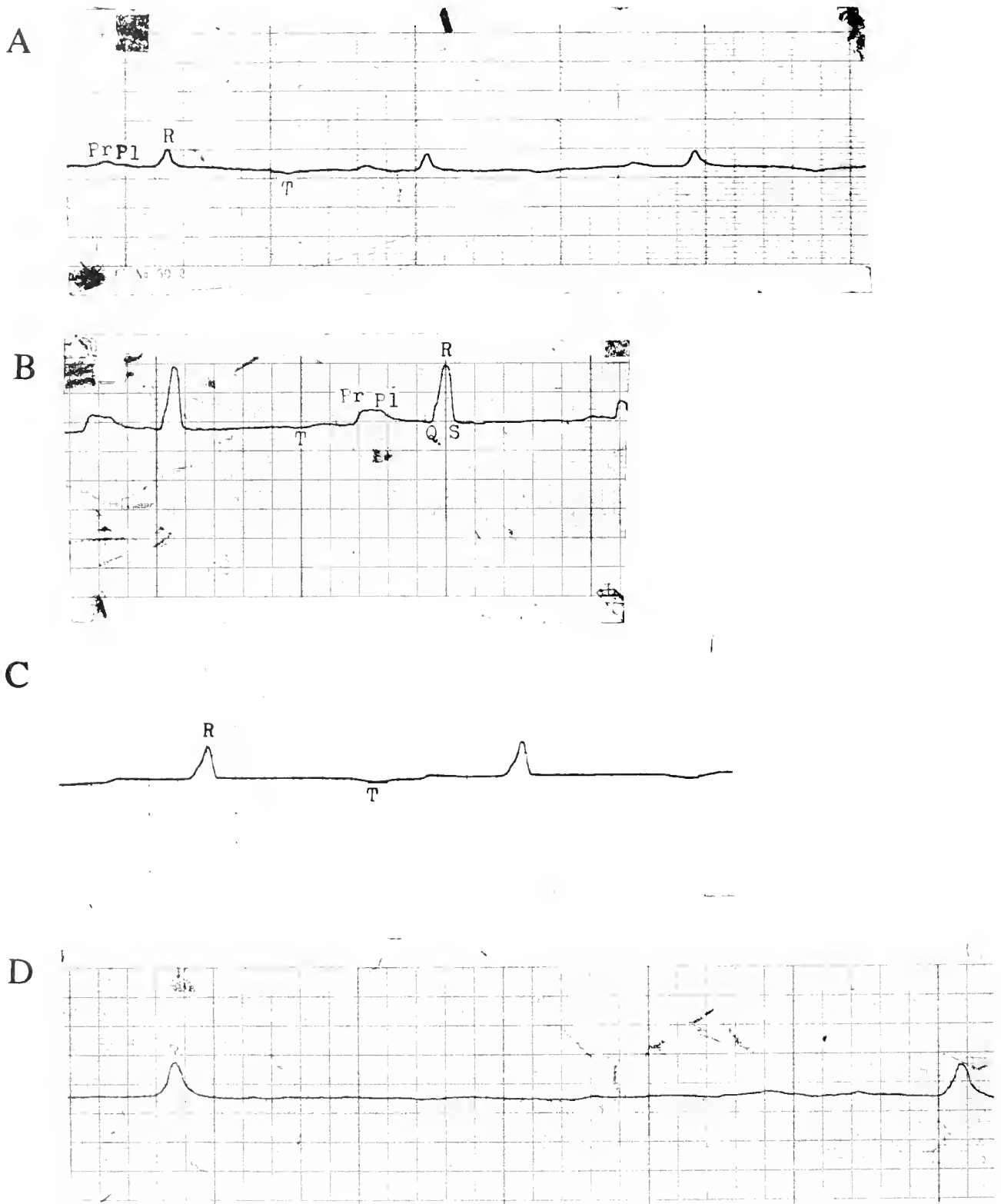


FIG. 1. The electrocardiogram of the Chinese Alligator (*Alligator sinensis*) under conditions of different temperatures as determined in 1988. A. April 8, 14° C. B. June 20, 21° C. C. Oct. 3, 16° C. D. Dec. 9, 4° C.



TABLE 1. Changes in the electrocardiogram of the Chinese Alligator at different temperatures.

	14°C (Apr. 8)	21°C (Jun. 20)	24°C (Sep. 13)	16°C (Oct. 3)	4°C (Dec. 9)
Amplitude (mv)	0.03	0.03	0.03	0.04	-
P Wave Time (s)	0.26	0.18	0.16	0.14	-
Rate of appearance (%)	0.02	96.40	100	87.14	0
Amplitude (mv)	0.19	0.28	0.37	0.35	0.25
R Wave Time (s)	0.12	0.12	0.13	0.24	0.32
Rate of appearance (%)	99	100	100	100	97
Amplitude (mv)	0.04	0.05	0.05	0.05	-
T Wave Time (s)	44	0.27	0.20	0.38	-
Rate of appearance (%)	0.02	98.11	97.06	83.56	0
Heart rate (frequency/min.)	9±13.72	17±7.64	31.09±2.79	13.00±2.37	6.89±0.51

wave, which is greater than the P wave and smaller than the R wave, is quite great. The time continued, which is an average of about 0.31 seconds, is the longest. The rate of appearance is the lowest (Table 1). The T wave does not appear during hibernation. The rate of appearance is the highest from May to June.

6). The heart rate is influenced by air temperature. The rate becomes faster when the temperature goes up and slower when the temperature goes down. We calculated the heart rate listed in table 1 from the formula: heart rate = 60(s)/average time between R and R (s) (Frequency/Minute).

7). We conclude that the electrical-axis is under normal conditions by range estimation.

### Discussion

1). Though the Chinese Alligator is a kind of elementary cold-blooded vertebrate, its heart is divided into two atriums and two ventricles. Heart beating is started by the sinus venosus, so the components of the Chinese Alligator's electrocardiogram, which consists of a P wave, QRS waves and a T wave, is closely related to those of other vertebrates.

2). The P wave is distinctly divided into Pr and Pl (∩). The fact that there is a time difference between the beating of the left and the right atriums leads to this situation. It is similar to the situation that the crests of the P wave is level and flat in determining the electrocardiogram of *Elaphe carinata*,

*Elaphe taeniura* and *Ptyas korros*. So we conclude that the two atriums of elementary vertebrates can not systole and diastole at the same time as in mammals, so there is only one P wave in electrocardiograms of mammals, while the P wave is divided into Pr and Pl in other vertebrates.

3). QRS waves are the reflection of the succession of several parts of the ventricle being excited one after another. From the fact that the rate of appearance of the R wave is the highest, we conclude that the ventricle is active all year round. Blood circulation was promoted by ventricle motion in order to maintain life even during hibernation. During that period, with the reduction of the Chinese Alligator's activities and a lowered metabolism, the amplitude of the P wave and the T wave becomes lower, so that it can not even be measured with an electrocardiogram.

4). More often than not, the main wave of the QRS waves and the T wave are of the same direction, showing that the part being excited earlier repolarized later, while the part being excited later repolarized earlier. But the fact that the T wave and the QRS waves are of different directions in the Chinese Alligator's electrocardiogram shows the muscle structure of its ventricles and the pressure change inside its ventricles when congested. This may be somewhat different from those of mammals.

5). The Chinese Alligator is cold-blooded, so air temperature has a great influence on its activities and its activities

depend largely on the external environment. When air temperature goes up, it becomes nimble, its heart rate quicker and its metabolism active; when the temperature goes down, it becomes sluggish, its heart rate gets slower and its metabolism drops.

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## Karyotypes of Two *Rana* from Xinjiang, China

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**Abstract.** -Karyotypes, C-bands, and Ag-NORs of *Rana ridibunda* (Ili River Valley, Xinjiang) and *R. altaica* (Altai Mountains, Xinjiang, China) are reported. The specimens of *R. ridibunda* from central Europe have a karyotype with chromosome nos. 8 and 11 being both metacentric. They have a telomeric C-band on almost every chromosome arm and a few interstitial C-bands on some chromosomes. The specimens from the Ili River Valley have a karyotype with chromosome no. 8 being submetacentric and no. 11 submetacentric, and no telomeric or interstitial C-bands. Chromosome polymorphism of the different populations of the same species may explain this. We suggest that *R. altaica* and *R. arvalis* are in a middle stage of chromosome evolution from a karyotype with  $2n=26$  to a karyotype with  $2n=24$  and chromosome no. 6 being submetacentric.

**Key words:** Amphibia, Ranidae, *Rana ridibunda*, *Rana altaica*, China, Xinjiang, karyotype, C-band, Ag-NORs, polymorphism, evolution.

### Introduction

The karyotype, C-band and Ag-NORs of *Rana ridibunda* from central Europe were investigated by Schmid (1978) and the karyotype and Ag-NORs of the same species from Korgas, Bole and Urumqi in Xinjiang Autonomous Region, China were investigated by Wu (1990). In the present study, the karyotype, C-bands and Ag-NORs of *R. ridibunda* were reexamined and those of *R. altaica* are examined for the first time.

### Methods

The frogs used in this study are: *R. ridibunda* Pallas, a male and a female from the Ili River region in Xinjiang, China and *R. altaica* Kastschenko, two males and two females from the Altai Mountains (= Altay Shan) region in Xinjiang. Both ends of the femur, tibio-fibula, and humerus bones were cut off, and the marrow cells were washed out with 0.46 M KCl for chromosome preparation by a centrifugal air-drying method. Testing of C-bands and Ag-NORs were carried out following the methods of Wei et al. (1990) and Xu et al. (1990).

### Results

Figure 1 depicts the karyotype, C-bands, and Ag-NORs of *R. ridibunda*. For the measurements of the karyotypes, see table 1.

The diploid number of *R. ridibunda* is  $2n=26$ , which can be divided into two groups. The large chromosome group includes chromosome nos. 1-5, with a relative length (R. L.) larger than 9%. Chromosome nos. 1, 2, 4 and 5 are metacentric and no. 3 is submetacentric. The small chromosome group consists of chromosome nos. 6-13, with R. L. less than 7%. Numbers 6, 7 and 11 are metacentric, nos. 9, 10, 12 and 13 are submetacentric and no. 8 is submetacentric. The only secondary constrictions can be readily observed on the long arms of no. 10.

With regard to C-bands, there is a centromeric C-band on each chromosome of *R. ridibunda*, but some of them are weakly stained and no interstitial or telomeric C-band can be observed. There are a pair of standard Ag-NORs on the long arms of no. 10, in the same position as the

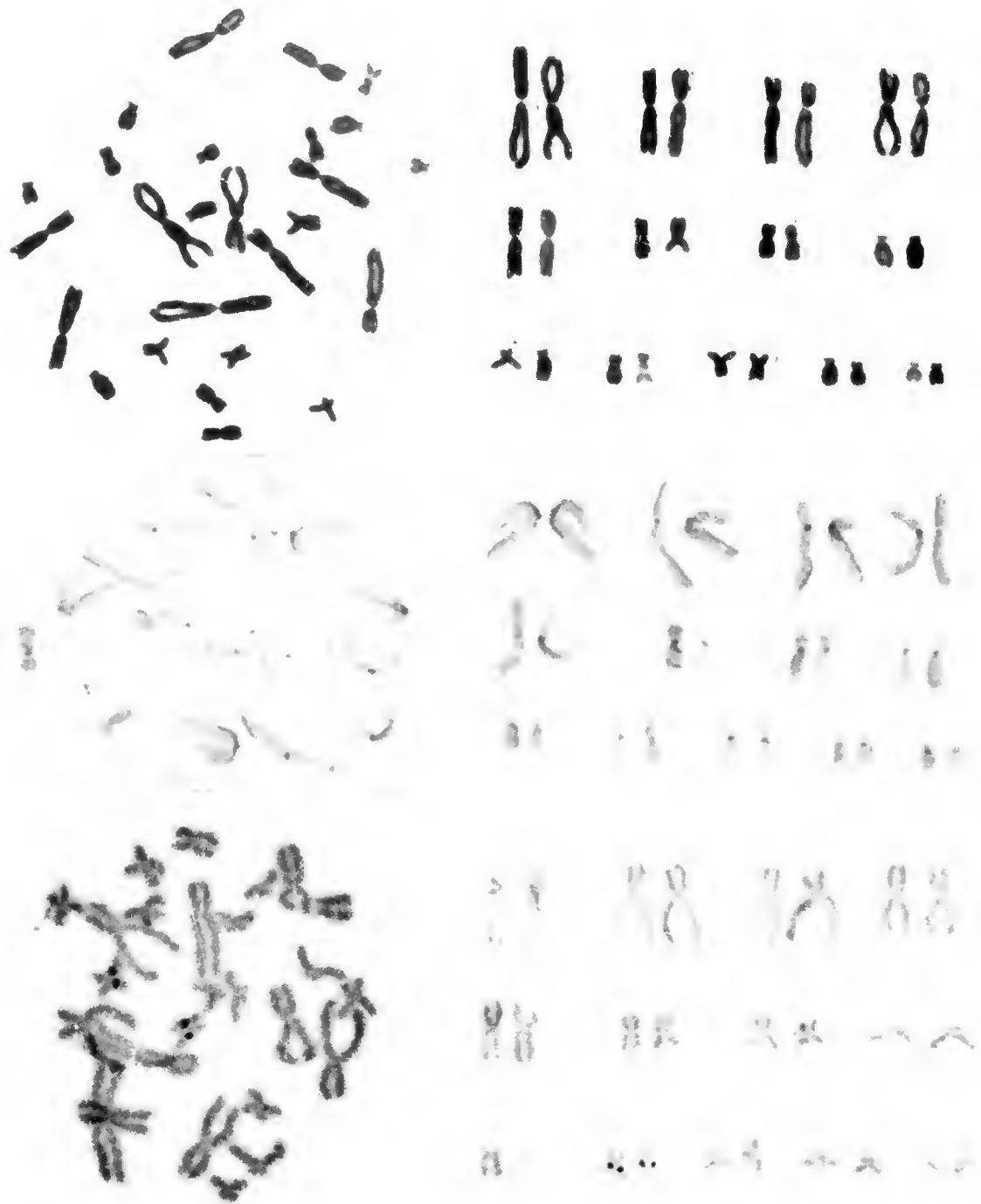


FIG. 1. The karyotype, C-band and Ag-NORs of *Rana ridibunda*.

secondary constrictions.

Figure 2 depicts the karyotype, C-bands, and Ag-NORs of *R. altaica*. The diploid number of *R. altaica* is  $2n=24$ , which are composed of three groups. The large chromosome group includes chromosome

nos. 1-5. All of them are metacentric. The prominent secondary constrictions can be readily observed on the long arms of no. 1, where the standard NORs are located. The middle sized chromosome group only includes chromosome no. 6, with the R. L. between 7-9%. It is also metacentric. The

TABLE. 1. Chromosome measurements of *R. ridibunda* and *R. altaica*.

Chromosome Number	<i>R. ridibunda</i>		<i>R. altaica</i>	
	Relative Length	Arm Ratio	Relative Length	Arm Ratio
1	15.60±1.07	1.20±0.08M	14.97±1.04	1.27±0.21M
2	12.63±0.68	1.61±0.22M	13.83±1.18	1.27±0.18M
3	11.79±0.66	2.20±0.31SM	12.34±0.84	1.58±0.25M
4	11.32±0.62	1.44±0.17M	11.26±0.60	1.31±0.23M
5	9.75±0.64	1.33±0.10M	9.80±0.64	1.28±0.16M
6	5.99±0.56	1.32±0.16M	8.82±0.71	1.25±0.21M
7	5.60±0.44	1.42±0.31M	6.26±0.52	1.40±0.23M
8	5.19±0.28	3.37±0.41ST	5.37±0.34	2.31±0.32SM
9	4.82±0.39	2.61±0.36SM	4.86±0.42	2.33±0.31SM
10	4.68±0.32	1.74±0.40SM	4.51±0.37	1.29±0.27M
11	4.40±0.38	1.61±0.37M	4.19±0.38	1.97±0.34SM
12	3.95±0.48	2.09±0.39SM	3.59±0.60	1.74±0.31SM
13	3.58±0.26	2.11±0.35SM		

small chromosome group includes chromosome nos. 7-12. Numbers 7 and 10 are metacentric. Numbers 8, 9, 11 and 12 are submetacentric. No heteromorphic chromosome is observed. In connection with C-bands, there is a weakly stained centromeric C-band on chromosome nos. 1, 2, 6, 8 and one homologous of nos. 3, 4. An obvious interstitial C-band can be observed on 1p. Some weakly stained interstitial C-bands could also be seen on 2p, 3p, 4p, 4q, 6p and 7q, and a C block on the long arm of one homologous of no. 9. It is noted that on the basis of C-band and arm ratio pairing, one homologous of chromosome no. 2 of the C-banding plate is much shorter than the other. The R. L. of the longer chromosome no. 2 is larger than that of chromosome no. 1. We suggest that translocation might have taken place between the two homologous of chromosome no.2.

### Discussion

*Rana ridibunda* is distributed in central Europe east of northwestern France, north to the southern shore of the Baltic Sea, south to northern Italy and the Balkans; southwestern Asia, east to ca. 81°E latitude in asiatic Russia and Xinjiang, China, south to Afghanistan and Pakistan (Frost, 1985). The type locality of *R. ridibunda* is the Caspian Sea, Volga and Jaico (USSR). The place where Schmid (1978) collected

specimens and the places where we collected are the nearly opposite margins of the distribution of *R. ridibunda*.

Comparing the results, we found that the differences between them are as follows: chromosome nos. 8 and 11 of Schmid's result are both metacentric, but for Wu's and our results, no. 8 is subtelocentric and no. 11 is submetacentric. Schmid's result indicates that a telomeric C-band is located at the end of each arm of every chromosome except the short arms of no. 6 and long arms of no. 12. An interstitial C-band is on 1q, 3p, 4p, 5q, 7q, 8p, 8q, and 11 q, but no telomeric or interstitial C-band could be observed in our result. The differences between them might be polymorphism of chromosomes between the different populations of the same species.

*Rana altaica* is distributed in northern Xinjiang (China) and southern Siberia (Russia). The type locality of it is Altai, USSR. It is a species of woodfrog, belonging to the *R. temporaria* group. In this group, *R. temporaria* is distributed throughout Europe east to the Urals, *R. arvalis* from the northeast of France to the west of Siberia (124° E). *R. chensinensis* is distributed from the Russian Far East to Sakhalin and southern Kurile islands; Hokkaido, Japan; Korea; eastern Mongolia; northeastern and central China, south to



FIG. 2. The karyotype, C-band and Ag-NORs of *Rana asiatica*.

Sichuan and Hubei. *R. dybowskii* is distributed from the Russian Far East; Korea, Tsushima Island., Japan and *R. ornativentris* on Honshu, Shikoku and Kyushu islands, Japan.

*Rana temporaria* have a karyotype with 26 chromosomes, divided into a large chromosome group (nos. 1-5, with R. L. > 9%) and a small chromosome group (nos. 6-13, with R. L. < 7%). However *R. arvalis*, *R. altaica*, *R. chensinensis*, *R.*

*dybowskii* and *R. ornativentris* each have a karyotype with 24 chromosomes, divided into a large chromosome group (nos. 1-5), a middle size chromosome group (no. 6 with R. L. 7-9%) and a small chromosome group (nos. 7-12). Chromosome no. 6 of *R. arvalis* and *R. altaica* is metacentric, while that of *R. dybowskii*, *R. ornativentris* and *R. chensinensis* is submetacentric (Wei and Chen, 1990). Considering that the distributional areas of *R. arvalis* and *R. altaica* are between *R.*

*temporaria* and the three other species, *R. chensinensis*, *R. dybowskii* and *R. ornativentris*, it is suggested that the two small chromosomes of the ancestor of *R. temporaria* merged into one middle sized, metacentric chromosome which is chromosome no. 6 of *R. arvalis* and *R. altaica*. This metacentric chromosome transformed into a submetacentric chromosome by inversion between arms and formed chromosome no. 6 of *R. chensinensis*, *R. ornativentris* and *R. dybowskii*.

### Acknowledgments

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## Karyotypic Studies of Nine Species of Chinese Salamanders†

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**Abstract.** -Four species of hynobiid salamanders, from three genera, possess bimodal and asymmetrical karyotypes with  $2n=64$  or  $2n=68$  chromosomes. Five species of salamandrids, from four genera, have  $2n=24$  and unimodal, symmetrical karyotypes with no microchromosomes or telocentric chromosomes. Karyologically, Hynobiidae is the most primitive and the Salamandridae is the most advanced family in the Caudata. The two families conform to different models of chromosome change.

**Key words:** Amphibia, Caudata, Hynobiidae, Salamandridae, China, karyotype.

TABLE 1. Locality, date of collection, and number of individuals (male, female) for the 9 species used in the karyotypic analyses.

Hynobiidae		F	M
<i>Batrachuperus karlschmidti</i>	Sichuan Prov., 1986	2	4
<i>B. yenyuanensis</i>	Mianning Co., Sichuan Prov., July 1986		2
<i>Liua shihi</i>	Wushan Co., Sichuan Prov., Mar. 1986	1	2
<i>Pachyhynobius shangchengensis</i>	Jinzhai Co., Anhui Prov., Apr. 1984	3	
Salamandridae			
<i>Tylotriton kweichowensis</i>	Weining Co., Guizhou Prov., Jun. 1986		3
<i>T. verrucosus</i>	Jingdong Co., Yunnan Prov., Aug. 1984		3
<i>Pachytriton labiatum</i>	He Co., Guangxi Prov., Jun. 1986		1
<i>Paramesotriton chinensis</i>	He Co., Guangxi Prov., Jun. 1986		1
<i>Cynops cyanurus yunnanensis</i>	Jingdong Co., Yunnan Prov., Aug. 1984		1

### Introduction

There are 33 species of salamanders known from China, including two suborders, three families and 12 genera (Zhao et al., 1988). Only a few of their karyotypes have previously been reported (Wang et al., 1983; Yang and Zhao, 1984; Yang et al., 1986a, 1986b; Zhu and Wei, 1981). Karyotypic studies among the Caudata (Kuro-o et al., 1987; Makino, 1932; Morescalchi, 1973, 1975; Morescalchi et al., 1977; 1979; Schmid, 1979; Sessions et al., 1982; Seto et al., 1986) have contributed evidence for the phylogeny of salamanders. The present paper reports the karyotypes of nine species belonging to the families Hynobiidae and Salamandridae, thereby providing

additional cytogenetic data towards understanding the phylogeny of Chinese salamanders.

### Methods

#### *Preparation of Chromosomes*

Animals used in this study were collected from Sichuan, Yunnan, Guizhou, Guangxi and Anhui Provinces, China from May 1983 to June 1986 (Table 1). Mitotic chromosomes were prepared using the methods of Kezer and Sessions (1979) with minor modifications. Animals were intraperitoneally injected with 20 mg/ml of colchicine solution about 40 to 60 hours before sacrifice using a dosage of 0.01 ml/g body weight. Liver and intestine were removed, washed with 1% sodium citrate, and sliced. Chromosome preparations were made by air-dry and squash techniques. Chromosomes were also obtained using the methods of Princee and

† This publication was previously published in Chinese by Yang (1990).



Boer (1983) and Wu (1982) with slight modifications (Yang et al., 1986a). Specimens were injected intraperitoneally with PHA solution (5 mg/ml) at a dosage of 0.09 ml/g body weight, administered once every 24 hours for three days. Twenty four hours after the third PHA injection, the specimens received a final injection of colchicine (3 mg/ml) with a dosage of 30 µg/g body weight about 14 hours before they were sacrificed. The spleen was removed, washed with 1% solution of sodium citrate, ground, and put into a hypotonic solution (0.4% KCl). A few drops of the final cell suspensions were used per slide, which was then placed in a large Petri dish. Following hypotonic treatment and fixation in the dish, the air-dried slides were stained with 5% Giemsa PBS (pH 6.8) for 30 minutes.

An intraperitoneal injection of colchicine solution (3 mg/ml) was given using a dosage of 30 µg/g body weight for 14-24 hours before the specimens were sacrificed. The testes were removed, rinsed with 1% sodium citrate, ground, and put into 0.4% KCl solution for 1.0-1.5 hours at room temperature. After centrifugation, the supernatant was discarded and the precipitate was fixed in a 3:1 solution of methanol:acetic acid for three periods of 30 minutes each. Slides were prepared by the air-dry method and stained with 5% Giemsa PBS (pH 6.8) for 1 hour.

### Karyotype Analysis

#### 1. Mitotic chromosomes.—

Chromosomes were numbered and the spreads which could be used for karyotypes were photographed. The karyotypes were prepared on the basis of relative lengths and arm ratios measured and calculated from the enlarged photographs. The chromosomes in tailed amphibians grade smoothly in size from the largest to the smallest, so that it is impossible to distinguish between the largest microchromosomes and the smallest macrochromosomes. No general criterion of microchromosomes exists to date (Morescalchi, 1973, 1975; Sessions et al, 1982; Wang et al, 1983). In addition, the

morphology of the microchromosomes varies with differences in the preparation techniques and the mitotic chromosomes of the cells analyzed. For the sake of consistency, I have defined the chromosomes less than 3.00% relative length (in percentage of total haploid length, including the microchromosomes) as microchromosomes according to the fact that the minimum value of relative lengths of the smallest chromosomes in Salamandridae, which is the most advanced family without microchromosomes in Caudata, is 3.00 (Table 2). The abbreviations of the chromosomes are as follows: M-metacentric; SM-submetacentric; ST-subtelocentric; T-telocentric; and m-microchromosome.

2. Meiotic chromosomes.—Bivalents in diakinesis were numbered and arranged. The relative lengths of the bivalents were calculated according to the principles of ISCN (1978). The arm ratio was not calculated due to the absence of C-band information. The relative chiasma numbers also were calculated (those having joined ends were also considered to be in chiasma) using the method presented by Imai and Moriwaki (1982). For chromosomes in metaphase II, the relative length and arm ratio were measured and calculated. The terminology for centromeric position followed Levan et al. (1964).

## Results

### Hynobiidae

*Batrachuperus*.—*B. karlschmidti* (2n=68) has 12 pairs of macrochromosomes and 22 pairs of microchromosomes, which is the highest chromosome number among species of Hynobiidae reported to date except for *Onychodactylus japonicus* (2n=78; Table 3). Nos. 1-3 are metacentric and the rest submetacentric among the macrochromosomes (Fig. 1, Table 4). This is a bimodal and asymmetrical karyotype with a formula of 6M + 18ST + 44M.

*B. yenyuanensis* (2n = 68), consisting

TABLE 2. Mitotic chromosome data for five species of Salamandridae.

Relative length ( $\bar{x} \pm S.D.$ )					
No.	Tk <sup>a</sup>	Tv <sup>b</sup>	Ta <sup>c</sup>	Pb <sup>d</sup>	Co <sup>e</sup>
1	12.24±0.55	12.2	12.8	12.54±0.61	12.17±0.86
2	11.20±0.33	11.5	10.8	11.63±0.41	11.40±0.59
3	10.52±0.53	10.8	11.2	10.52±0.55	10.49±0.58
4	10.13±0.55	10.7	10.1	10.56±0.59	10.13±0.59
5	9.45±0.49	9.5	9.4	9.89±0.42	9.59±0.37
6	8.62±0.73	9.0	8.8	9.17±0.60	9.08±0.57
7	8.07±0.54	7.8	7.7	8.20±0.62	8.27±0.71
8	7.36±0.50	7.6	8.1	7.92±0.73	8.17±0.76
9	6.53±0.58	6.3	6.0	5.89±0.55	6.28±0.48
10	5.81±0.36	5.5	5.6	5.42±0.41	5.63±0.49
11	5.33±0.41	5.4	5.0	4.81±0.34	5.09±0.43
12	4.44±0.58	3.8	3.0	3.21±0.49	3.94±0.52
Arm ratio ( $\bar{x} \pm S.D.$ )					
No.	Tk	Tv	Ta	Pb	Co
1	1.2±0.16	1.08	1.13	1.11±0.09	1.07±0.08
2	1.3±0.13	1.22	1.08	1.25±0.16	1.19±0.11
3	1.3±0.32	1.08	1.38	1.62±0.20	1.51±0.18
4	1.3±0.36	1.27	1.08	1.13±0.08	1.11±0.08
5	1.4±0.39	1.08	1.17	1.20±0.12	1.14±0.10
6	2.5±1.20	2.03	2.33	1.42±0.19	1.28±0.14
7	1.4±0.31	2.70	2.85	2.93±0.56	2.35±0.32
8	1.8±0.48	1.33	1.38	1.20±0.15	1.13±0.06
9	1.4±0.08	1.22	1.38	1.67±0.19	1.44±0.17
10	1.5±0.36	1.38	1.70	2.64±0.58	2.57±0.33
11	2.9±1.50	1.70	1.86	2.88±0.44	2.33±0.38
12	3.6±2.30	3.76	3.76	2.00±0±22	2.20±0.31
Centromere position					
No.	Tk	Tv	Ta	Pb	Co
1	M	M	M	M	M
2	M	M	M	M	M
3	M	M	M	M	M
4	M	M	M	M	M
5	M	M	M	M	M
6	SM	SM	SM	M	M
7	M	SM	SM	SM	SM
8	SM	M	M	M	M
9	M	M	M	M	M
10	M	M	SM	SM	SM
11	SM	SM	SM	SM	SM
12	ST	ST	ST	SM	SM

a. Tk = *Tylotriton kweichowensis*, (present paper); b. Tv = *T. verrococus*, (Seto et al., 1982); c. Ta = *T. andersoni*, (Seto et al., 1982); d. Pb = *Pachytriton brevipes*, (Zhu and Wei, 1981); e. Co = *Cynops orientalis*, (Zhu and Wei, 1981).

of 11 pairs of macrochromosomes and 23 pairs of microchromosomes. Among the macrochromosomes, nos. 1-2 are metacentric, no. 4 is submetacentric, and the rest are subtelocentric (Fig. 1, Table 4). The karyotype is bimodal and asymmetrical, with a formula of 4M + 2SM

+ 16ST + 46m.

*Liua*.—*L. shihi* ( $2n = 64$ ). The karyotype consists of 11 pairs of macrochromosomes and 21 pairs of microchromosomes, nos. 1-3 being metacentric, no. 7 submetacentric and the

TABLE 3. Chromosome data of some species in Hynobiidae.

Species	2n	Telocentric Macro- chromosomes	Micro- chromosomes	References
<i>Hynobius dunni</i>	56	0	16	Morescalchi et al. 1979
<i>H. retardatus</i>	40	4	0	Morescalchi et al. 1979
<i>Salamandrella keyserlingii</i>	62	24	24	Morescalchi et al., 1979
<i>Ranadon sibericus</i>	66	18	38	Morescalchi et al., 1979
<i>Batrachuperus mustersi</i>	62	10	38	Morescalchi et al., 1979
<i>B. karlschmidti</i>	68	0	44	Present paper
<i>B. yenyuanensis</i>	68	0	46	Present paper
<i>Onychodactylus fischeri</i>	>66	6	>22	Session et al., 1982
<i>O. japonicus</i>	58+2	0	18	Morescalchi et al., 1979
<i>O. japonicus</i>	78	?	?	Yamamoto, 1982
<i>Liua shihi</i>	64	10	42	Present paper
<i>Pachyhynobius shangchengensis</i>	64	18	40	Yang et al., 1986

rest telocentric among the macrochromosomes (Fig. 1, Table 4). The karyotype is bimodal and asymmetrical, with a formula of 6M + 2SM + 4ST + 10T + 42M.

*Pachyhynobius*.—*P. shangchengensis* (= *Xenobius melanonychus*), (2n = 64). There are 12 pairs of macrochromosomes and 20 pairs of microchromosomes. Numbers 1 and 5 are metacentric, no. 2 is subtelocentric, and the rest of the macrochromosomes are telocentric (Fig. 1, Table 4). This is a bimodal and asymmetrical karyotype with a formula of 4M + 2ST + 18T + 40M.

#### Salamandridae

*Tylototriton*.—*T. kweichowensis* (2n=24) has 8 pairs of metacentric (nos. 1-5, 7, 9-10), 3 pairs of submetacentric (nos. 6, 8 and 11) and 1 pair of subtelocentric chromosomes (no. 12), without microchromosomes (Fig. 2, Table 2). This

is a unimodal and symmetrical karyotype. Twelve chromosomes in metaphase II and twelve bivalents in diakinesis were seen on the meiotic preparations (n=12). The relative lengths of chromosomes in metaphase II are larger than those of chromosomes in mitotic metaphase (Tables 2 and 5). Both nos. 11 and 12 chromosomes in metaphase II are submetacentric, the arm ratios being 1.7 and 2.6 respectively, while no. 11 is submetacentric and no. 12 is subtelocentric for the chromosomes in mitotic metaphase, the arm ratios being 2.6 and 3.6 respectively. The differences might show the different degree of chromosome contraction during meiosis and mitosis (Figs. 2, Tables 2 and 5). The relative lengths and relative chiasma number of the bivalents are larger than those of chromosomes in mitotic and less than those of chromosomes in metaphase II. The relationship of chiasma numbers and lengths of the bivalents is not a straight line, for instance, the relative lengths of



FIG. 1. Karyotypes of four species of hynobiid salamanders. 1) *Batrachuperus karlschmidti*, 2) *B. yenyuanensis*, 3) *Liua shihi*, 4) *Pachyhynobius shangchengensis*.

nos. 1 and 12 are 12.47 and 5.41, while their relative chiasma numbers are 7.96 and 8.47 respectively.

*T. verrucosus* ( $2n = 24$ ). The haploid chromosome number is 12. Accordingly, the diploid chromosome number expected is 24, which is consistent with those of *T. andersoni* and *T. verrucosus* from different localities (Ferrier and Beetschen, 1973; Morescalchi, 1973; Seto et al, 1986). The relative lengths of chromosomes in metaphase II are larger than those of bivalents in diakinesis (Tables 5 and 6). The chromosomes in metaphase II are metacentric except nos. 6, 8 and 12 of submetacentric chromosomes and there are no microchromosomes. The karyotype is unimodal and symmetric. 2). The relative chiasma numbers are not proportional to relative lengths, for example, the relative

lengths are 9.36 and 5.25 respectively (Table 6).

*Pachytriton*.—*P. labiatum* ( $2n = 24$ ). There are 12 bivalents in diakinetive cells ( $n=12$ ). Accordingly, the diploid chromosome number should be 24 (Fig. 2), in accord with that of *P. brevies* (Zhu and Wei, 1981). The relative chiasma numbers of nos. 1-6 bivalents vary basically with their relative lengths, while the relative chiasma numbers of nos. 7-12 are more constant (Table 6).

*Cynops*.—*C. cyanurus yunnanensis* ( $2n=24$ ). There are 12 bivalents in diakinetive cells and 12 chromosomes in metaphase II cells (Fig. 2). Consequently, the  $2n$  should be 24. The chromosomes in metaphase II are metacentric except no. 8 (SM), without microchromosomes (Fig.

TABLE 4. Macrochromosome data for four species of Hynobiidae.

Relative length ( $\bar{x}\pm S.D.$ )				
No.	Ps <sup>a</sup>	Ls <sup>b</sup>	Bk <sup>c</sup>	By <sup>d</sup>
1	11.95±1.15	13.06±0.76	12.28±1.03	13.87±3.95
2	7.80±0.60	11.19±0.44	9.88±0.79	9.66±0.44
3	7.43±0.55	8.13±1.30	7.51±0.89	8.10±0.82
4	6.94±0.47	7.45±0.35	6.93±0.85	7.52±1.18
5	6.80±0.47	6.87±0.33	6.37±0.79	7.07±0.52
6	5.80±0.33	6.33±0.37	5.24±0.52	6.29±0.43
7	5.27±0.42	5.54±0.55	4.49±0.56	4.78±0.86
8	4.42±0.39	4.93±0.41	3.94±0.51	4.00±0.31
9	3.79±0.25	4.18±0.66	3.56±0.20	3.52±0.16
10	3.62±0.22	3.41±0.47	3.27±0.24	3.36±0.23
11	3.29±0.18	3.18±0.35	3.08±0.16	3.15±0.29
12	3.06±0.19	-	3.00±0.13	-
Arm ratio ( $\bar{x}\pm S.D.$ )				
No.	Ps	Ls	Bk	By
1	1.3±0.50	1.3±0.20	1.3±0.14	1.2±0.13
2	3.7±0.75	1.2±0.13	1.3±0.23	1.3±0.17
3	-	1.5±0.22	1.4±0.20	3.0±0.60
4	-	8.0±0.67	4.7±1.50	2.1±1.30
5	1.5±0.07	7.3±1.37	4.5±1.50	3.0±1.30
6	-	6.6±1.09	4.2±1.40	4.2±1.00
7	-	2.4±0.25	4.1±1.24	3.7±0.30
8	-	5.5±1.95	3.1±1.49	3.7±1.60
9	-	-	3.6±0.75	4.1±0.38
10	-	-	3.6±0.78	4.0±2.02
11	-	-	3.6±0.98	4.5±1.56
12	-	-	3.1±0.81	-
Centromere position				
No.	Ps	Ls	Bk	By
1	M	M	M	M
2	ST	M	M	M
3	T	M	M	ST
4	T	T	ST	SM
5	M	T	ST	ST
6	T	ST	ST	ST
7	T	SM	ST	ST
8	T	ST	ST	ST
9	T	T	ST	ST
10	T	T	ST	ST
11	T	T	ST	ST
12	T	-	ST	-

a. Ps=*Pachyhynobius shangchengensis*; b. Ls=*Liua shihi*;  
 c. Bk=*Batrachuperus karlschmidti*; d. By=*B. yenyuanensis*

2). This is a unimodal and symmetrical karyotype, which is in accord with those of other species in the same genus (Zhu and Wei, 1981). The relative chiasma numbers do not vary with the relative lengths, for instance, the relative lengths of nos. 2 and 5 are 11.30 and 9.42, but their relative chiasma numbers are 9.14 and 9.63

respectively.

*Paramesotriton*.—*P. chinensis* ( $2n=24$ ). Twelve bivalents were seen in the diakineti cells. The diploid number of 24 (Fig. 2) is the same as that of *P. hongkongensis* (Morescalchi, 1975). The relative lengths and the relative chiasma numbers are

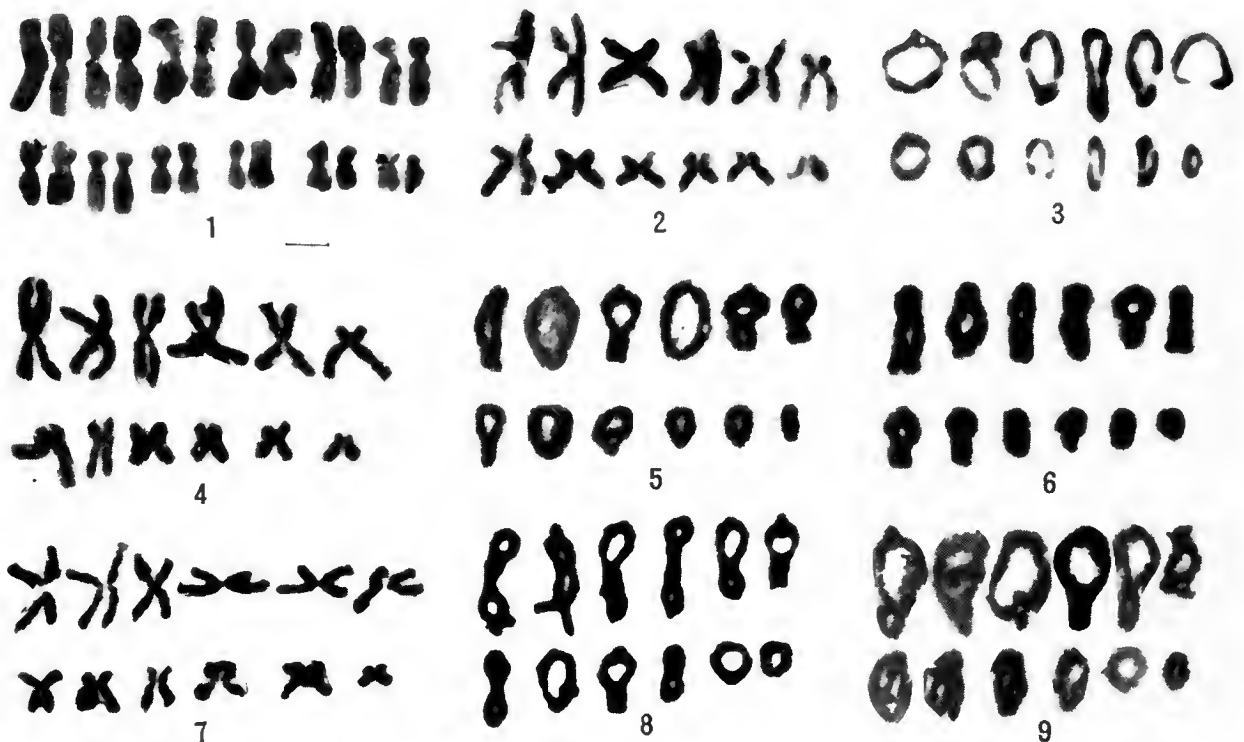


FIG. 2. Karyotypes of five species of salamandrid salamanders. 1-3) *Tylototriton kweichowensis*, mitotic chromosomes (1), chromosomes in metaphase II (2), and meiotic bivalents (3). 4, 5) *T. verrucosus*, chromosomes in metaphase II (4), and meiotic bivalents (5). 6) Meiotic bivalents of *Pachytriton labiatum*. 7, 8) *Cynops cyanurus yunnanensis*, chromosomes in metaphase II (7), and meiotic bivalents (8). 9) Meiotic bivalents of *Paramesotriton chinensis*.

shown in table 6. The relationship of chiasma numbers and the lengths of the bivalents is not a straight line, for example, the relative lengths of the nos. 2 and 12 are 11.89 and 3.55 respectively, while their relative chiasma numbers are the same, 8.10.

### Discussion

It has been suggested from karyotypic data that Hynobiidae is the most primitive group of salamanders, while Salamandridae is the most advanced group in Caudata (Morescalchi, 1973, 1975; Morescalchi et al., 1979). The same conclusion is derived from morphological comparisons (Zhao and Hu, 1984). There are some differences in the evolutionary ways of the two groups.

#### *Karyotypic Evolution in Hynobiidae*

The bimodal (with macrochromosomes

and microchromosomes) and asymmetrical (with metacentric and telocentric chromosomes) karyotype is considered to be primitive (Morescalchi, 1975) in reference to the karyotypic evolution in Caudata. Among some species of Hynobiidae, the diploid numbers are 40-66 and their karyotypes are bimodal and asymmetrical except for *Hynobius retardatus* [= *Satobius retardatus* (Adler and Zhao, 1990)], (Table 3). The karyotypes of the four species (in three genera) I studied here are all bimodal and asymmetrical, with  $2n=64$  or 68 chromosomes. *Batrachuperus* is one of 2 hynobiid genera in China that are aquatic for their entire lives and different from other genera morphologically. The diploid number of *B. karlschmidti* and *B. yenyuanensis* is 68, the second highest number among species of Caudata studied so far (Table 3). *Onychodactylus* is more derived and allied with *Ranodon* and

TABLE 5. Metaphase II chromosome data for 3 species of Salamandridae.

Chromosome No.	Relative length ( $\bar{x}\pm S.D.$ )		
	<i>T. verrucosus</i>	<i>T. kweichowensis</i>	<i>C. c. yunnanensis</i>
1	13.10 $\pm$ 1.67	13.14 $\pm$ 1.48	12.03 $\pm$ 0.75
2	11.39 $\pm$ 0.83	12.01 $\pm$ 1.63	11.23 $\pm$ 0.54
3	10.92 $\pm$ 1.05	10.64 $\pm$ 1.14	10.24 $\pm$ 0.39
4	10.27 $\pm$ 0.90	10.08 $\pm$ 1.23	10.07 $\pm$ 0.39
5	9.56 $\pm$ 0.50	9.39 $\pm$ 1.24	9.46 $\pm$ 0.38
6	7.81 $\pm$ 0.91	8.62 $\pm$ 1.26	8.91 $\pm$ 0.34
7	7.48 $\pm$ 0.80	8.54 $\pm$ 1.33	8.28 $\pm$ 0.41
8	7.33 $\pm$ 0.82	7.61 $\pm$ 0.90	7.63 $\pm$ 0.58
9	6.87 $\pm$ 0.77	6.66 $\pm$ 0.86	6.66 $\pm$ 0.58
10	5.60 $\pm$ 0.86	6.24 $\pm$ 0.84	5.98 $\pm$ 0.60
11	5.23 $\pm$ 0.81	5.69 $\pm$ 0.72	5.32 $\pm$ 0.43
12	4.45 $\pm$ 0.90	4.92 $\pm$ 0.61	4.28 $\pm$ 0.25
Chromosome No.	Arm Ratio ( $\bar{x}\pm S.D.$ )		
	<i>T. verrucosus</i>	<i>T. kweichowensis</i>	<i>C. c. yunnanensis</i>
1	1.2 $\pm$ 0.15	1.2 $\pm$ 0.20	1.3 $\pm$ 0.11
2	1.3 $\pm$ 0.17	1.3 $\pm$ 0.23	1.2 $\pm$ 0.14
3	1.5 $\pm$ 0.53	1.3 $\pm$ 0.28	1.2 $\pm$ 0.08
4	1.4 $\pm$ 0.10	1.2 $\pm$ 0.10	1.3 $\pm$ 0.19
5	1.4 $\pm$ 0.13	1.4 $\pm$ 0.43	1.4 $\pm$ 0.32
6	1.7 $\pm$ 0.36	2.1 $\pm$ 0.55	1.3 $\pm$ 0.39
7	1.9 $\pm$ 0.76	1.4 $\pm$ 0.44	1.5 $\pm$ 0.89
8	1.7 $\pm$ 0.58	1.8 $\pm$ 0.24	2.0 $\pm$ 0.26
9	1.6 $\pm$ 0.26	1.6 $\pm$ 0.24	1.6 $\pm$ 0.28
10	1.4 $\pm$ 0.26	1.5 $\pm$ 0.25	1.6 $\pm$ 0.39
11	1.4 $\pm$ 0.05	1.7 $\pm$ 0.24	1.6 $\pm$ 0.38
12	2.5 $\pm$ 0.81	2.6 $\pm$ 1.11	1.5 $\pm$ 0.32
Chromosome No.	Centromere Position		
	<i>T. verrucosus</i>	<i>T. kweichowensis</i>	<i>C. c. yunnanensis</i>
1	M	M	M
2	M	M	M
3	M	M	M
4	M	M	M
5	M	M	M
6	SM	SM	M
7	SM	M	M
8	SM	SM	SM
9	M	M	M
10	M	M	M
11	M	SM	M
12	SM	SM	M

*Batrachuperus* (Zhao and Hu, 1984), in accordance with the fact that *O. fischeri* has  $2n>66$  chromosomes (Sessions et al., 1982) and *O. japonicus* has  $2n=78$  (Yamamoto, 1982). The diploid number of *B. musteri* (Morescalchi et al., 1979), *B. pinchonii* and *B. tibetanus* (Yang and Zhao, 1984) is all 62, distinctly different from those of *B. karlschmidti* and *B. yenyuanensis*. Both *B. karlschmidti* and *B. yenyuanensis* have  $2n=68$  chromosomes,

but differ in chromosome component and morphology (Tables 3 and 4). The former has one more macrochromosome pair and one less microchromosome pair than the latter. In addition, the latter has one pair of subtelocentric chromosomes, while the former has none. It is obvious that the karyotypic evolution in *Batrachuperus* is more complex.

*Pachyhynobius shangchengensis*, which

TABLE 6. Bivalent data for 5 species of Salamandridae.

Relative length ( $\bar{x}\pm S.D.$ )					
No.	Tv <sup>a</sup>	Tk <sup>b</sup>	Pc <sup>c</sup>	Pl <sup>d</sup>	Ccy <sup>e</sup>
1	12.49±0.83	12.47±1.79	13.27±1.25	12.62±1.08	11.92±0.31
2	11.65±0.79	11.33±0.64	11.89±0.82	11.85±0.53	11.30±0.51
3	11.07±0.62	10.53±0.69	11.01±0.45	11.09±0.29	10.58±0.37
4	10.24±0.54	9.99±0.76	10.10±0.68	10.25±0.50	10.10±0.45
5	9.36±0.52	9.32±0.56	9.60±0.88	9.57±0.47	9.42±0.29
6	8.66±0.50	8.71±0.35	8.67±0.64	9.11±0.48	8.83±0.31
7	7.80±0.62	7.81±0.55	7.95±0.67	8.02±0.49	8.16±0.25
8	7.23±0.57	7.39±0.72	7.30±0.60	7.49±0.54	7.46±0.47
9	6.28±0.48	6.50±0.72	6.35±0.33	5.97±0.41	6.60±0.24
10	5.77±0.39	5.86±0.63	5.65±0.43	5.36±0.49	5.86±0.27
11	5.25±0.38	5.41±0.80	4.66±0.54	4.85±0.49	5.42±0.32
12	4.21±0.45	4.67±0.66	3.55±0.64	3.79±0.36	4.37±0.47

Relative chiasma number ( $\bar{x}\pm S.D.$ )					
No.	Tv	Tk	Pc	Pl	Ccy
1	10.29±1.62	7.96±1.32	10.94±1.67	11.20±2.13	11.65±1.33
2	8.29±2.11	8.91±1.22	8.10±0.32	10.00±1.73	9.14±2.21
3	9.36±1.93	8.47±0.41	8.65±1.30	9.23±1.73	9.16±2.36
4	8.81±1.23	8.47±0.41	8.67±1.50	8.53±1.86	9.77±2.05
5	7.92±0.57	8.91±1.22	8.10±0.32	7.82±0.22	9.63±2.10
6	8.44±1.73	8.47±0.41	8.10±0.32	8.12±1.24	7.82±0.90
7	7.38±1.31	8.47±0.41	7.48±1.39	7.73±0.30	7.92±1.70
8	7.92±0.57	7.98±1.42	7.53±1.59	7.73±0.30	7.23±1.01
9	8.89±1.90	8.47±0.41	8.10±0.32	7.32±1.13	6.92±0.72
10	7.38±1.31	8.47±0.41	8.10±0.32	7.32±1.13	7.21±0.75
11	7.92±0.57	8.47±0.41	8.10±0.32	7.73±0.30	6.92±0.72
12	7.40±1.42	6.95±2.89	8.10±0.32	7.73±0.30	6.92±0.72

a. Tv = *Tylotriton verrucosus*; b. Tk = *T. kweichowensis*; c. Pc = *Paramesotriton chinensis*; d. Pl = *Pachytriton labiatum*; e. Ccy = *Cynops cyanurus yunnansis*.

is a genus and species of Hynobiidae described on morphological characteristics (Fei and Ye, 1983), has  $2n=64$ . The karyotype differs from those of other species in Hynobiidae, providing the cytogenetic evidence for establishing the new genus and species.

*Liua* is a genus established by Zhao and Hu (1983), based on morphological characteristics. *Liua shihii*, which is the only species, has  $2n=64$ , the same as *P. shangchengensis*. However, there are some differences between them in chromosome component and morphology. *Liua shihii* has 11 pairs of macrochromosomes, including 3 pairs of metacentric, 1 pair of submetacentric, 2 pairs of subtelocentric, and 5 pairs of telocentric chromosomes, while *P. shangchengensis* has 12 pairs of macrochromosomes, consisting of 2 pairs

of metacentric, 1 pair of subtelocentric and 9 pairs of telocentric chromosomes (Fig. 1 and Table 4).

The predominant mode of karyotypic evolution in Caudata is that the unimodal symmetrical karyotypes with low chromosome number are derived from the bimodal and asymmetrical karyotypes with high chromosome number, through Robertsonian centric fusions and pericentric inversions (Morescalchi, 1975). Robertsonian centric fusions, which could occur between telocentric macrochromosomes, between stable microchromosomes, and between telocentric macrochromosomes and stable microchromosomes, reduce the diploid number and/or the microchromosome number and increase the metacentric chromosomes. Consequently, the karyotypes tend toward stability.



Pericentric inversions do not change the diploid number, but could increase the number of metacentric chromosomes and the stability of karyotypes.

*B. karlschmidti* and *B. yenyuanensis* possess 22 and 23 pairs of microchromosomes respectively and lack telocentric macrochromosomes. Contrastingly, *P. shangchengensis* and *L. shihii* have 21 and 20 pairs of microchromosomes and 5 and 9 pairs of telocentric macrochromosomes. It is concluded that the karyotypic evolution of the 4 species above has involved Robertsonian centric fusion as well as pericentric inversion. However, the phylogeny of the 4 species could not be established based on the present data. It is necessary to have information from chromosome banding and biochemistry in order to define the structures and functions of microchromosomes and telocentric chromosomes.

#### *Karyotypic Evolution in Salamandridae*

The 5 salamandrid species studied here all have  $2n=24$  chromosomes, lack microchromosomes, and possess unimodal and symmetrical karyotypes (Fig. 2, Tables 2 and 5) as consistent (Ferrier and Beetschen, 1973; Seto et al., 1986; Zhu and Wei, 1981). Morescalchi (1975) suggested that all species studied possess similar karyotypes that differ very little even at the intergeneric level. The differences between these karyotypes predominantly concern the absolute size of chromosomes and quantity of DNA. Accordingly, the karyotypic diversity among the species has chiefly resulted from pericentric inversions that result in differences between individual chromosomes by changing the telocentric chromosomes into metacentric ones, or changing the metacentric chromosomes into submetacentric, subtelocentric and telocentric chromosomes. The difference, which occurred not only at the intergeneric level, but also at the intrageneric level, are as follows: 1. The data of chromosomes in mitotic metaphase: as shown in table 2, the no. 12 chromosomes of 3 species in

*Tylostotriton* are all subtelocentric, while the karyotypes of *C. orientalis* and *P. brevipes* have no subtelocentric chromosomes, only metacentric and submetacentric chromosomes. In addition, the chromosome differences in morphology were seen among 3 species in *Tylostotriton*, 4 pairs of submetacentric chromosomes in *T. andersoni*, 3 pairs in *T. kweichowensis* and 2 pairs in *T. verrucosus*. 2. The data of chromosomes in meiotic metaphase II (Table 5): *C. cyanurus yunnanensis* has only 1 pair of submetacentric chromosomes, while there are 4 pairs in both *T. verrucosus* and *T. kweichowensis*. Numbers 6, 7, 8, and 12 are submetacentric chromosomes in *T. verrucosus* and nos. 6, 8, 11, and 12 in *T. kweichowensis*. 3. The data of bivalents in diakinesis (Table 6): the relative lengths of no. 1 bivalents of *T. verrucosus* and *T. kweichowensis* are similar, 12.49 and 12.47 respectively, but 13.27, 12.62 and 11.92 in *P. chinensis*, *P. labiatum* and *C. cyanurus yunnanensis* individually. The relative chiasma numbers of no. 1 bivalents reveal the intergeneric and intrageneric variations. It is noteworthy that the interspecific and intraspecific variations of individual bivalents on relative chiasma number in 2 species of *Tylostotriton* are more distinctive than those in other genera and species. The relative chiasma numbers are apparently not directly proportional to the relative lengths.

*Tylostotriton* has karyotypically been considered to be the most primitive genus in Salamandridae, based on the fact that there are more subtelocentric chromosomes in mitotic metaphase, more submetacentric chromosomes in meiotic metaphase II, and more variations of relative chiasma numbers in diakinesis. The same conclusion was reached based on morphological comparisons (Zhao and Hu, 1984). However, as shown in table 2, *T. andersoni* has 2 more submetacentric chromosomes pairs (nos. 10-11) than *T. kweichowensis* and 1 more submetacentric chromosomes pair (no. 10) than *T. verrucosus*. The relative length of chromosome no. 1 is largest and the relative length of no. 12 is the shortest in *T.*

*andersoni* among the 3 species above. These data could provide cytogenetic evidence for reestablishing *Echinotriton*. The mitotic chromosome number and morphology of *C. orientalis* are the same as those of *P. brevipes*, but the color, size and distribution of C-bands are different from each other. Consequently, the authors proposed that the differences of heterochromatic components and distributions on chromosomes of different genera could be the block of interspecific fertilization (Zhu and Wei, 1981).

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## GUIDELINES FOR MANUSCRIPT PREPARATION AND SUBMISSION

### Summary

Manuscripts must:

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- 2) be of letter quality (typewritten on bond paper).
- 3) include camera ready figures (if any).
- 4) include complete and accurate literature citations.
- 5) include complete and accurate localities with latitude and longitude.
- 6) include a camera ready map illustrating regions discussed (when applicable).

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*Asiatic Herpetological Research* publishes articles concerning but not limited to Asian herpetology. The editors encourage publications from all countries in an attempt to create an open forum for the discussion of Asian herpetological research.

Articles should be in standard scientific format and style. The following sections should be included:

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**Key Words.** Key words provide an index for the filing of articles. Key words provide the following information (when applicable): 1) Taxonomy (e.g. Reptilia, Squamata, Gekkonidae, *Gekko gecko*). 2) Geography (e.g. China, Thailand). 3) Subject (e.g. taxonomic validity, ecology, biogeography). The order of taxonomy, geography, and subject should be observed.

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Manuscripts following standard format should include introduction, methods, results, and discussion sections. While other formats are acceptable, the editors encourage the use of standard format. **Please do note type in all capital letters** (headings, Fig., Table, and authors names in the Literature Cited section).

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For example, "My results also incorporate literature records (Marx et al., 1982; Marx and Rabb, 1972; Mertens, 1930; Pope, 1929; Wall, 1909, 1910a, 1910b, 1910c)."

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*Abstract of oral presentation*

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FIG. 2. Lateral view of live *Psammodynastes pulverulentus* holding a prey lizard (*Anolis carolinensis*). Note buccal tissue surrounding the enlarged anterior maxillary and dentary teeth of the snake.

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**Joint Meeting 1992.**—The Asiatic Herpetological Research Society (AHS), the Society for the Study of Amphibians and Reptiles (CSSAR), the Amphibian and Reptile Specialist Group of Species Survival Committee of International Herpetological Society (of the former USSR), and the International Society for the Study and Conservation of Amphibians (ISSCA), including the 1992 International Conference on Oriental Amphibians will hold a joint meeting in Hanoi, Vietnam from 15 July to 20 July. Members of these societies and others are invited to attend. A number of general topics will be covered in the fields of amphibian and reptile biology, herpetological studies of various Asian regions, venomous snakes, and captive reproduction. Registration information is available from the following:

**China:** Dr. Huang Jie-tang, Qimen Institute of Snakebites, Qimen, China. **Independent Republics of the Commonwealth of Independent States:** Dr. Ilya Darevsky, Zoological Institute, Russian Academy of Sciences, Moscow, Russia. **In the USA and all other countries:** Dr. Theodore J. Papenfuss, Department of Vertebrate Zoology, University of California, Berkeley, CA

**Second World Congress of Herpetology.**—The Second World Congress of Herpetology will be held at the University of Adelaide, South Australia, Australia from 10 to 15 January 1994. Information is now available concerning the congress before and after the meeting. For information contact: Secretariat, Second World Congress of Herpetology, Dept. of Zoology, University of Adelaide, GPO Box 497, Adelaide, South Australia.

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Page 162 of volume 4 was left out by the printers. A copy is included here.

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Y. S. Pp. 1-12. Holotype of *Dibamus greeri* (ZIN 20011) from Hanoi, Vietnam. Chen, Yuancong, Dawei Zhang, and Rui Wang. Pp. 58-61. *Agkistrodon strauchii* from 3150 m, sandstone mountains of Waqên (33° 03' N 102° 37' E), Aba (Ngawa) Zangzu Autonomous Prefecture, Sichuan Province, China. Photo by J. Robert Macey. Semenov, Ilya, and Boris Borzhenko. Pp. 99-112. *Teratoscincus przewalskii* from Dunhuang (40° 10' N 94° 50' E), Jiuquan Prefecture, Gansu Province, China. Nuzimni, Sergius L. Pp. 123-131. *Mertensiella caucasica* from 10 km SSE of Borzhomi (41° 51' N 43° 23' E), Georgia. Photo by J. Robert Macey.



## ANNOUNCEMENTS

**Asian Herpetological Meeting 1992.**—The Asiatic Herpetological Research Society (AHRS), the Chinese Society for the Study of Amphibians and Reptiles (CSSAR), the Chinese Amphibian and Reptile Specialist Group of Species Survival Committee of I.U.C.N., the All Union Herpetological Society (of the former USSR), and the International Society for the Study and Conservation of Amphibians (ISSCA), including the Second International Conference on Oriental Amphibians will hold a joint meeting in Anhui Province, China from 15 July to 20 July. Members of these societies and others are invited to attend the meeting. A number of general topics will be covered in the fields of biology and conservation, herpetological studies of various Asian regions, venomous snakes and snakebite, and captive reproduction. Registration information is available from the following: **Within China:** Dr. Huang Jie-tang, Qimen Institute of Snakebites, Qimen, Anhui Province, China. **Independent Republics of the Commonwealth of Independent States:** Dr. Ilya Darevsky, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia. **In the USA and all other countries:** Dr. Theodore J. Papenfuss, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA.

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PLATE 1.—Darevsky, Ilya S. Pp. 1-12. Holotype of *Dibamus greeri* (ZIN 20011) from 850 m, Kontarang, Gilai-Contum Province, Vietnam. Chen, Yuancong, Dawei Zhang, Kexian Jiang, and Zhonghui Wang. Pp. 58-61. *Agkistrodon strauchii* from 3150 m, sand dunes, 7.0 km north of Waqên (33° 03' N 102° 37' E), Aba (Ngawa) Zangzu Autonomous Prefecture, Sichuan Province, China. Photo by J. Robert Macey. Semenov, Dimitri V., and Leo J. Borkin. Pp. 99-112. *Teratoscincus przewalskii* from Dunhuang Sand Dunes, Dunhuang (40° 10' N 94° 50' E), Jiuquan Prefecture, Gansu Province, China. Kuzmin, Sergius L. Pp. 123-131. *Mertensiella caucasica* from 10 km SSE of Borzhomi (41° 51' N 43° 23' E), Georgia. Photo by J. Robert Macey.

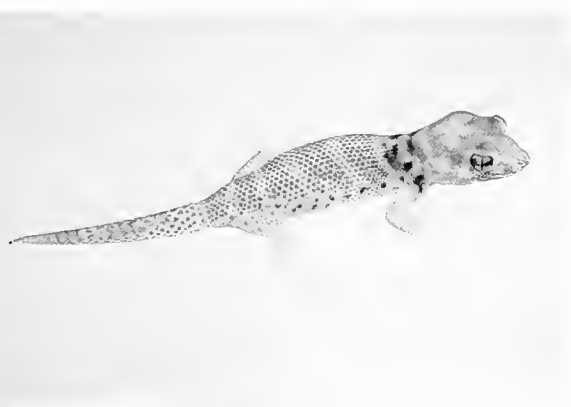




*ibannus greeri*  
arevsky



*Agkistrodon strauchii*  
Chen, Zhang, Jiang, and Wang



*eratoscincus przewalskii*  
emenov and Borkin



*Mertensiella caucasica*  
Kuzmin



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