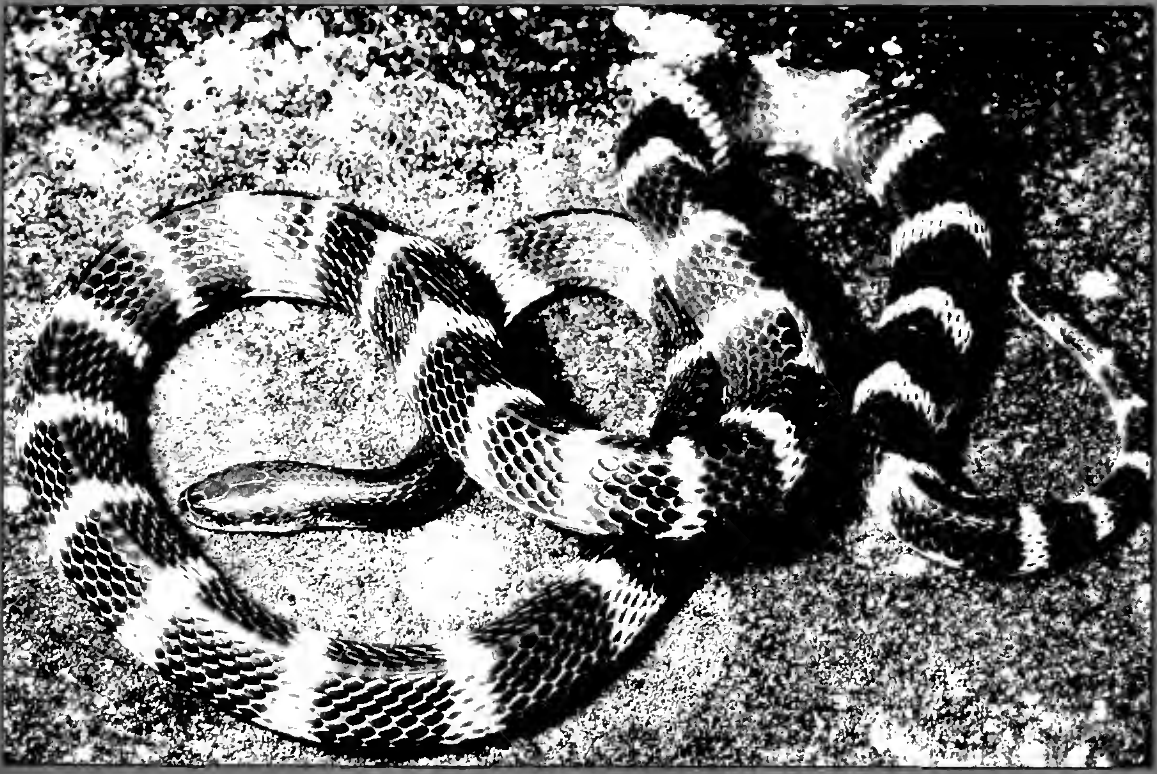
Asiatic Herpetological Research



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Cover: *Bungarus multicinctus*. Tam Dao, northernVietnam. Photo by Nikolai Orlov.

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Anurans Collected in West Malaysia

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Abstract. - Distributional records and natural history notes are given for anurans collected in West Malaysia 1976. *Rana baramica* was observed when it was caught by an *Ahaetulla nasuta* (Serpentes: Colubridae). *Rhacophorus leucomystax*, *Limnonectes limnocharis* and *Microhyla heymonsi* were all found at night on September 16-17, when they were spawning in shallow ditches, formed by the wheels of a truck. *Amolops larutensis* were day active and occurred in the shadow, among stones in a forest stream, particularly close to water falls and rapids. Several white foam nests with a diameter of 5-7 cm were deposited on the same stones just above the water surface on August 27. Other species observed were *Bufo melanostictus*, *Bufo asper*, *Leptobrachium hasseltii*, *Kaloula pulchra*, *Limnonectes laticeps*, *Limnonectes macrodon*, *Rana erythraea*, *Rana glandulosa*, *Rana nicobariensis*, and *Rhacophorus prominanus*.

Key words: Amphibia, Anura, West Malaysia.

Figure 1. West Malaysia: The collecting sites are marked with a dot (•). Scale bar = 100 km.

Introduction

The amphibian fauna of peninsular Malaysia is covered by some books (Berry 1975; Boulenger 1912; Smith 1930) and articles published thereafter (e.g., Arak 1984; Dring 1979; Kiew 1979; Inger 1980a, b; Lim 1990). New species have been described in the area during the last decades, e.g., *Kalophrynus palmatissimus* Kiew, 1984b, *Rana malesiana* Kiew, 1984c and *Rhacophorus tunkui* Kiew, 1987, which indicates that much more work still remains to be done. Most of the existing publications deal with systematics. The fauna is rich and contains many interesting species, however, most of them are not studied in detail according to aspects of their distribution, natural history and ecology.

The nature in Malaysia is now undergoing radical and large-scale changes. Most of them are effects of an increasing human population, industrialization, changes of the vegetation over large areas, and the massive use of biocides (Aiken and Leigh 1992; Cranbrook 1988; Cubitt and Payne 1990; Yussof 1987). These factors probably threaten the amphibians (Kiew 1984a) in similar ways as, e.g., the fish fauna (M. Zakaria-Ismail 1994; Ng et al. 1994; Rösler 1988). An increased field work is therefore motivated, so that the degree of habitat destruction is documented and necessary conservation measures can be done. This contribution contains some notes on the geographical distribution and natural history of several amphibians collected in Malaysia 1976.

Material and Methods

Collecting sites are listed in Table 1, and marked on the map (Fig. 1). The positions were plotted from the map of Malaysia, published by the Director of National Mapping, Malaysia, 1976, series 1307, edition 5-PPNM, sheet 1, scale 1:760,000. The specimens were preserved in formalin, identified by the use of Berry (1975), verified by Dr. Lim Boo-Liat, and deposited at Department of Medical Ecology, Institute

Table 1. Sampling stations.

Field Study Center, University of Malaysia, Ulu Gombak, Selangor	101°45'E; 3°17'N
Biological Field Station, Kota Tinggi, Johore	103°50'E; 1°50'N
Kuala Brang, Trengganu	103°01'E; 5°04'N
Kuin, about 4 miles SW of Marang, Trengganu	103°10'E; 5°09'N
Bukit Besar, Kuala Trengganu, Trengganu	103°07'E; 5°20'N
Malacca Youth Hostel, 9 miles north of Malacca city	102°10'E; 2°14'N
Portugese settlement, Malacca	102°17'E; 2°10'N
Kuala Lumpur Youth Hostel, Jalan Ipoh, Kuala Lumpur, Selangor	101°44'E; 3°09'N

for Medical Research in Kuala Lumpur, Malaysia. The nomenclature follows Frost (1986) and later changes summarized by Duellman (1993).

Results

Bufo melanostictus Schneider, 1799

Malacca Youth Hostel, July 29, 1976 (3 specimens); Portugese settlement, Malacca, July 29, 1976 (1 specimen); Kuala Lumpur Youth Hostel, August 5, 1976 (1 specimen), and September 29, 1976 (4 specimens). All specimens were found in urban areas or other environments affected by human activities.

Bufo asper Gravenhorst, 1829

Kuala Brang, August 27, 1976 (1 adult specimen), and August 28, 1976. (1 juvenile specimen); Field Study Center of the University of Malaysia, Gombak, September 14, 1976 (1 juvenile specimen). Several other adult specimens, except the collected one, were observed in the day, sitting on rocks 2-3 m above a small river. They were very shy and jumped into the water when disturbed, but returned to their rocks, within 10-30 minutes. The juvenile specimens were collected on the ground at night.

Leptobrachium hasselti Tschudi, 1838

Kuin, August 24, 1976 (1 specimen). It was found on the ground close to a stream in a primary forest.

Kaloula pulchra Gray, 1831

Kuala Lumpur Youth Hostel, August 6, 1976. (1 specimen).

Microhyla heymonsi Vogt, 1911

Kuala Brang, August 26, 1976 (1 specimen); Field Study Center of the University of Malaysia, Gombak, September 17, 1976 (6 specimens). The specimen from Kuala Brang was jumping in the leaf litter of an open secondary forest. The specimens from Gombak were 3 pairs in amplexus found in shallow ditches between 8.30 and 10.30 p.m.

Amolops larutensis (Boulenger, 1899)

Kuala Brang, August 27, 1976 (13 specimens). The frogs were active in the day, jumping in the shadow between the stones (Fig. 2) in a rapid stream particularly close to waterfalls (Fig. 4), and disappeared in the water when disturbed. Several white foam nests with a diameter of 5-7 cm were found on the same stones, just above the water level (Fig. 3).

Limnonectes laticeps (Boulenger, 1882)

Field Study Center of the University of Malaysia, Gombak, September 17, 1976 (1 specimen). It was found in the day, jumping in the leaf litter in a primary forest not far from a stream.

Limnonectes limnocharis (Boie, 1835)

Portugese Settlement, Malacca, July 30, 1976 (5 specimens); Kuin, August 23, 1976 (3 specimens); Kuala Brang, August 25, 1976 (1 specimen) and August 28, 1976 (3 specimens); Bukit Besar, Kuala Trengganu, September 27, 1976 (1 specimens); Field Study Center of the University of Malaysia, Gombak, September 17, 1976 (8 specimens); Biological Field Station, Kota Tinggi, September 20, 1976 (1 specimens). They were all found in areas affected by human activities. The 8 specimens from Gombak were males, actively croaking in water filled ditches.

Figure 2. *Amolops larutensis*, Kuala Brang, Trengganu. The day active frog jumped in the shadow among the stones in a stream.

Figure 4. Habitat for *Amolops larutensis*, Kuala Brang, Trengganu.

Figure 3. Egg mass of *Amolops larutensis*, Kuala Brang, Trengganu

Figure 6. *Rana macrodon*, lateral view, the same individual as in Fig. 5

Figure 5. *Rana macrodon*, dorsal view, Trengganu, Kuin.

Limnonectes macrodon (Duméril and Bibron, 1841)

Kuin, August 23, 1976 (2 specimens). They were found at night, sitting on stones in a small stream in a primary forest (Figs. 5-6).

Rana baramica Boettger, 1901

Kuin, August 24, 1976 (1 specimen). The specimen was observed when it was caught by the colubrid snake *Ahaetulla nasuta* (Lacepede, 1789), in a primary forest close to a stream.

Rana erythraea (Schlegel, 1837)

Bukit Besar, Kuala Trengganu, August 29, 1976 (1 specimen), and September 27, 1976 (1 specimen); Biological Field Station, Kota Tinggi, September 20, 1976 (4 specimens). All specimens were found in the dense vegetation in shallow lakes, some of them also populated with fish.

Rana glandulosa Boulenger, 1882

Biological Field Station, Kota Tinggi, September 20, 1976 (2 specimens). They were found in a logged, swampy area with a dense, secondary vegetation.

Rana nicobariensis (Stoliczka, 1870)

Biological Field Station, Kota Tinggi, September 20, 1976 (2 specimens). They were found croaking at night, in a logged, swampy area with dense, secondary vegetation. They climbed up in the vegetation, 0.5-1 m above the ground.

Rhacophorus leucomystax (Boie, 1829)

Field Study Center of the University of Malaysia, Gombak, September 16, 1976 (29 specimens), and September 17, 1976 (34 specimens); Biological Field Station, Kota Tinggi, September 21, 1976 (3 specimens), and September 22, 1976 (1 specimen). The specimens from Gombak were found in small water-filled pits or wheel tracks, or in the vegetation above them. Several pairs were found in amplexus, and yellow foam nests with whitish eggs were found on the water surface, or on the vegetation about 10 cm above the surface (Fig. 7).

Rhacophorus prominanus Smith, 1924

Kuala Brang, August 27, 1976 (1 specimen). It was found in primary forest, close to a little river.

Discussion

The identity of *Limnonectes macrodon* has been uncertain (Kiew 1978). Kiew (1984c) described a closely related species, *Rana malesiana* (now *Limnonectes malesianus* according to Duellman 1993) earlier confused with *L. macrodon*. The species found by me is *L. macrodon* (Kiew 1984c; Frost 1985) (Fig. 5-6).

Some aspects on the reproduction in *Amolops larutensis* are mentioned, seemingly for the first time, since no information was found in the literature. The reproduction in *Microhyla heymonsi* is studied by Berry (1964) in Singapore and occurs during all times of the year. Additional information is given by Pope (1931). The reproductive pattern of *Rhacophorus leucomystax* varies within its large distributional area. Berry (1964) and Flower (1899) note that they seem to breed at almost all times of the year in Singapore and Malaysia, but Zeller (1960) reported a synchronous periodicity in the reproduction in Java, and Kiyasetuo and Khare (1986) found it to have an annual breeding cycle, with spawning in June, in northeastern India. The reproduction has also been reported by Yorke (1983), Arak (1984), Feng and Narins (1991).

Acknowledgments

I would like to express my sincere thanks to Dr. Kiew Bong-Heang and Dr. Lim Boo-Liat, Kuala Lumpur, for valuable help and advice. I am also most grateful to Mr. Mohammad Zaharan bin Razak, B.Sc., Kuala Trengganu, for the time we spent together in the nature. Professor Immanuel Vigeland invited me to the Biological Field Station, Kota Tinggi. Mr. Ragnar Cedhagen kindly lent me a camera and provided film. Dr. Mats Olsson, Göteborg, critically commented on an earlier version of this manuscript.

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A Catalogue of Non-Metrical Variations in Skull Bones of *Vipera lebetina* (Reptilia, Viperidae)

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Abstract.- This paper presents a description, codes, and figures of 16 variations of non-metrical characters of 122 skull bones of *Vipera* (*Macrovipera*) *lebetina* inhabiting Central Asia and the Caucasus. Statistical characteristics of the number of teeth on the pterigoideum and dental bones for several populations of the three subspecies of the levantine viper are provided.

Key words: Reptilia, Ophidia, Viperidae, *Vipera lebetina obtusa*, *V. l. turanica*, *V. l. cernovi*, Uzbekistan, Turkmenistan, Caucasus, osteology, skull bones.

Introduction

Currently, the use of non-metrical variation in cranial structures for the identification of differences and the determination of whether an individual belongs to some populational group, subspecies or larger taxon, is widely used in zoological studies (Berri, 1975; Yaletsky, 1978; Shubin and Sedokova, 1982; Larina and Eremina, 1988; Zerova and Chikin, 1992). While working on a catalogue of non-metrical variations of the cranial traits of *Vipera lebetina* L., 1758, I attempted to identify the range of variability, systematize the data, and unify techniques for distinguishing, describing, and coding traits and their variations.

Material and Methods

An osteological collection in the Institute of Zoology of the Uzbek Academy of Sciences as well as some skulls from Moscow State University were the basis for this work. A total of 268 skulls of the Levantine viper of different ages and sexes from various localities in both Central Asia and Azerbaistan were used. These populations are attributed by modern taxonomists to the following subspecies:

1. *Vipera* (*Macrovipera*) *lebetina obtusa* Dwigubsky, 1832, 35 specimens;
2. *V.* (*M.*) *l. turanica* Chernov, 1940, 175 specimens;
3. *V.* (*M.*) *l. cernovi* Chikin and Szczerbak, 1992, 58 specimens.

The ordinal numbers of the subspecies correspond to those in the fourth column of Tables 1 and 2 of this catalogue and in the first column of Tables 3 and 4.

Variations of the characters were revealed and illustrated while comparing the bones using the binocular MBI-9 at different magnifications and with a magnifier. The characters are arranged in groups to be presented in the tables: the characters of the bony elements in Table 1 as foramenal characters in Table 2. Table 3 provides statistical characteristics, calculated using standard techniques (Lakin, 1990), of the numbers of the teeth in the pterigoideum and dental bones separately for males and females, and their total; the total number of teeth is given in Table 4. The populations of *V.* (*M.*) *l. turanica* —one from the eastern and western parts of the Nuratau Ridges (EN, WN) and Turkestan (T), the Malguzar Ridge (M), and Gobduntau (G)—are characterized in Tables 3 and 4.

Names of bones and bony elements are given as described by Gurtovoy et al. (1978), Groombridge (1980), Mbrkevitch and Tatarko (1983), and Szyndlar (1984). The names of the characters are coded by the letter symbols (initial letters of their Latin names).

Results

The following non-metrical variations are described in this catalogue: (Table 1) variability in the shape of most cranial bones, (Table 2) foramenal characters, (Table 3) the number of teeth (and whether a subspecies shows variations in this or that trait), and (Table 4) some schematic drawings (Figs. 1–16), illustrating the variations described.

Some of the variations may be considered as insignificant anomalies (rare phenes), which characterize only individual populations of a subspecies. However, the variations are common, i.e., found in each of the subspecies, and are "normal" for a species, though their occurrence is different in each populational group. Naturally-occurring heterogeneity of bilateral structures is not reflected in the catalogue except the characters *Mcp* and *Fpa* on the parietal bone. These combinations, assessed by means of the values of fluctuating asymmetry and observed even on a single (nonpaired) bone, are independent characteristics of stable development and its description is not supposed here.

It is noteworthy that separate variations (Mpa, Mcp), expanding the range of variability, can be in fact considered as the age characteristics and it is this case that necessitates a study on transformations of the characters in ontogeny.

This catalogue cannot be considered comprehensive and should be treated as a scheme, which, when used by researchers, will enable them to amplify it in the following:

(1) description of variability of the other bones;

(2) incorporation of new traits and variations; and

(3) identification of known traits and variations to individuals in various populational and taxonomic groupings, both living and fossil.

Discussion

This publication of the Catalogue is a slightly extended variant of my previous work (Chikin, 1993), which, due to its limited distribution, is inaccessible to most scientists. I will be grateful to my readers for their remarks and glad to have followers.

Acknowledgments

The author is indebted to Galina A. Zerova for discussions resulting in this work. My thanks are extended to Valentina F. Orlova and Evgeny Dunayev (Zoological Museum of Moscow State University) for the specimens from their collection, Dzhavkhar Khodzhaev for translation of the manuscript and Kraig Adler for reviewing it.

Appendix I

Figures 1-16

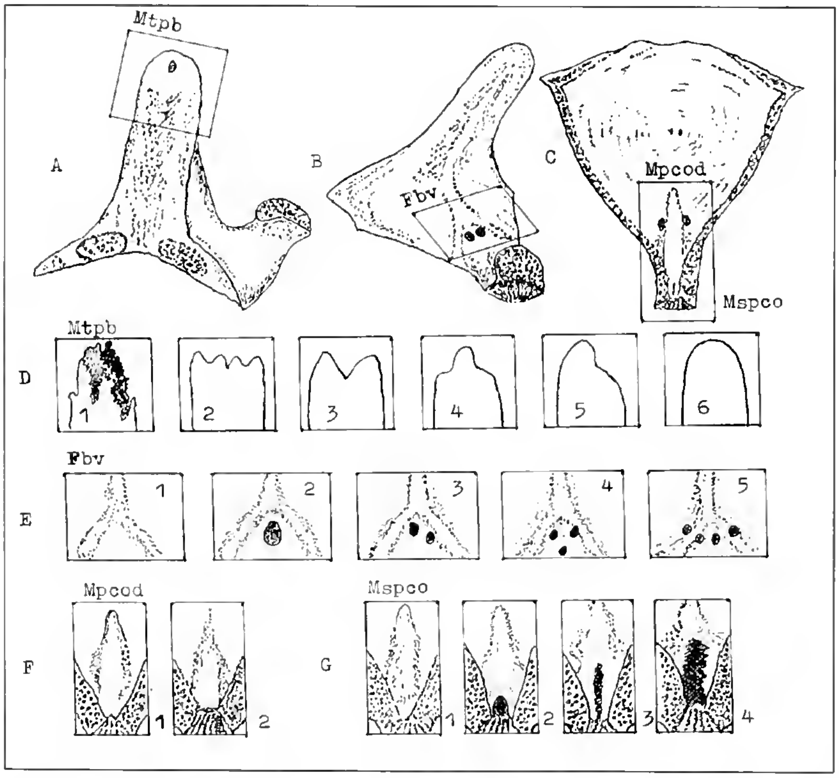

Figure 1. Basioccipital bone. A, B and C are the location of the characters; the numbers of variations correspond to those in Tables 1 and 2.

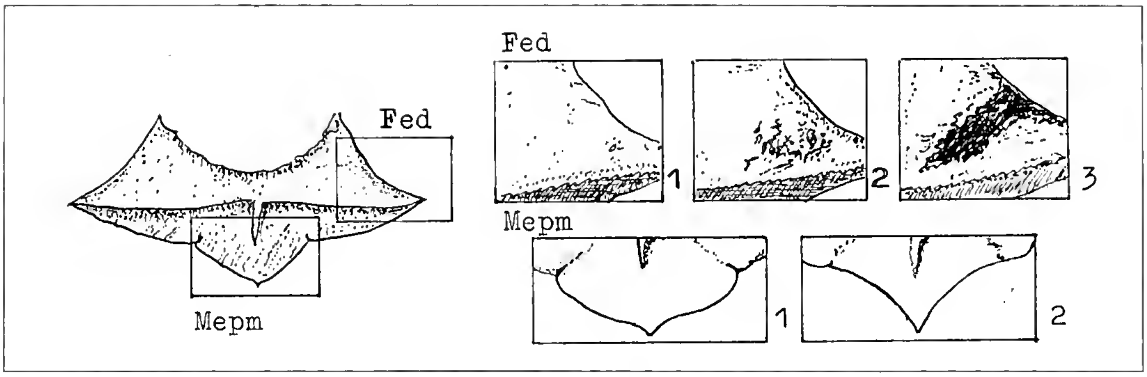

Figure 2. Supraoccipital bone (dorsal view). Location of the characters and their variations.

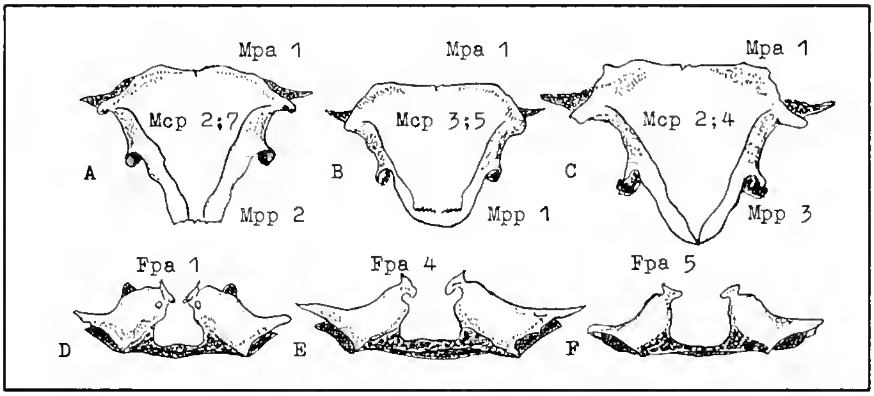

Figure 3. Parietal bone. A, B, and C are the variations of the form of the parietal crest and posterior margin. D, E, and F are the foramina and notches or the anterior edge of the descending part of the bone.

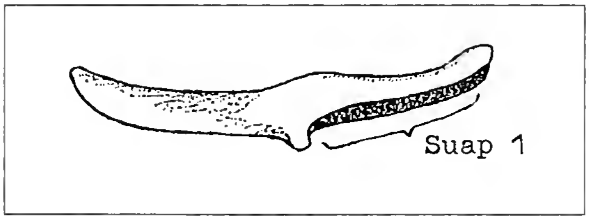

Figure 4. Postfrontal bone, showing the surface that joins with the parietal bone.

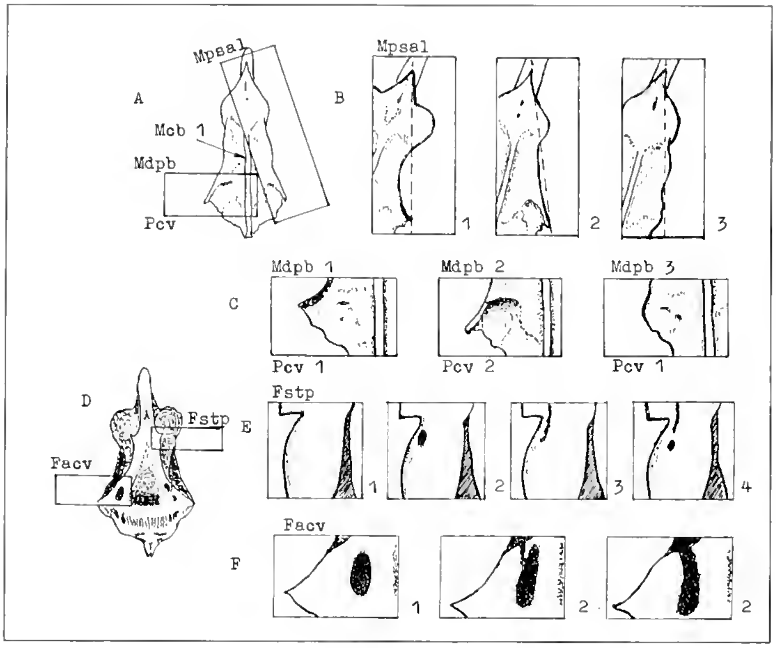

Figure 5. Basiparasphenoid bone. Location of the characters: A - inferior; D - superior views; B, C, E, F - variations.

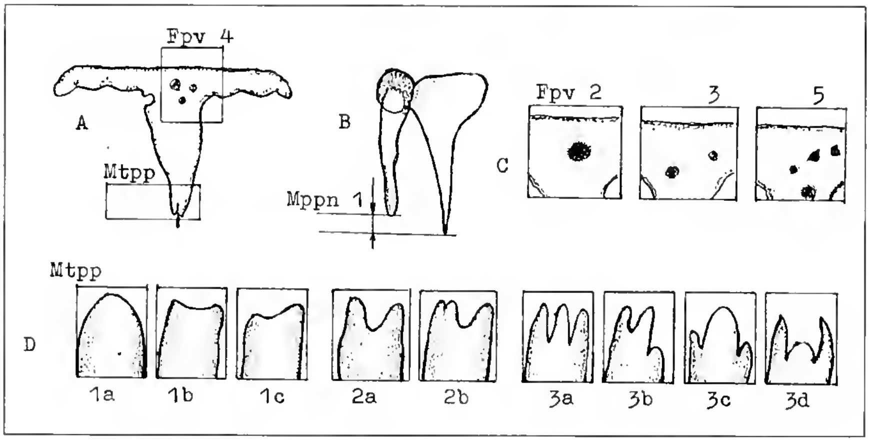

Figure 6. Premaxillary bone: A - inferior, B - lateral views. Location of the characters and (C, D) variations observed.

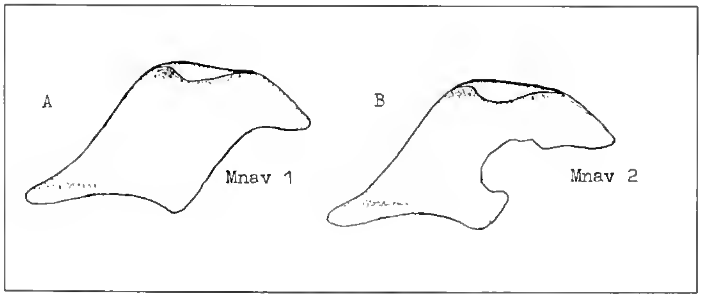

Figure 7. Nasal bone. Variations in the form of the anterior edge.

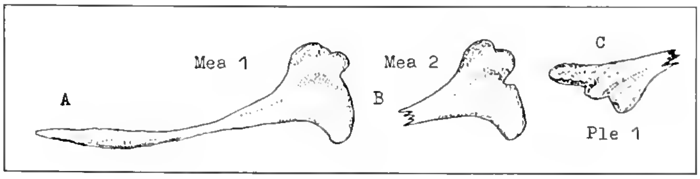

Figure 8. Variations of the anterior margin of the ectopterygoid (A, B); C- external lateral prominence.

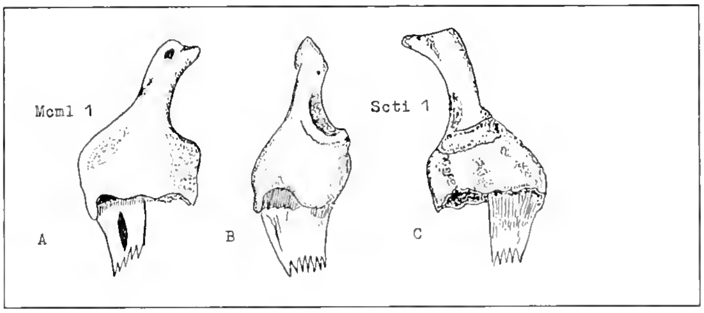

Figure 9. Maxillary bone. A - anterior, B - lateral, C - dorsal views.

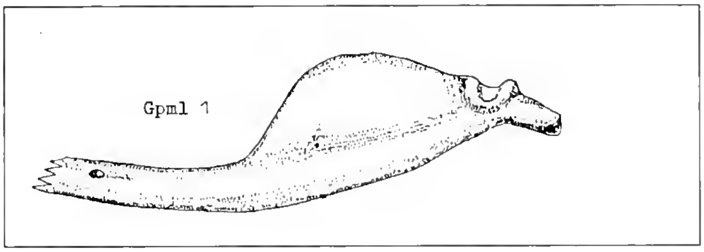

Figure 10. Articular bone. a Proximal part from the external lateral view.

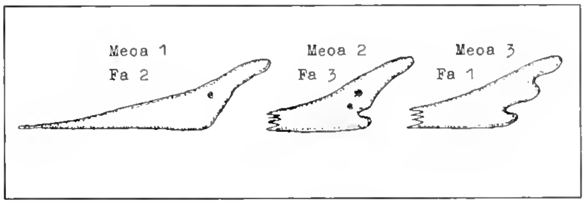

Figure 11. Angular bone. Variations in the form of the anterior margin and foramina.

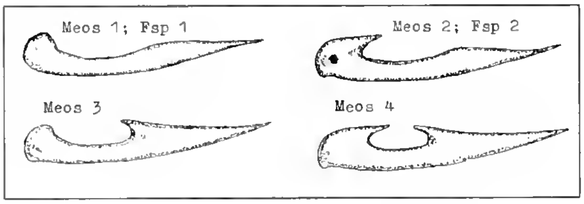

Figure 12. Splenial bone. Variations of the noch or the dorsal part and of the openings.

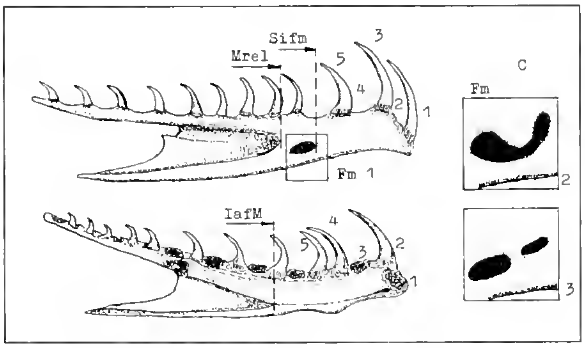

Figure 13. Dental bone. A - external lateral side; the position of the notch margin of the articular bone and mental foramen. B - the internal lateral side, where Mekkel's groove begins to expand. C- variations in the form of the mental foramen. 1 - 5 - numbers of the teeth.

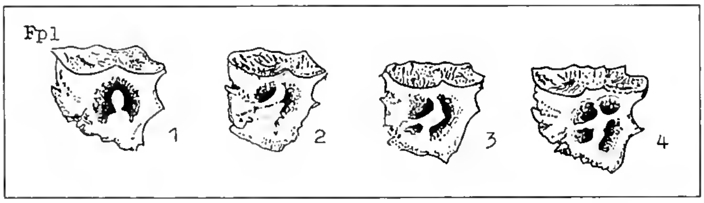

Figure 14. Prooticum (left bone). Variations of the foramina at the external lateral side.

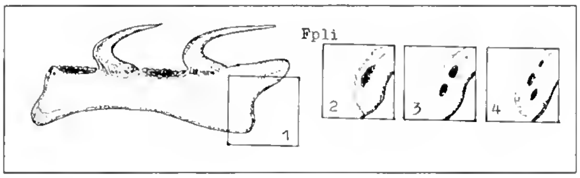

Figure 15. Palatal bone. Variations of the foramina at the dorsal part of the internal lateral surface.

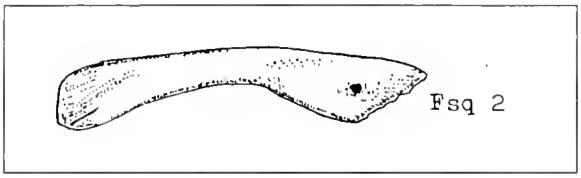

Figure 16. Squamosum bone. A variant with the foramen.

Appendix II

Tables 1-4

TABLE 1. Form of the skull bones in the Levantine Viper.

Character	Description of variations	Code	Subspecies
The main occipital bone—basioccipitale (Fig. 1)			
Margo terminationis processus basioccipitalis (Mtpb)	Coral-shaped	Mtpb 1	2
	Saw-shaped	Mtpb 2	2; 3
	V-shaped	Mtpb 3	1; 2; 3
	Projection in the middle	Mtpb 4	1; 2; 3
	Truncated	Mtpb 5	1; 2; 3
	Roundish	Mtpb 6	1; 2
Margo prominentiae condyli occitocondilaris, pars dorsalis (Mpcod)	Margin of prominence sharply extending above the bone	Mpcod 1	1; 2
	Margin of prominence gently extending above the bone	Mpcod 2	1; 2; 3
Margo sinus prominentiae condili occitocondilaris (Mspco)	Groove absent	Mspco 1	1; 2; 3
	Groove chink shaped	Mspco 2	1; 2
	Groove oval	Mspco 3	1
	Groove irregular	Mspco 4	2; 3
Supraoccipital bone—exoccipitale (Fig. 2)			
Facies exoccipitalis, pars dorsalis (Fed)	Surface is smooth or slightly wavy	Fed 1	1; 3
	Surface with hollows	Fed 2	1

(Continued)

Character	Description of variations	Code	Sub-species
	Surface with deep grooves	Fed 3	2
Margo exoccipitalis posterior, pars medialis (Mepm)	Margin salient	Mepm 1	2
	Margin concave	Mepm 2	3
	Margin straight	Mepm 3	1
Parietal bone—parietale (Fig. 3)			
Margo parietalis anterior (Mpa)	Margin straight	Mpa 1	1; 2; 3
	Margin slightly concave	Mpa 2	2 (juv)
Margo crista parietalis (Mcp)	Crest absent	Mcp 1	2 (juv)
	Crest reaches the posterior margin of the bone	Mcp 2	1; 3
	Crest does not reach the posterior margin of the bone	Mcp 3	2
	Left and right parts of the crest join at acute angles	Mcp 4	3
	Parts of the crest join at right angles	Mcp 5	2
	Parts of the crest do not join	Mcp 6	1
Margo parietalis posterior (Mpp)	Margin roundish	Mpp 1	1; 2
	Margin right-angled	Mpp 2	1; 2; 3
	Margin obtuse-angled	Mpp 3	1; 3
Postfrontal bone—postfrontale (Fig. 4)			
Sutura articuli ossis postfrontale (Suap)	Suture starts at the projection in midpart	Suap 1	1; 2; 3
Basiparasphenoid bone—basiparasphenoid (Fig. 5)			
Margo cristae basiparasphenoidis (Mcb)	Crest long with rounded top	Mcb 1	1; 2; 3
Margo processus suborbitalis et areae lateralis (Mpsal)	Suborbital appendix is big, in the form of a semicircle projecting beyond the line and the margin of the lateral surface passes near the line in the form of a concave arc	Mpsal 1	1
	Suborbital appendix is small, projecting beyond the line in the form of a small sector of a circle or obtuse angle, and the margin of the lateral line parallel with the line or on it	Mpsal 2	1; 2
	Suborbital appendix small, parasphenoid and suborbital appendices project beyond the line, as well as most of the lateral line	Mpsal 3	3

(Continued)

Character	**Description of variations**	**Code**	**Subspecies**
Margo et directio processus basipterigoidis (Mdph)	Appendix sharp and directed upward and to the side	Mdpb 1	1; 2
	Appendix sharp and directed downward, forming outer margin of deep groove	Mdpb 2	1; 2
	Appendix obtuse (not manifested), the groove is shallow or absent	Mdpb 3	2; 3
Pesten canalis vidianus (Pcv)	Crest absent	Pcv 1	1; 2; 3
	Crest present	Pcv 2	1; 2; 3
Premaxillary bone—premaxilla (Fig. 6)			
Margo terminationis processus palatinus (Mtpp)	One-bladed: (a) rounded	Mtpp 1a	1; 3
	(b) flat	Mtpp 1b	1; 2; 3
	(c) truncated	Mtpp 1c	1; 3
	Two-bladed: (a) V-shaped	Mtpp 2a	1; 2, 3
	(b) V-shaped with a hollow	Mtpp 2b	1; 2
	Three-bladed: (a) equal trident	Mtpp 3a	2
	(b) one of the last teeth is smaller than the others	Mtpp 3b	2
	(c) the last teeth are smaller than the middle tooth	Mtpp 3c	2
	(d) the last teeth are bigger than the middle tooth	Mtpp 3d	2
Magnitudo processus palatinus et processus nasalis (Mppn)	Palatal process is smaller than the nasal	Mppn 1	1; 2; 3
Nasal bone—nasale (Fig. 7)			
	Edge straight	Mnav 1	1; 2; 3
Margo nasalis anterior, pars verticalis (Mnav)	Edge with notch	Mnav 2	1
Ectopterygoid bone—ectopterygoid (Fig. 8)			
Margo ectopterigoidis anterior (Mea)	Margin with projection	Mea 1	1; 2
	Margin with projection and groove	Mea 2	1; 2; 3
Prominentia lateralis exterior (Ple)	Downward-turning projection	Ple 1	1; 2; 3
Maxillary bone—maxillare (Fig. 9)			
Margo corpus maxillare, pars lateralis (Mcml)	Bone expanded with large shoulder-shaped projection	Mcml 1	1; 2; 3

(Continued)

Character	Description of variations	Code	Sub-species
Sinus et crista transversus dorm salts, pars interior (Scti)	Opening rectangular; crest well developed	Scti 1	1; 2; 3
Articular bone—articulare (Fig. 10)			
Gradus evolutionis processes medialis et processus lateralis (Gpml)	The medial process is significantly larger; the lateral process is small and smooth	Gpml 1	1; 2; 3
Angular bone—angulare (Fig. 11)			
Margo exiguus ossis angulares (Meoa)	Margin even (no projection observed)	Meoa 1	2; 3
	Margin with process below	Meoa 2	1; 2; 3
	Margin with processes below and in the middle	Meoa 3	1; 3
Splenial bone—spleniale (Fig. 12)			
Margo emarginaturae ossis spleniale (Meos)	Notch not restricted by the projections	Meos 1	1; 2; 3
	Notch posteriorly restricted by the projection	Meos 2	2; 3
	Notch anteriorly restricted by the projections	Meos 3	1; 2
	Notch both anteriorly and posteriorly restricted by the projections	Meos 4	1; 2; 3
Dental bone—dentale (Fig. 13)			
Magnitudo relativa emarginaturae ossis articulare, pars lateralis exterior (Mrel)	Margin of notch reaches 7th tooth	Mrel 1	2
	Margin reaches 8th tooth	Mrel 2	1; 2; 3
	Margin reaches 9th tooth	Mrel 3	1; 2; 3
	Margin reaches 10th tooth	Mrel 4	1; 2; 3
	Margin reaches 11th tooth	Mrel 5	1; 2; 3
	Margin reaches 12th tooth	Mrel 6	1; 3
Initialio apertionis fissurae Mekkelii (IafM)	Fissure opens under 7th tooth	IafM 1	1; 2
	Fissure opens under 8th tooth	IafM 2	1; 2; 3
	Fissure opens under 9th tooth	IafM 3	1; 2; 3

TABLE 2. Foramenal traits of the skull bones in Levantine Viper.

Character	Description of variations	Code	Subspecies
The main occipital bone-basioccipitale (Fig. 1)			
Foramen ossis basioccipitale, pars ventrale (Fbv)	Foramen not present	Fbv 1	2; 3
	One foramen	Fbv 2	1; 2; 3
	Two foramina	Fbv 3	1; 2
	Three foramina	Fbv 4	1
	Four foramina	Fbv 5	1
Prooticum bone-prooticum (Fig. 14)			
Foramen ossis prooticum, pars lateralis (Fpl)	One foramen	Fpl 1	1
	Two foramina	Fpl 2	1; 2; 3
	Three foramina	Fpl 3	1; 2; 3
	Four foramina	Fpl 4	2
Parietal bone-parietale (Fig. 3)			
Foramens et emarginaturas ossis parietale, pars anterior (Fpa)	Two completely closed foramina	Fpa 1	2
	One of the foramina is not closed	Fpa 2	2
	Two open foramina, rupture in the wall smaller than the diameter of the foramen	Fpa 3	2; 3
	Two open foramina, rupture in the wall larger than or equal to the diameter of the foramen	Fpa 4	3
	Of equal size on both sides	Fpa 5	1
Basiparasphenoid bone-basiparasphenoid (Fig. 5)			
Foramen et sulculus processes trabecularis (Fspt)	Both foramen and sulcus missing	Fspt 1	1; 2; 3
	Foramen present	Fspt 2	2
	Sulcus present	Fspt 3	1; 2; 3
	Both a groove and sulcus present	Fspt 4	1
Foramen anterior canalis vidianis (Facv)	One fossa	Facv 1	1; 2
	External edge of foramen not closed (partition has sulcus, canal)	Facv 2	1; 3
Premaxillary bone-premaxilla (Fig. 6)			

(Continued)

Character	Description of variations	Code	Sub-species
Foramen ossis premaxilla, pars ventralis (Fpv)	Foramen not present	Fpv 1	2
	One foramen	Fpv 2	1; 2; 3
	Two foramina	Fpv 3	1; 2; 3
	Three foramina	Fpv 4	1; 2; 3
	Four foramina	Fpv 5	1
Palatine bone-palatinum (Fig. 15)			
Foramen ossis palatinum, pars lateralis interior (Fpli)	Foramen not present	Fpli 1	1; 2
	One foramen	Fpli 2	1; 2; 3
	Two foramina	Fpli 3	1; 2; 3
	Three foramina	Fpli 4	1; 2; 3
Squamose bone squamosum (Fig. 16)			
Foramen squamosum (Fsq)	No foramen	Fsq 1	1;2;3
	One foramen	Fsq 2	2;3
Angular bone-angulare (Fig. 11)			
Foramen angulare (Fa)	No foramen	Fa 1	1;2;3
	One foramen	Fa 2	2
	Two foramina	Fa 3	2
Splenial bone spleniale (Fig. 12)			
Foramen spleniale (Fsp)	No foramen	Fsp 1	1;2;3
	One foramen	Fsp 2	2
Dental bone-dentale (Fig.13)			
Foramen mentale (date, form)(Fm)	One foramen, oval	Fm 1	1;2;3
	One half-moon-shaped foramen	Fm 2	2
	Two oval foramina	Fm 3	2;3
Situs foramen mentale (Sifm)	One foramen under 5th tooth	Sifm 1	1
	One foramen under 6th tooth	Sifm 2	1;2;3
	One foramen under 7th tooth	Sifm 3	1;2;3
	One foramen under 8th tooth	Sifm 4	3
	Two foramina under 4th and 7th teeth	Sifm 5	2
	Two under 5th and 6th teeth	Sifm 6	2
	Two under 5th and 7th teeth	Sifm 7	2

(Continued)

Character	Description of variations	Code	Sub-species
	Two under 6th and 7th teeth	Sifm 8	2
	Two under 6th and 8th teeth	Sifm 9	2
	Two under 7th and 8th teeth	Sifm 10	2;3

TABLE 3. Statistical characteristics of tooth number on the pterigoideum and dental bones of the levantine viper

		Pterigoideum bone indices				Dental bone indices			
Sub-species	Sex	n	Range	x±Sx	CV	n	Range	x±Sx	CV
1	♂	16	11-15	13.2±0.33	10.1	16	15-19	16.4±0.23	5.7
	♀	40	11-16	13.4±0.16	7.6	40	14-19	16.3±0.22	8.5
	Σ	56	11-16	13.3±0.15	8.4	56	14-19	16.3±0.17	7.8
2 WN	♂	59	12-15	13.7±0.10	5.5	59	16-21	18.2±0.14	5.9
	♀	43	12-15	13.9±0.12	5.7	42	17-21	18.0±0.16	5.6
	Σ	102	12-15	13.8±0.08	5.6	101	18-21	18.1±0.10	5.8
2 EN	♂	30	12-17	13.8±0.18	7.1	29	16-20	17.7±0.17	5.1
	♀	14	12-15	13.7±0.21	5.8	14	16-20	17.4±0.28	6.0
	Σ	46*	12-17	13.8±0.13	6.8	45*	16-20	17.6±0.15	5.5
2 M	♂	21	12-17	14.1±0.27	8.8	21	16-23	18.9±0.34	8.2
	♀	8	12-14	13.4±0.25	5.2	8	17-19	17.9±0.21	3.4
	Σ	29	12-17	13.9±0.22	8.4	29	16-23	18.6±0.26	7.7
2 G	♂	16	11-15	13.4±0.25	7.4	16	17-19	17.7±0.15	3.3
	♀	2	14	—	—	2	18	—	—
	Σ	20*	11-15	13.4±0.24	8.0	19*	16-19	17.6±0.15	3.8
2 T	♂	44	12-16	13.8±0.13	6.2	42	17-20	18.2±0.14	5.1
	♀	23	12-16	13.8±0.23	7.9	24	16-23	17.9±0.28	7.7
	Σ	79*	12-16	13.9±0.10	6.7	77*	16-23	18.1±0.12	6.0
3	♂	40	12-17	14.3±0.16	7.0	38	17-20	18.3±0.14	4.8
	♀	34	13-16	14.7±0.15	6.1	29	17-20	18.3±0.13	3.9
	Σ	94*	12-17	14.4±0.10	6.9	83*	17-20	18.3±0.09	4.6

* - The bones of the snakes of unknown sex were added; x - mean; Sx - Standard error; CV - coefficient of variation

TABLE 4. Total tooth number on the skull in the Levantine Viper.

Bone **Subspecies:**	**1**	**2, EN**	**2, WN**	**2, M**	**2, G**	**2, T**	**3**
Maxilare (left+right)	1+1	1+1	1+1	1+1	1+1	1+1	1+1
Palatinum (left+right)	4+4	4+4	4+4	4+4	4+4	4+4	4+4
Pterygoideum (x*2)	26.6	27.6	27.6	27.8	26.8	27.8	28.8
Upper jaw segment	36.6	37.6	37.6	37.8	36.8	37.8	38.8
Dentale (x*2)	32.6	36.2	35.2	37.2	35.2	36.2	36.6
Total teeth	69.2	73.8	72.8	75.0	72.0	74.0	75.4

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A New Gecko of the Genus *Gonydactylus* (Sauria: Gekkonidae) with a Key to the Species from Vietnam

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Abstract: *Gonydactylus paradoxus* sp. nov from a small off-shore island in South Vietnam distinctly differs from all other known species of the genus *Gonydactylus* in the absence of preanal and femoral pores in males and females. The occurrence in a new insular species of a feature so unusual for the genus *Gonydactylus* may be an external manifestation of founder effect sensu E. Mayr (1942).

Key words: Lizards, Gekkonidae, *Gonydactylus*, femoral pores

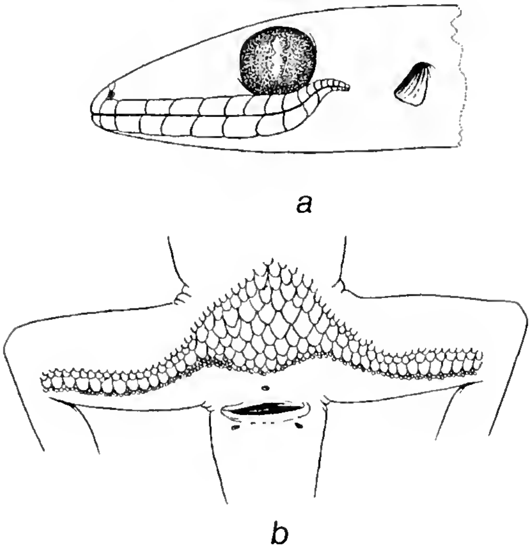

Figure 1. Lateral view of head (a) and preanal and femoral areas (b) of a holotype of *Gonydactylus paradoxus* sp. nov. Note the rows of enlarged preanal and femoral scales.

Introduction

The validity of the genus *Gonydactylus* Kuhl et van Hasselt, 1822, originally described at the beginning of the last century and long regarded as a synonym of the genus *Cyrtodactylus* Gray, 1827, has recently been advocated by Kluge (1991). According to the latter author and current literature *Gonydactylus* comprises 62 species widely distributed within the South and South-Eastern Asia. Some of them have been only recently described from the Borneo (Hikida, 1990) and from Thailand (Ulber, 1993).

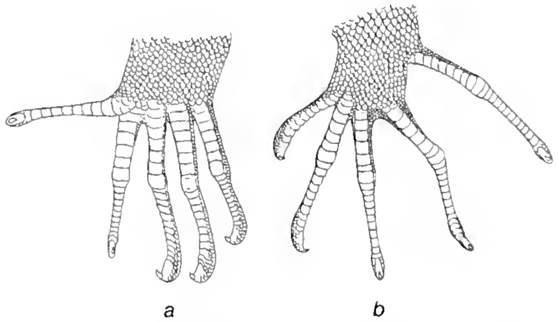

Figure 2. Lower surface of the right manus (a) and right pes (b) of a holotype of *Gonydactylus paradoxus* sp. nov.

Among the most important diagnostic characters in the genus are the pattern of disposition and number of femoral and preanal pores, which are present in specimens of all known species of *Gonydactylus*. Some years ago on a small offshore island of South Vietnam the first author collected a series of specimens of a species of *Gonydactylus* totally devoid of both femoral and preanal pores. A more detailed examination has shown that these lizards constitute a rare new species of the genus *Gonydactylus*. A description of this form is provided below.

The following acronyms and abbreviations are used: ZIL - Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZMK - Zoological Museum, Ukranian Academy of Sciences, Kiev; SVL - snout-vent length; TL - tail length.

Gonydactylus paradoxus sp. nov. (Figures 1-3)

Holotype: ZIL 20310, Hon Thom Isle near south point of Phu Quoc Island, Kieng Giang Province,

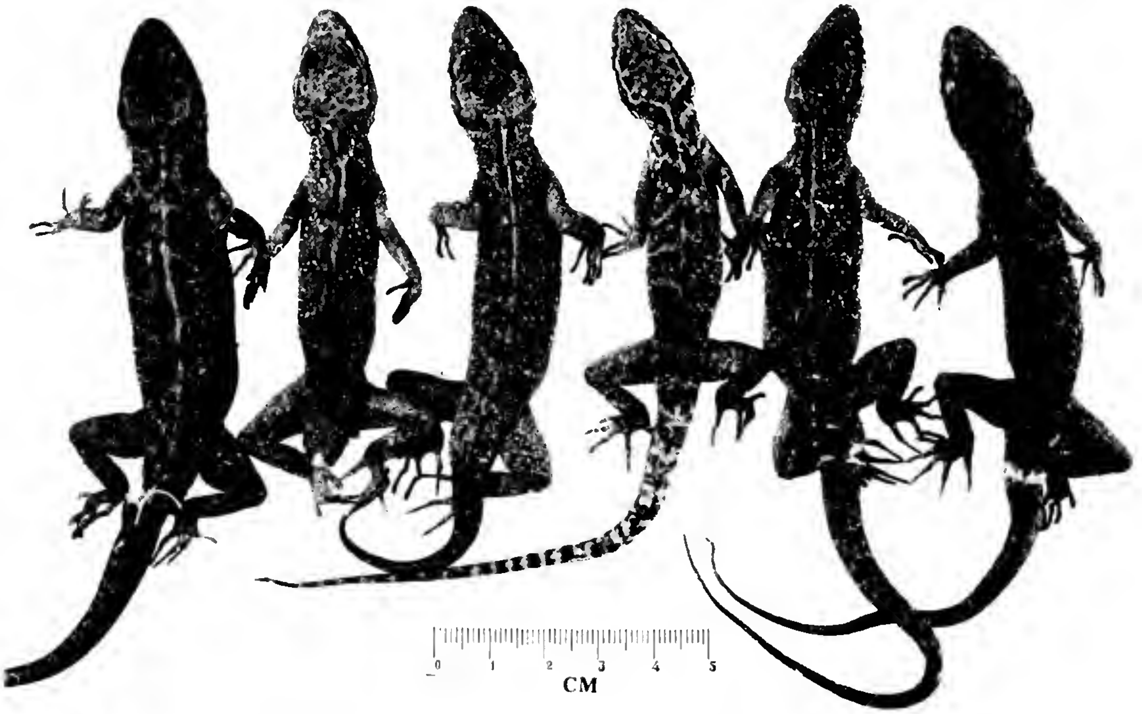

Figure 3. Dorsal coloration variability in six paratype specimens of *Gonydactylus paradoxus* sp. nov.

South Vietnam, coll. I. Darevsky, April 13, 1987, adult male.

Paratypes: ZIL 20311-20315, 204-21, 20422, 20479-20481; ZMK Re 22, 23a (7 males, 6 females). Same data as for holotype.

Etymology: The species name derives from the Greek word "*paradoxos*" - unusual, strange; in the present case referring to the lack of femoral and preanal pores.

Diagnosis: A medium-sized species of *Gonydactylus* with an adult body size of 45-84 mm in SVL; no preanal groove, no preanal and femoral pores in males or females; enlarged femoral scales distinct; 26-36 midventral scale rows between indistinct lateral folds; 17-23 subdigital lamellae under fourth toe; a median series of transversely widened subcaudal scales; irregular crossbands on the dorsum.

Description of the holotype: Adult male, 80 mm SVL; 95 mm TL; head oviform; forehead concave; snout obtusely pointed; ear opening oval; eye with vertical *Gekko*-type pupil; rostral large, quadrangular, partially split by a median vertical cleft, contacting nostrils, first upper labials and three enlarged internasals; first upper labial, two postnasals, supranasal and rostral forming border of nostril; scales on snout three or more times larger than on occiput or interorbital area; approximately 44 granules between palpebral borders of eyelids at the middle of the orbits; granules on the back of the head intermixed with few small conical scales; 10/9 supralabials; mental triangular with labial border wider than labial border of rostral; 9/9 lower labials; one large pair of postmental about 1/2 the size of the first; four gular scales bordering first postmentals between second postmentals followed by small gular granules. Dorsal surface of the body with fine scales mixed with about 16 irregular rows of small rounded conical or trihedral tubercles; small tubercles developed on dorsal part of legs; ventrolateral folds feebly indicated by low rounded tubercles; ventral scales small, cycloid, equal in size; about 30 scalerows between ventrolateral folds; approximately 135 scales in a row from chin shields to vent at medial ventral line; one row of enlarged smooth femoral scales on underside of thighs; no femoral and preanal pores; tail round in cross-section, verticilate, covered dorsally and laterally with small granules, with 4-6 low tubercles near posterior part of each segment; a median series of transversely widened subcaudals.

Color (in life): Head and body yellow-brown above, lighter below; back with seven brown-bordered light undulating transverse bands, divided by a narrow lon-

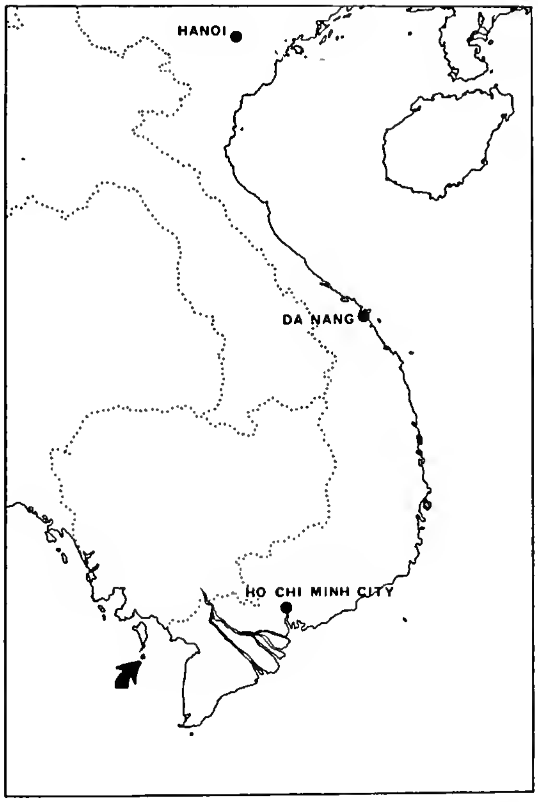

Figure 4. Type locality (indicated by arrow) of *Gonydactylus paradoxus* sp. nov. at Thom Island, Kien Giang Province, South Vietnam.

gitudinal vertebral stripe; tail with dark rings separated by narrow light interspaces.

Variation: The paratype specimens resemble the holotype in all major characters. SVL of seven mature males 41.0-84.0 mm and 50.3-78.0 mm for mature females; scale rows between ventrolateral folds 30-34; scales in a row from chin shields to vent 188-144. Variations in dorsal coloration are shown in Fig. 3.

Distribution: All specimens are known only from the type locality on Hon Tom Island in South Vietnam (Fig. 4). It can be assumed that this island species also occurs one some of the neighboring small islands in the Gulf of Siam.

Field notes: All specimens from the type series were collected at night on dry rocks under the canopy of a secondary dipterocarp forest. By day, however, no geckos were detected at the same place.

Reproduction: Four females kept in terraria laid 2 eggs repeatedly. Following about 55 days of incubation, young geckos 45-47 mm in total length were hatched. A peculiar coloration of the young involves the presence of bright white transverse rings on the tail, which are hardly noticed in the adults.

Comparative notes: The intrageneric systematics of the genus *Gonydactylus* has been largely based on the pattern of scuttelation of the preanal and femoral areas. The presence of more or less well developed preanal or femoral pores is characteristic of all of previously-described representatives of the genus, the number and disposition of these pores significantly varying in different species. The pores are commonly present in males only, although these may occasionally be distinguishable in females too. Some species display both femoral and preanal pores, whereas others possess either the former or the latter.

There are 15 species of *Gonydactylus* in Indochina, four of which are known from Vietnam. All of them, with the exception of *G. paradoxus* exhibits the presence of preanal pores. As mentioned above, this new species has no pores at all, and thus differs from other representatives of the genus. In this regard *G. paradoxus* exhibits some similarity to some Thai specimens of *G. oldhami* whose males have generally 1-4 preanal pores, but which may lack pores entirely (Smith, 1935; Taylor, 1963; Ulber, 1993). However, *G. oldhami* definitely differs from *G. paradoxus* in a number of other characters, particularly in possessing a non-segmented tail and characteristic white spots on the back. Among other Indochinese species, the new species, according to its coloration and some other markers, seems to be somewhat close to *G. angularis* Smith from south Thailand, but differs from it in some characters, in particular in a larger number (40-48) of ventral scale rows between a ventrolateral folds (versus 30-34 in *G. paradoxus*). On the basis of the majority of its characters the newly described species obviously also differs from *G. condorensis* (Smith, 1921), a Vietnamese endemic insular species from Pulo Condore (Con Dao) Island in the South China Sea. Literature records (Bobrov, 1995) citing *G. philippinicus* from Vietnam are not confirmed by voucher material and seem to be erroneous.

As is generally known, insular animals, in particular some reptile species, often display unusual morphological characters (Mertens, 1934), which may be regarded as a manifestation of the so called "founder effect", originally formulated by E. Mayr (1942). This principle attributes genetic uniformity and phenotypic specificy of specimens within an isolated population to an origin from a small founding population, perhaps a single fertilized female, which might possess certain features not characteristic of the species. It is assumed that the insular population of *Gonydactylus* on Hon Thom may have originated from an accidentally introduced female having some genes controlling the formation in ontogeny of femoral or preanal pores (Darevsky et al., 1991).

Key to the species of *Gonydactylus* in Vietnam

1 (6) Underside of tail with transversely enlarged plates.

2 (3) Body banded with four distinct dark light-edged dorsal cross-bars . . . . *G. intermedius* Smith.

3 (2) Body without distinct banded pattern.

4 (5) Males with a group of 4 to 7 preanal pores; 35-40 scales across the belly . . . . . *G. condorensis* Smith.

5 (4) Males and females without preanal pores; 30-34 scales across the belly. . . . . *G. paradoxus* sp. nov.

6 (1) Underside of tail with numerous roundish scales . . . . *G. irregularis* Smith.

Acknowledgments

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Rediscovery of *Lipinia macrotympanum* (Stoliczka, 1873) from the Nicobar Islands, India

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Abstract.- Stoliczka's (1873) *Mocoa macrotympanum*, known from the holotype collected over 120 years ago from the Andaman Islands, India, is redescribed on the basis of two specimens from Little and Great Nicobar Islands, India. The species is diagnosed by: small body size (SVL up to 38.1 mm); tympanum exposed; disk on lower eyelid translucent; prefrontals separate; the failure of the adpressed hind limbs to meet the fore limbs; 21-23 smooth midbody scale rows; 15-17 subdigital scansors under toe IV; three pairs of nuchals; four supraoculars; seven supralabials (supralabial V in midorbit position); six infralabials; and lateral bands starting from the nostrils.

Key words.- *Lipinia macrotympanum*, Sauria, Scincidae, Great Nicobar, Little Nicobar, India.

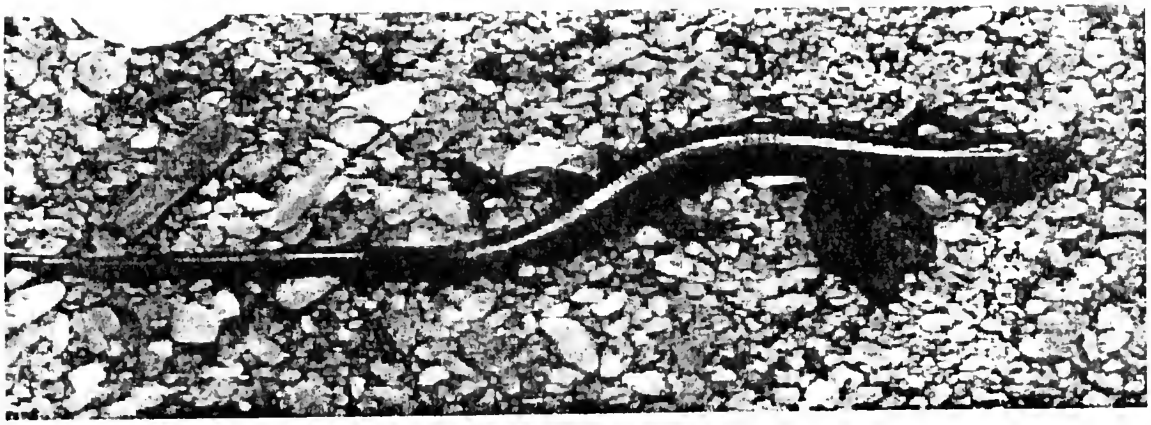

Figure 1. *Lipinia macrotympanum* (MCZ R-176760) from Pulo Ulan (07 03'N; 93 35'E), Little Nicobar, India, in life.

Introduction

Mocoa macrotympanum was described by Stoliczka (1873), based on a single example from "South Andaman....on a sandy beach in Macpherson's Straits" (11º 31'N; 92º 39'E), which lie between South Andamans and Rutland Island, that was deposited in the collection of the Asiatic Society of Bengal, in Calcutta. The holotype is now in the collection of the Zoological Survey of India (ZSI 5571). No further examples of this distinctive species have come to light. In Mittleman's (1952) synopsis of scincids, the species was assigned to the genus *Scincella*, although Greer (1974) subsequently placed Stoliczka's species in the genus *Lipinia*, now known to include 20 nominal species (Austin, 1995; Greer, 1974; Greer and Mys, 1987) that are diagnosable by their small (SVL 56 mm) size, generally slender body, lack of a postorbital bone and a dorsal color pattern of striking light, and dark longitudinal stripes. Their distribution includes the insular regions of south-east Asia, including the Sundas east to the Philippines, New Guinea, with one species (*L. noctua*) reaching Polynesia, further east (see Fig. 45 in Greer, 1974, and Fig. 8 in Zweifel, 1979) that is suspected to be spread through human agencies (Greer, 1989). Only one species (*L. vittigera*) has been recorded from the Asian mainland (Greer, 1974).

The collection of an example (Fig. 1) of *Lipinia macrotympanum* during field work conducted in the Nicobars in 1994 and an examination of another Nicobarese specimen (from Great Nicobar), referred to *Sphenomorphus quadrivittatum*, although with some hesitation, by Biswas and Sanyal (1977), provide an opportunity to both enlarge the description of the species based on the two Nicobarese specimens and announce its rediscovery after over 120 years.

Material and Methods

The material from Little Nicobar was fixed in 10% formalin for two weeks, soaked in distilled water to remove the formalin for a day and finally preserved in 70% ethanol. The following measurements were taken 13-14 months (for the material from Little Nicobar) and 29 years (the material from Great Nicobars) after collection, with dial vernier caliper (to the nearest 0.1 mm): snout-vent length (SVL; from the tip of the snout to the vent), tail length (TL; from the vent to the tip of the unregenerated tail), tail width (TW; measured at the base of the tail); head length (HL; the distance between the angle of the jaws and the snout-tip), head width (HW; measured at the angle of the jaws), head depth (HD; the maximum height of the head, from the forehead to the throat), tympanum diameter (TYD; the greatest [vertical] diameter of the tympanum), body width (BW; the greatest width of the body), axilla to groin length (A-G; the distance between the posterior edge of the fore limb and the anterior edge of the hind limb), eye diameter (ED; the greatest diameter of the orbit), eye to nostril distance (E-N; the distance between the anterior-most point of the eyes and the nostrils), eye to snout distance (E-S; the distance between the anterior-most point of the eyes and the tip of the snout), eye to ear distance (E-E; the distance from the anterior edge of the ear opening to the posterior corner of the eyes), greatest ear length (EL; the greatest diameter of the ear opening), internarial distance (IN; the distance between the upper eyelids), fore limb length (FOL; the length of the outstretched fore limb, from axilla to the tip of its longest finger), and hind limb length (HIL; the length of the outstretched hind limbs, from vent to the tip of its longest toe).

Institutional abbreviations follow Leviton *et al.* (1985). Color nomenclature is that suggested by Smith (1974; 1981) and taken from Kodak Gold film. Nomenclature of dorsal striping is after Storr *et al.* (1981).

Lipinia macrotympanum (Stoliczka, 1873)

Material examined: MCZ R-176760, Pulo Ulan (07 03'N; 93 35'E), Little Nicobar, India. Coll. Indraneil Das and Satish Bhaskar, 31 March, 1994; ZSI 22508, Campbell Bay (06 50'N; 93 50'E), Great Nicobar, India. Coll. A. Daniel, Great Nicobar Expedition, 1966.

Diagnosis.- A member of the genus *Lipinia* (fide Greer, 1974), differentiable from congeneric species in possessing the following suite of characteristics: small body size (SVL up to 38.1 mm); tympanum exposed; disk on lower eyelid translucent; prefrontals separate; failure of the adpressed hind limbs to meet the fore limbs; 21-23 smooth midbody scale rows; 15-17 subdigital scansors under toe IV; three pairs of nuchals; four supraoculars; seven supralabials (supralabial V in midorbit position); six infralabials; and lateral bands starting from the nostrils.

Redescription.- In general form, a supple skink, the body elongated with fairly well-developed limbs. Head relatively small (HL/SVL ratios 0.15 and 0.16), snout acute, the sides converging to a distinctly rounded tip; head relatively more slender than the body, with a distinct neck, and longer than wide; head and body slightly depressed dorso-ventrally; tail long (TL/SVL ratios 1.20 and 1.41), rounded in cross section and tapering to a sharp point.

Rostral enlarged and visible dorsally, broader than high, forming a straight suture with frontonasal; supranasals absent; postnasals contact supralabial II; two loreals contact supralabials II and III; two preoculars, smaller (preocular I) in contact with supralabial IV; supralabials seven; infralabials eight; presubocular in contact with both supralabials IV and V; supralabial IV in midorbital position; last supralabials horizontally split; frontonasal broader than long, broadly in contact with the rostral anteriorly and with the prefrontals posteriorly; prefrontals not in contact with each other; supraoculars four; frontal long, spear-shaped, in contact with supraoculars I and II; fused fronto-parietals; interparietal triangular, with apex partially dividing parietals, and covering a relatively large and distinct parietal eye; supracilliaries 10; two pre-temporals; two primary temporals; two secondary temporals; three pairs of smooth nuchals; mental wider than long, in contact with infralabials I and II; postmental longer than wide, in contact with infralabials II and III; three pairs of chin shields follow the postmental on each side, the first pair in contact with each other, the second pair divided medially by the a single row of ventral scale, and the third pair separated by three rows of ventral scales; tympanum exposed, longer vertically, its greatest length more than half eye diameter (ED/EL ratios 1.30 and 1.64), shallow, lacking lobules.

Body slender (BW/SVL ratios 0.12 and 0.13); fore and hind limbs well developed (FOL/SVL and HIL/SVL ratios 0.22 and 0.23, and 0.32 and 0.33, respectively), adpressed hind limbs fail to touch fore limbs.

Dorsally, the scales on body, limbs and tail are smooth; ventrally, scales imbricate with three to four very fine striations; midbody scale rows 21 and 23;

Table 1. Meristic data (in mm) on the two Nicobarese specimens of *Lipinia macrotympanum*

	MCZ R-176760	ZSI 22508
Snout-vent length	38.1	36.5
Tail length	53.6	43.9
Tail width	3.3	3.6
Head length	5.8	5.8
Head width	3.9	3.7
Head depth	3.2	3.4
Body width	4.7	4.7
Axilla to groin distance	20.2	21.3
Eye diameter	1.8	1.3
Eye to nostril distance	1.6	1.5
Eye to snout distance	2.7	2.9
Eye to ear distance	2.9	2.6
Ear length	1.1	1.0
Internarial distance	1.7	1.3
Fore limb length	8.4	8.4
Hind limb length	12.5	11.7

ventral scale rows (postmental to anal) 62; preanals not enlarged; tripartite, the inner scales overlapping the outer; ventrally, tail scales smooth, with imbricate scales, the median series not being enlarged; scales on palms and soles flattened and rounded. Subdigital lamellae (MCZ R-176760) are as follows: (right fore limb) finger I: 5; finger II: 9; finger III: 11; finger IV: 11; finger V: 7; (right hind limb) toe I: 7; toe II: 12; toe III: 13; toe IV: 16; toe V: 11, transversely enlarged, pad-like.

Measurements (in mm) of the two Nicobarese specimens are in Table 1. Subdigital formulae: 4 > 3 > 2 > 5 > 1 (manus); 4 > 3 > 2 > 5 > 1 (pes).

Color.- Vertebral stripe trogon yellow; paravertebral stripes blackish neutral gray; dorsals trogon yellow; dorsolateral stripes blackish neutral gray; snout cinnamon; ventrally, the body is an unpatterned cream; tail beyond cloaca burnt orange both dorsally and ventrally; upper surfaces of limbs Pratt's rufous; undersurface of manus and pes gray-brown (in preservative).

Ecological notes.- Of the specimen from Great Nicobars, no field data are on record. Stoliczka's type was taken from a beach, as was MCZ R-176760, which was found moving with great agility over sand, into which it made no attempts to burrow. Anecdotal notes, and in certain cases, more detailed observations on most of its congeners suggest however that members of the genus *Lipinia* are largely arboreal (e.g., Brown and Fehlmann, 1958, for *L. leptosoma;* Loveridge, 1948:360, for *L. miotis;* Brown and Alcala, 1980:95-96, for *L. pulchella*, Brown and Alcala, 1980:87, for *L. quadrivittata*, Greer and Mys, 1987, for *L. rouxi;* Brown and Alcala, 1980:100, for *L. semperi*, Brown and Alcala, 1980:89, for *L. subvittata* Smith, 1930:36; 1935:307, for *L. vittigera*), although *L. noctua*, which is arboreal elsewhere (Greer and Mys, 1987; Loveridge, 1948:358), is substrate dwelling on some of the islands of Fiji (Zug, 1991) and Hawaii (Oliver and Shaw, 1953; McMorris, 1970). The holotype of *Lipinia macrotympanum* contained two eggs (Smith, 1935).

Variation.- The differences between the holotype and hitherto only known specimen, as given by Stoliczka (1873) and the fresh material from the Nicobars are understandable, given the distance between the two island groups. The holotype showed 15 lamellae under the fourth toe (as opposed to 16 and 17) and 22 midbody scale rows (vs 21 and 22 in the Nicobarese material). In addition, the color notes taken by Stoliczka (1873) indicate that the ventral surface of his specimen (a gravid female) was livid carneous tinged with orange, while the Nicobarese specimens have an unpatterned cream belly.

Acknowledgments

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On the Distribution of Diploid and Tetraploid Green Toads of the *Bufo Viridis* Complex (Anura; Bufonidae) in Southern Kazakhstan

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Abstract. -115 specimens of Green Toads belonging to the *Bufo viridis* complex were sampled from 8 populations in south Kazakhstan during the breeding seasons of 1994 and 1995. Subsequent karyological analysis revealed a single diploid population (Kopa) with a 2n=22 karyotype and large snout-vent length. All other seven populations proved tetraploid with a 4n=44 karyotype and smaller size. Information on the distribution of diploid and tetraploid toads in southern Kazakhstan is discussed in connection with previous data.

Key words: Amphibia, Bufonidae, diploid *Bufo viridis*, tetraploid *Bufo danatensis* Kazakhstan, geographic distribution.

Introduction

Following the discovery of some polyploid Asiatic Green Toad populations (Masik et al. 1976) and the description of a new species, *Bufo danatensis* Pisanetz (Pisanetz 1978), two distinct species, diploid *Bufo viridis* and tetraploid *Bufo danatensis*, have been known to occur in ex Soviet central Asia, where only *Bufo viridis* Laurenti, 1768 was formerly recognized.

Using literature data on a number of populations (Bachmann et al. 1978; Pisanetz 1978; Pisanetz and Szczerbak 1979; Pisanetz et al. 1985; Toktosunov 1984), as well as their own data, Borkin et al. (1986a) have drawn a preliminary map of the distribution of diploid and tetraploid Green Toads of the *Bufo viridis* complex in the territory of the ex Soviet Union. Only 3 records of tetraploid *Bufo danatensis* were known for Kazakhstan at the time, whereas diploid *Bufo viridis* had not yet been reported from this region (Borkin et al. 1986a, p. 141).

During the following nine years many more data became available on the distribution of diploid and tetraploid Green Toads in Middle Asia, including Kazakhstan and its bordering countries (China, Mongolia) (Borkin et al. 1986a, 1986b, 1986c, 1996; Fichtman 1989; Orlova and Terbish 1986; Orlova and Uteshev 1986; Schneider and Egiasaryan 1995; Wu Min and Zhao Yajiang 1987; Fichtman 1989; Zhao Ermi 1995). Although some of these data relate to Kazakhstan, however, the vast territory of this Republic is still very poor studied in this respect.

In 1994-1995 a combined expedition by the Department of Animal Biology of the University of Torino (Italy) and the Department of Biology of Kazakh State University at Almaty (Kazakhstan) carried out some field work on the *Bufo viridis* complex in south Kazakhstan. One of the aims of this expedition was to obtain new data on the geographic distribution of diploid and tetraploid toads in this territory.

Materials and Methods

115 Green Toads were sampled from 8 populations in South Kazakhstan (Fig. 1) during the breeding seasons (May-June) of 1994 and 1995. Preliminary species identification was based on morphometric comparisons and records of mating calls. In order to obtain the exact determination of the ploidy level of each specimen a karyological analysis was subsequently carried out at Naples University. From each specimens 100-200 μl of venous blood were incubated for 4 days at 25• C in MEM (Minimal Eagle Medium, GIBCO) with 20% calf serum and 3% Phytoaemogglutinin M. Chromosome preparations were produced by conventional air-drying method, using KCl 0.075 M as hypotonic solution. Standard staining method were performed using Giemsa 5% in phosphate buffer pH 7.

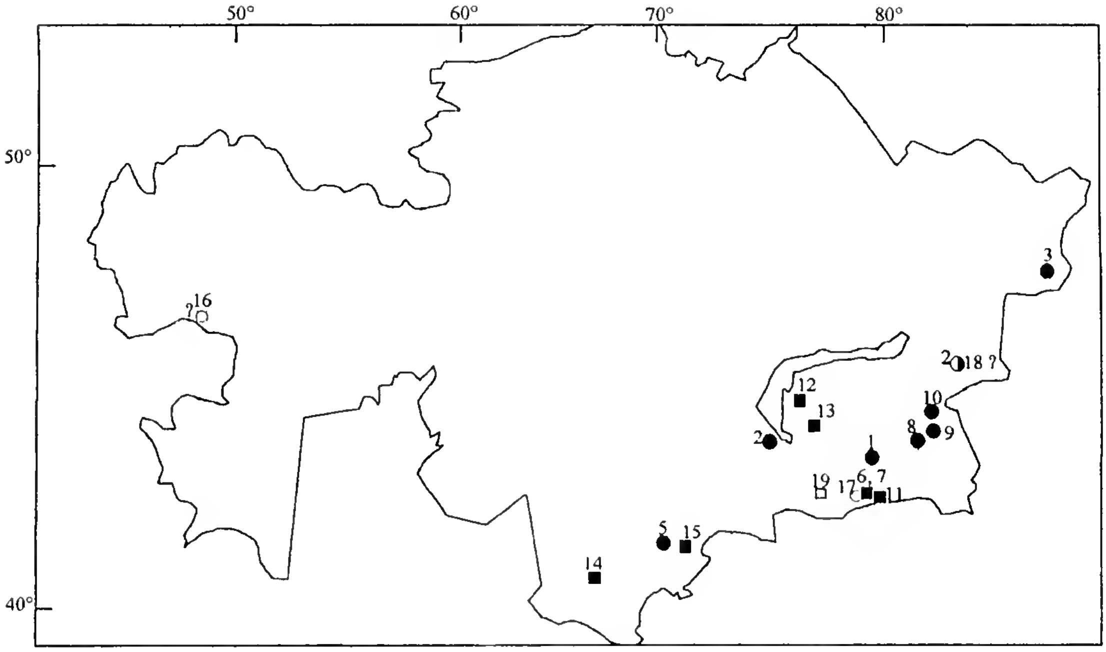

Figure 1. Known localities of diploid and tatraploid green toads, *Bufo viridis* complex in Kazakhstan. [Circle = date from literature; Square = our own findings. Dark = *Bufo danatensis* (4n); light = *Bufo viridis* (2n); hemidark = sympatric locality of *Bufo danatensis* and *Bufo viridis*. ? = attibution not supported by karyological analysis]

Bufo danatensis: 1 - Kapchagai, Ili River (Borkin et al., 1986a); 2 - desert near Burubaital Village, to the soutwest of the Balkhash Lake (Egemberdieva, 1983); 3 - Aksiir Farm, 12 km to the northwest of the Maikapchagay Village, Zaissan Depression (Szczerbak, Golubev, 1981); 4 - Chindzhaly River near Andreyevka Village, Taldy-Kurgan Region (Golubev, 1990); 5 - Chimkent Town, Chimkent Region (Mezherin, Pisanetz, 1991); 6, 7 - Almaty (Borkin et al., 1996; our data); 8 - Baschii Village, 1 km to the south of the Altyn-Emel Mountain Range (44 10'N; 78 45'E), Taldy-Kurgan Region (Borkin et al., 1996); 9 - Koyandytau Mountain Range, Taldy-Kurgan Region (Borkin et al., 1996); 10 - Ayan-Saz Point, the Borokhudzir River Valley, Taldy-Kurgan Region (Borkin et al., 1996); 11 - Big Almaty Lake, Zailijsky Alatau Range; 12 - Karaoj Village, to the south of the Balkhasn Lake; 13 - Zhidely Channel, Ili River delta; 14 - Kizilkum Desert, 50 km to the southwest of the Bairkum Village, Chimkent Region; 15 - Jabagly Village, Chimkent Region (11-15, our data).

Bufo viridis viridis: 16 - Chornaya Rechka near Guryev Town, Guryev Region (Schneider, Egiasaryan, 1995).

Bufo viridis turanensis: 17 - Almaty (Mezherin, Pisanetz, 1991); 18 - Chindzhaly River near Andreyevka Village, Taldy-Kurgan Region (Golubev, 1990); 19 - a point in 20 km to the south of the Kopa Station, Almaty Region (our data).

Table 1. Some preliminary results of the study of green toad of *Bufo viridis* complex in South Kazakhstan. In 1994 and 1995, specimens have been collected in two different regions of Almaty town and are, therefore, considered as distinct samples

Locality	Year	Longitude	Latitude	Altitude (m)	Sample size males/females	Karyotype	SVL min-max mm
Almaty*	1994	76° 55’	43° 15’	900	13/1 (14)	4n	68.49-79.87
Almaty*	1995	76° 55’	43° 15’	900	15/14(29)	4n	68.48-90.88
Big Almaty Lake	1994	77° 00’	43° 04’	2300	12/1 (13)	4n	62.14-83.62
Kopa	1994	75° 47’	43° 25’	750	15/3 (18)	2n	85.15-106.33
Karaoj Village	1995	74° 47’	45° 54’	350	11/5 (15)	4n	59.06-65.24
Zhidely Channel	1995	75° 12’	45° 18’	370	3/1 (4)	4n	49.35-71.8
Kizil-kum Desert	1995	67° 25’	42° 02’	250	7/0 (7)	4n	67.87-78.79
Jabagly Village	1995	70° 32’	42° 25’	1100	11/2 (13)	4n	68.02-77.80

A map of the distribution of diploid and tetraploid Green Toads of the *Bufo viridis* complex was made by program Automap 1.1 (programmers V. Dubjansky and A. Kazimirov). Since the main purpose of this paper is to present some new information on the distribution of diploid and tetraploid toads in Kazakhstan, only a brief review of other results obtained has been summarized in Table 1.

Results and Discussion

Of 8 populations, only one, sampled near Kopa, in south eastern Kazakhstan, proved to have a diploid karyotype. As it is normally the case, this population also shows the largest snout-vent length (see Table 1).

Until now, diploid Green Toads were reported for the territory of Kazakhstan from 3 localities only, but only Mezherin and Pisanetz (1991) and Pisanetz (1991) supported the occurrence of *Bufo viridis turanensis* at Almaty with a karyological study. The record by Golubev (1990) of the presence of *Bufo viridis* in cohabitation with *Bufo danatensis* on the Chindzhily River, near the village of Andreyevka (eastern Kazakhstan) (Fig. 1) was based on differences in the breeding behaviour of two groups of specimens and lacks any karyological confirmation. Finally, Schneider and Egiasaryan (1995) cited *Bufo viridis viridis* from Chornaya Rechka, near the town of Guryev (north western Kazakhstan, Fig. 1) on the basis of some advertisement-call characters. Although the mating calls and behaviour of some populations of *Bufo viridis* have been studied in full detail, a karyological analysis remains necessary for exact determination.

Records of tetraploid toads in Kazakhstan are more numerous (Fig. 1). Two of them, however, respectively from the Zaissan region (Szczerbak and Golubev 1979) and the Chindzhily River, near Andreyevka Village (Golubev 1990) need karyological confirmation.

Our karyological data show that, apart from a single locality (Kopa), all other populations examined consist of tetraploid specimens. The finding of tetraploid toad populations at the Zhidely Canal of the Ili River delta and at Karaoj Village concurs with data by Borkin et al. (1986a; 1996) in that the territory south of Lake Balkhash and the area along the Ili River are inhabited by tetraploid toads only (Fig. 1). Specimens from Zhidely Canal and Karaoj also show the smallest snout-vent lengths in comparison with toads from all other populations sampled in 1994 and 1995 (Table 1).

Our record of tetraploid toads within the town of Almaty (Table 1) is in an agreement with data by Borkin et al. (1996), who identified a tetraploid population in the same area by flow cytometry analysis, but may contradict data of Mezherin and Pisanetz (Mezherin and Pisanetz 1991; Pisanetz 1991, see above) who reported the presence of diploid *Bufo viridis turanensis* from Almaty. A high mountain population from the Big Almaty Lake (Transvalley Alatau Range, 2300 m) also has a tetraploid 4n=44 karyotype (Table 1). For the time being, however, we cannot exclude the possibility of the presence in the Almaty region of diploid and tetraploid synthopic populations and further investigations are necessary in order to settle this point.

Mezherin and Pisanetz (1991) were first to report on the presence of a tetraploid population in the southeast region of Kazakhstan, near the town of Chimkent. All specimens from the south east examined by us (Kizilkum Desert and Jabagly Village, Fig. 1) are indeed tetraploid. They share a similar snout-vent length (Table 1) but inhabit ecologically different biotopes. At Kizilkum, toads were found at a pond located in a sand-dunes area and formed by water overflowing from a water hole (altitude 250 m). At Jabagly, toads were caught in small ponds and in a stream, by a mountain village, at an altitude of 1100 m.

Acknowledgments

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Phylogeny of Genus *Scutiger* (Amphibia: Megophryidae): A Re-evaluation

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Abstract. - A re-analysis of a published data set from Ye et al. (1992) indicates that their phylogeny for the genus *Scutiger* does not reflect the most parsimonious explanation of the data. The consensus of the resulting trees from the original data set is a "bush" with only three resolved nodes. A re-evaluation of the character states, and their respective polarizations, resulted in alternative phylogenetic hypotheses. However, measures of homoplasy and data consistency for the re-evaluated topologies were relatively low, suggesting that little confidence could be obtained in these relationships. More data are needed to generate a defensible hypothesis of the relationships within the genus *Scutiger*.

Key words: Amphibia, Anura, Pelobatoidea, Megophryidae, *Scutiger*, morphology, phylogeny, parsimony

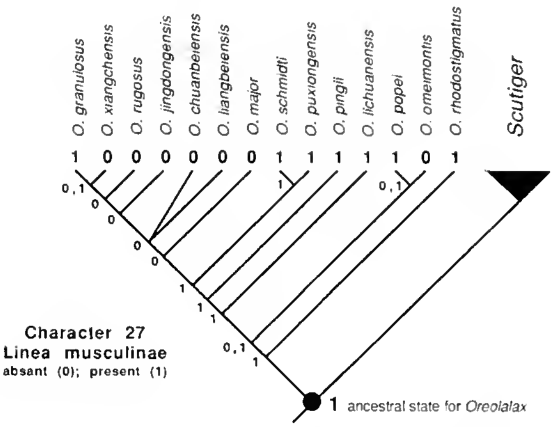

Figure 1. Phylogeny of *Oreolalax* with the character states of linea musculinae optimized on the tree. The primitive condition of linea musculinae for the phylogeny of *Scutiger* is 1.

Introduction

Frogs in the family Megophryidae have long captivated many herpetologists, especially Chinese colleagues, partly because of their supposed transitional position between "primitive" and "advanced" frogs (Lynch, 1973, Ford and Cannatella, 1992) and also because of asthetic appeal. The phylogeny of pelobatoids is largely unknown, and we now realize that the concepts of "primitive" and "advanced" taxa are phylogenetically flawed and hence unacceptable; only character states have these attributes.

Thirty-two species of *Scutiger* occur in the high altitudes of the Tibet Plateau in southwestern China, Burma, Nepal, and northern India. A phylogeny of this group has been wanting. The genealogical relationships of this group would be useful for assessing theories of the geologic events that have been linked with the uplift of this region.Recently, Fei and Ye (1990) and Xu et al. (1992) investigated the relationships of megophryids. Of particular interest, Ye et al. (1992) presented a phylogeny of genus *Scutiger* using 29 morphological characters. Unfortunately, some invalid methods were employed in both the character analysis and tree selection, and these nullify their hypothesis. We performed a re-evaluation of the Ye et al. (1992) data, and examined their proposed phylogeny of *Scutiger*.

Methods

The data of Ye et al. (1992) consisted of 29 morphological characters for 16 species of *Scutiger*, and one outgroup taxon (Appendix I). Initially, we analyzed these data without modification. Following Ye et al. (1992), five species, *Scutiger ningshanensis*, *S. maculatus*, *S. nepalensis*, *S. occidentalis*, and *S. adungensis*, were excluded from the analysis owing to many unknown character states (Appendix II). We used outgroup analysis (Maddison et al., 1984) to reassess character state polarizations. *Oreolalax* was used as the outgroup and polarizations of the character states were determined from previous work (Fu and Murphy, in press). From this phylogeny, we were able to identify pleisomorphic character states for *Oreolalax*, which were then used to polarize the character states for scutigers. For example following Maddison et al. (1984) and Wiley et al. (1991), we assigned character states for the terminal branches down the tree until reaching the root node (see Fig. 1 for the optimization of Linea Musculinae).

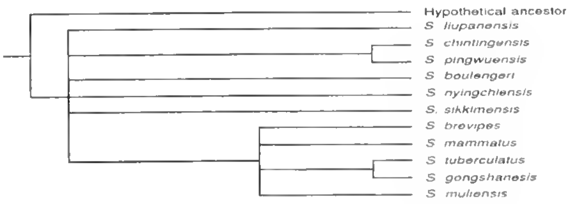

Figure 2. Strict consensus tree of the phylogeny of *Scutiger*, derived from our reanalysis of Ye et al.'s (1992) original data.

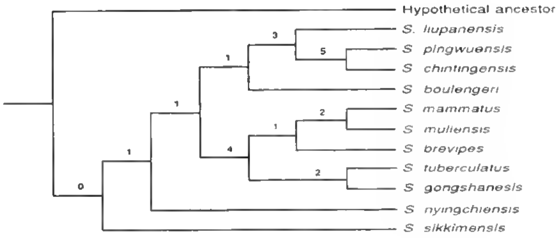

Figure 3. One of 20 MPTs depicting the phylogeny of *Scutiger* that was derived from our reanalysis of Ye et al.'s (1992) original data. When the outgroup condition was not known, the original character state polarizations of Ye et al. were used. This topology was reached by successive approximations (Farris, 1969); numbers indicate unambiguous synapomorphies occuring at each corresponding node.

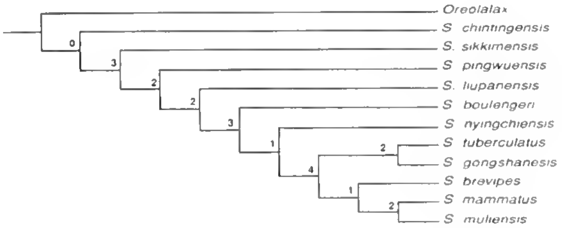

Figure 4. Phylogeny of *Scutiger*. One of 16 MPTs derived from Ye et al.'s (1992) data using *Oreolalax* as the outgroup. When the outgroup condition was not known, the original character state polarizations of Ye et al. were used. This topology was reached by successive approximations; numbers indicate unambiguous synapomorphies occuring at each corresponding node.

Phylogenetic analyses were conducted using (PAUP) version 3.1.1 (Swofford, 1993) and employing an heuristic search with stepwise addition. Tree optimization was performed using the tree bisection-reconnection branch swapping option, steepest descent, and retaining all most parsimonious trees. Tree topologies were analyzed in MacClade 3.04 (Maddison and Maddison, 1992). To choose among the most parsimonious trees, we employed successive approximations (Farris, 1969). Decay analysis (Bremer, 1988) was used to assess nodal stability.

Results

Our initial evaluation of the phylogeny of *Scutiger* using the unmodified original data of Ye et al. (1992) resulted in 20 most parsimonious trees (MPTs), each with a consistency index (ci) of 0.46, retention index (ri) of 0.53 and a length of 62 steps. A strict consensus tree revealed only three consistent nodes (Fig. 2). *Scutiger gongshanensis* with *S. tuberculatus* were resolved as sister species, as were *S. pingwuensis* and *S. chintingensis*. Only the latter relationship and the association of *S. mammatus*, *S. brevipes*, *S. muliensis*, *S. tuberculatus* and *S. gongshanensis* were resolved by Ye et al. (1992). Excluding these relationships, all others were ambiguous. The topology of Ye et al. requires 63 steps to explain the data, one steps longer than our most parsimonious tree. A successive approximations evaluation resolved a single tree, one of the original 20 MPTs (Fig. 3).

Re-examination of the character polarizations of Ye et al. (1992) shows that characters 3 and 27 were incorrectly polarized in the original work. We were unable to polarize character 25 because both states occur in the outgroup; the presence or absence of spinal patches on the forelimbs are equally probable as a plesiomorphy for *Scutiger*. Characters 1 and 26 have autapormorphic states only, making them phylogenetically uninformative; they were excluded from subsequent analyses. Polarization of characters 7, 8, 9, 10, 11, 15, and 17 was not possible using outgroup criterion because the state(s) in the outgroup are not known. These characters were treated both using the original polarizations of Ye et al. (1992), and subsequently by treating them as missing data in the outgroup.

Our analysis using the polarizations of Ye et al. (1992) for characters 7–11, 15, and 17 resulted in 16 MPTs, 60 steps in length (ci = 0.45, ri = 0.53). The strict consensus tree is identical to that of the original analysis with only three nodes resolved. Using successive weighting resulted in a single MPT which is one of the 16 MPTs (Fig. 4). When supporting characters were mapped on the phylogeny, most of the nodes received very little unambiguous support from these data.

The alternative approach treated character states that were unknown in the outgroup as missing data. This resulted in 1 most parsimonious tree (Fig. 5), ci =

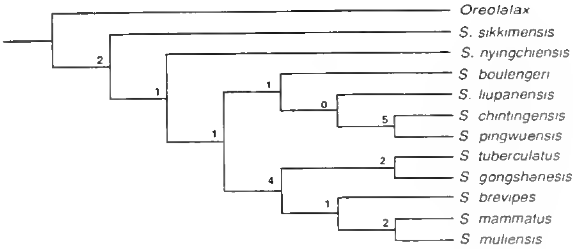

Figure 5. A single MPT for the relationships of *Scutiger*. The data in which unknown states for the outgroup are left as missing. Numbers indicate unambiguous synapomorphies occuring at each node.

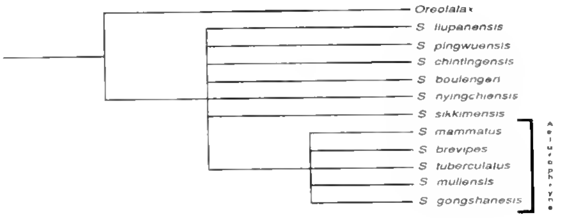

Figure 6. The resulting strict consensus tree of *Scutiger* after saving all trees one step longer than the shortest tree, from the data set where unknown outgroup states were left as missing.

0.49, ri = 0.57 and 59 steps. In this topology, like the others, few unambiguous changes have occurred.

Discussion

Ye et al. (1992), recognized two subgenera in the genus *Scutiger*: *Scutiger* and *Aelurophryne*. They identified three synapomorphies for the latter, and based on the derived relationships and current distributions, drew conclusions about the origin of the scutigers.

Our results show that the phylogeny of Ye et al. (1992) was not the most parsimonious explanation of their data. We resolved 20 trees that were more parsimonious. A strict consensus of our shortest trees resulted in a tree with only three nodes resolved. As was true in Ye et al.'s tree, *Aelurophryne* was monophyletic and supported by three synapomorphies. Within this clade the sister relationships of only two species, *S. tuberculatus* and *S. gongshanensis*, could be unambiguously resolved. The remaining scutigers formed a single basal polytomy with the *Aelurophryne*, but two species were resolved, *S. chintingensis* and *S. pingwuensis*. This sister relationship was also seen in Ye et al.'s tree. our analysis did not resolve the subgenus *Scutiger* as a monphyletic group.

Ye et al. (1992) apparently used a hypothetical ancestor rather than *Oreolalax* as the outgroup, some characters were incorrectly polarized. Consequently, we believe that any conclusions derived from either their phylogeny or our reanalysis of the original data set are invalid.

The proper ordering and polarizations of character states using the outgroup criterion proved very important. Failure to defensibly order states of multistate characters resulted in the resolution of less parsimonious solutions. Even though we changed the polarizations of two characters, seven other characters could not be polarized. Consequently, subsequent analyses either left the polarization as assumed by Ye et al (1992), or we treated the outgroup states as missing, thereby treating the characters as unpolarized. The former analysis resulted in 16 MPTs in which the strict consensus tree was identical to our first analysis. The latter analysis resulted in one tree depicting *Aelurophyrne* as monophyletic, and *S. chintingensis* and *S. pingwuensis* as sister species. It did not resolve the subgenus *Scutiger* as a monophyletic assemblage.

It is desirable to assess the support for individual nodes and the entire phylogeny. Several methods have been proposed. One procedure, bootstrap (BS) analysis (Felsenstein, 1985), assesses relative support for each node of a phylogeny (for criticisms of the method see Carpenter, 1992; Hillis and Bull, 1993; Kluge and Wolf, 1993; Trueman, 1993). One prerequisite to a BS analysis often overlooked, is that a minimum three characters per node is required to obtain a statistically significant BS value. Unfortunately, our MPTs do not have enough unambiguous character changes at each node to generate statistically meaningful BS values.

Decay analysis (Bremer, 1988), an alternative method, keeps all trees that are a specified length longer than the MPTs. It permits the assessment of nodal support by identifying only those monophyletic groups that are common to all of the possible trees. This method presumes that all relationships receiving sound support from these data will be present in a strict consensus tree of all trees one or two steps longer. When we held all MPT plus those one step longer, 241 trees were retained. The resulting strict consensus tree showed no resolution; all of the ingroup taxa were resolved from a single node. However, when the ambiguously polarized states were coded as missing data in the outgroup, the MPTs and those one step longer included 27 trees, and the strict consensus tree broke into one ingroup clade, *Aelurophryne* (Fig. 6). Holding all trees two steps longer resulted in 362 trees and a single polytomy.

The status of the subgenera *Aelurophryne* and *Scutiger* has been debated (Myers and Leviton, 1962; Noble, 1931; Pope and Boring, 1940; Liu, 1950) and *Aelurophryne* was previously diagnosed by the absence of maxillary teeth. Meyers and Leviton (1962) stated that the absence of teeth actually reflected a graded trend within the genus *Scutiger*, and could not be used to separate *Scutiger* from *Aelurophryne*. This is also true for two of the three characters used by Ye et al. (1992) to define *Aelurophryne*. However, the presence of a robust metacarpal bone can be used to distinguish *Aelurophryne* from other scutigers.

Ye et al. (1992), used their phylogeny to discuss the evolution and specialization of *Aelurophryne*. They described the subgenus as having become more specialized for an aquatic lifestyle, and recognize three synapomorphies: robust metacarpal bone, thick humerus, and the no keritanized spines on the dorsum. Two problems exist. First, the latter two synapomorphies are also derived in *S. nyingchiensis*. Second, one synapomorphy, no keritanized spines, is an actual loss of a character. It is more preferable when reconstructing phylogenies to use characters that are uniquely derived and not represented by the absence of characters. Moreover, characterizing a group based on the absence of traits should be avoided. Numerous scenarios can be developed to explain the loss of a character and its homologue can never be identified with certainty. However, the presence of a character may be scrutinized at a greater detail, often making it possible to recognize homologous counterparts.

Because the subgenus *Scutiger* cannot be diagnosed, it is possible, if not likely that this subgenus is a polyphyletic assemblage of species. Therefore, our analysis requires that the subgenus *Aelurophryne* not be recognized if a holophyletic classification is to be maintained.

One problem that permeates the data base is the selection of highly homoplastic characters. Homoplastic characters tend to provide no definitive resolution. However, we cannot comment on the quality of characters until we can see how they perform during a defensible phyletic estimation. We are certain that too few characters were used to generate support for any of the relationships on the phylogeny.

The information summarized by Ye et al. (1992) forms the initial ground work for understanding the evolutionary relationships *Scutiger*. Given that so little is known about these frogs, any advances should be deemed valuable. However, additional data are required to confidently resolve the phyletic relationships of scutigers, and to identify the corresponding plesiomorphic condition in *Oreolalax*. Once a sound phylogeny of the genus has been achieved, it will be possible to address biogeographical, ecological, and behavioral questions.

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Appendix I

Modified data set of Ye et al (1992). Characters were polarized using *Oreolalax* as the outgroup. Those characters in bold were omitted from the analysis because they are apomorphic.

Character	1 11111 11112 22222 **2**222
number	**1**2345 67890 12345 67890 12345 **6**789
Oreolalax	00100 00000 00000 00000 0000– 0100
S. liupanensis	11101 00011 10101 01101 11010 0000
S. pingwuensis	01111 00111 10001 00101 11011 0011
S. chintingensis	00111 01101 00001 01001 11001 0011
S. boulengeri	01101 10000 10100 01100 11010 0000
S. nyingchiensis	01001 00001 01000 11011 10000 0001
S. sikkimensis	01100 11111 00000 01111 11000 1001
S. mammatus	01001 10010 01110 10100 10100 0001
S. brevipes	01101 10000 01110 10101 10000 0001
S. tuberculatus	01011 10000 01110 11101 10000 0011
S. muliensis	01011 10000 01110 10101 10100 0001
S. gongshanensis	00111 10011 11110 11110 00000 0111

Appendix II

Character used by Ye et al (1992).

1. Head width to length
   0: width > length, 1: width < length
2. Maxillary teeth
   0: well developed, 1: very small or absent
3. Nasal and sphenethmoid
   0: articulated, 1: seperated
4. Columella
   0: present 1: absent
5. Quadratojugal
   0: long, articulated or overlapped with maxilla, 1: short, wildly seperated from maxilla
6. Prootic and exoccipital bone
   0: seperated, 1: fused
7. Hyoid plate plus anterior process (HPAP) and the distance between the out flank of the anterior process (DFAP)
   0: HPAP < DFAP, 1: HPAP > DFAP
8. Hyoid fenestra
   0: present 1: absent
9. Cricoid cartilage
   0: complete circle, 1: circle incomplete
10. Omosternum and xiphisternum
    0: Width of omosternum < width of xiphisternum, 1: width of episternum >width of xiphisternum
11. Omosternum
    0: partially ossified, 1: entirely cartilage
12. Humerus in male
    0: length/width > 4, 1: length/width < 4
13. Inner crest of radioulna in male
    0: absent, 1: present
14. Inner two metacarpals and phalanges in male
    0: normal, 1: robust
15. Prepollex
    0: ossified, 1: cartilage
16. Dorsal skin
    0: with horny spines, 1: without horny spines
17. Large warts near vent
    0: absent, 1: present
18. Post-femoral gland
    0: present, 1: absent
19. Webbing between toes
    0: present, 1: absent
20. Metatarsal tubercle
    0: absent, 1: present
21. Vocal sac
    0: present, 1: absent
22. Spiney patches on the chest
    0: one pair, 1: two pair
23. Spines on the chest
    0: small, 1: big
24. Spinal warts on belly
    0: absent, 1: present
25. Spinal patches of forelimb
    0: absent, 1: present
26. Nuptial spines
    0: small, 1: big
27. Linea musculinae
    0: absent, 1: present
28. Labial margin of tadpole
    0: narrow, with many tubercles, 1: wide, with few or no tubercles
29. Labial teeth formula of tadpole. Number of tooth rows
    0: ≥I:5-5/I:5-5, 1: < I:5-5/I:5-5.

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Phylogeny of Chinese *Oreolalax* and the Use of Functional Outgroups to Select Among Multiple Equally Parsimonious Trees

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Abstract. -Re-analysis of a published data set from Xu et al. (1992) reveals that their proposed phylogenetic tree is not the most parsimonious explanation. Ten shorter, most parsimonious solutions are derived from these data. The progressive functional outgroup approach found a single tree from among the ten to be the best explanation of the data. Such an approach may prove to be a powerful method for dealing with multiple equally parsimonious trees.

Key words: Amphibia, Anura, *Oreolalax*, China, Phylogeny, Functional outgroups

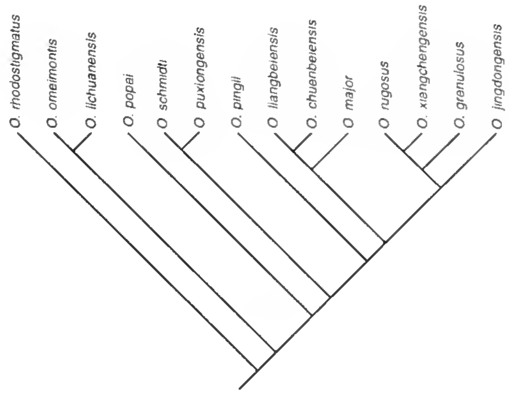

Figure 1. Phylogenetic Cladogram of *Oreolalax* proposed by Xu et al. (1992).

Introduction

Although considerable interest has been shown in the evolution of pelobatid frogs relatively recently, the phylogeny of many pelobatids remains largely enigmatic. Xu et al. (1992) proposed a phylogeny for fourteen species of *Oreolalax* (Fig. 1). This genus of pelobatid frogs is endemic to China and most of the 15 described species occur at high elevations (1500 to 3300m). Xu et al. used 29 morphological characters in their analysis (Appendix I), and these were gathered for the 14 species known at the time of their analysis. Subsequent to the proposed phylogeny, a new species, *O. multipunctatus*, was described (Wu et al., 1993). However, the phylogenetic relationships of this new species were not considered in the description; its position among the other species remained uncertain. Consequently, we undertook a re-examination of the phylogeny of *Oreolalax* using data provided by Xu et al. (1992) and Wu et al. (1993).

Our initial examination of Xu et al. (1992) showed several problems in their analysis potentially invalidating their conclusions. Because of this, we first pursued a re-evaluation of their data, and subsequently incorporated the new species into our analysis to obtain a more defensible phylogenetic estimation for the genus *Oreolalax*.

Materials and Methods

The data set from Xu at al. (1992) was used in our initial analysis (Appendix II). Our phylogenetic analysis was undertaken using Hennig86 (version 1.5; Farris 1988), Random Cladistics (version 2.0; Siddall 1994) and PAUP (version 3.1.1, Swofford 1993). Branch and bound algorithm (Hendy and Penny 1982) as provided in these software packages was used for all tree searching. The resulting trees were rooted initially by a hypothetical ancestor scored plesiomorphic for all characters based on the hypotheses of Xu et al. (1992). Using Random Cladistics, a permutation tail probability test (PTP; Faith and Cranston 1991) was used for assessing the presence of pattern in the data set, which we assume to represent phylogenetic structure. Bootstrap values (BS; Felsenstein 1985) were used for assessing the relative strength of support for monophyletic groups. Examination of character state distributions on trees was accomplished using MacClade (version 3.04; Maddison and Maddison 1992).

Initial estimations of phylogenetic analysis were accomplished using the unaltered data of Xu et al. (1992). Three methods were exploited for dealing with multiple most parsimonious trees (MPTs): con-

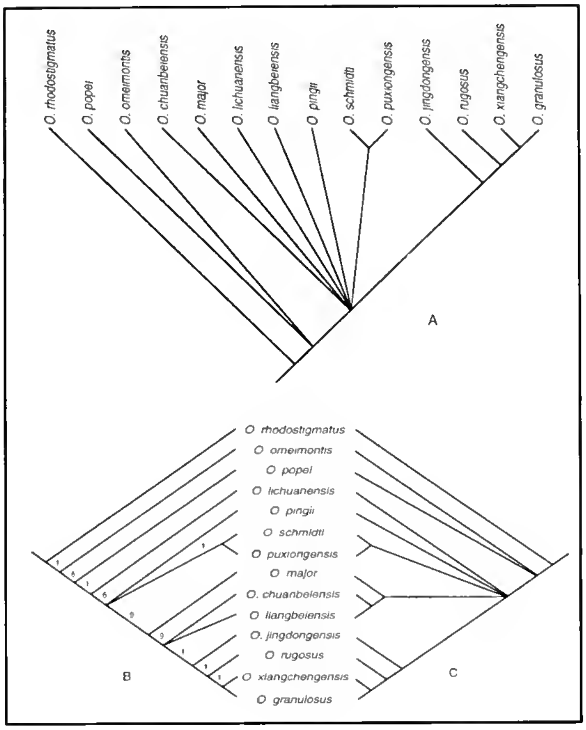

Figure 2. A: Strict consensus tree of 10 MPTs resulting from the original analysis with 7 unresolved nodes. B: 50% majority rule consensus tree with 2 unresolved nodes: 6=0.6; 9=0.9; 1=1.0. C: Adams consensus tree with 4 unresolved nodes.

sensus evaluation, successive approximations weighting (SAW; Farris 1969, 1988), and functional outgroup approach (FOG) modified from Watrous and Wheeler (1981). Following resolution of the tree for the initial 14 species treated by Xu et al., the position of *Oreolalax multipunctatus* relative to the other species was estimated.

Results

Our PTP test showed the data set of Xu et al. has pattern which is significantly different from random. A PTP value of $p<0.001$ was obtained based on 999 randomized data sets. The minimum length tree derived from the randomized data was 64 steps whereas the minimum length tree from the original data was 58 steps. We interpret this pattern to reflect the presence of phylogenetic structure.

Ten MPTs of 58 steps were found, each with a consistency index (CI; Kluge and Farris 1969) of CI = 0.50, and a retention index (RI; Farris 1989) of RI = 0.59. When the data are mapped onto the tree of Xu et al., their tree was observed to have a length of 61 steps (CI = 0.47; RI = 0.54). Using PAUP, we found no fewer than 7000 equally or more parsimonious solutions having 61 steps; we terminated the program after 30 minutes analysis.

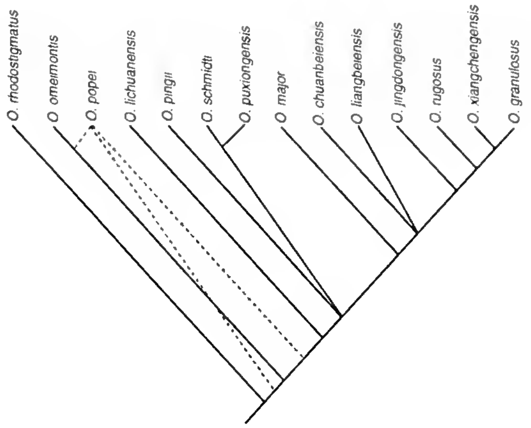

Figure 3. Three MPTs resulting from successive approximations weighting. The unstable position of *O. omeimontis* and *O. popei* is responsible for the three trees.

A strict consensus tree, Adams consensus tree (Adams 1972), and 50% majority consensus tree were generated from the ten MPTs respectively. The strict consensus tree (Fig. 2a) showed low resolving power. Only seven of 13 nodes were resolved demonstrating much conflict among various patterns of relationships. The Adams consensus tree (Fig. 2b) gave a slightly better resolution with four nodes unresolved. Finally, the 50% majority consensus tree (Fig. 2c) left only two nodes unresolved. In all analyses, *O. rhodostigmatus* always appeared at the base of the ten MPTs.

As another means of selecting a preferred tree from among the ten MPTs, we used SAW. Following the successive re-weighting of characters based on the RI, three trees were found. When the character weights were re-set to 1, each tree had a length of 58 steps, and thus all fall within the suite of initial MPTs. Among the three trees, the position of *O. omeimontis* and *O. popei* were unstable, accounting for three alternative trees, and two other nodes were resolved as polytomys (Fig. 3).

We had concern that the plesiomorphic states may not have been correctly identified as no outgroup was used in the analysis, although the ancestral states theoretically represent the conditions observed in *Leptobrachium*. Given this, and the observation that, in general, the closer the outgroup is to the ingroup the more likely the polarization of character states will be accurately determined, we used a functional outgroup (FOG) approach (Watrous and Wheeler 1981) to

Figure 4. Strict consensus tree of 2 MPTs resulting from using Oreolalax rhodostigmatus as functional outgroup.

Figure 5. Resulting tree using Oreolalax lichuanensis as functional outgroup.

examine the data. Because *O. rhodostigmatus* always appeared at the base of the ten MPTs, this species was used as our FOG. We excluded the hypothetical ancestor from our secondary and subsequent analyses.

Our FOG approach revealed two equally parsimonious trees, each with 53 steps (=58 steps with HA; CI = 0.54, RI = 0.60). Neither tree was the same as resolved from our SAW evaluation but both were among our original ten MPTs. The strict consensus tree shows two unresolved nodes (Fig. 4). For resolving the ambiguous nodes, a closer FOG, *Oreolalax lichuanensis*, was selected. Taxa below the FOG (*O. rhodostigmatus*, *O. popei* and *O. omeimontis*) were excluded from this analysis. A single MPT with 37 steps was found (=58 steps with the deleted taxa; CI = 0.67, RI = 0.70) (. 5). It is one of the ten MPTs from the original analysis. Examination of character state distributions on this tree showed no potential for further resolution to the relationships of *O. chuanbeiensis*, *O. liangbeiensis* and more terminal taxa. Combining the results of our progressive FOG analysis, a single cladogram emerged as our preferred tree (Fig. 6). Thus, our tree is left with one unresolved polytomy.

Bootstrap (BS; Felsenstein 1985; Siddall 1994) was used to assess strength of support of monophyletic groups. The BS value based on 999 randomized data sets was mapped on the resulting tree (Fig. 6). Three nodes were shown to be well supported by BS that have values over 0.5. The *O. schmidti* and *O. puxiongensis* clade has a highest value of 0.840, while the *O. jingdongensis*, *O.rugosus* and *O. granulosus* clade has the second highest value of 0.732. The ingroup member excluding *O. rhodostigmatus* from the clade and has a high value of 0.634. The weakest support from BS is the *O. popei* and *O. omeimontis* clade that has a value as low as 0.061.

Finally, the data for *Oreolalax multipunctatus* were combined with those of Xu et al. (1992: Appendix II). From the characters available for all ingroup taxa, *O. multipunctatus* was resolved as either the sister group of *O. schmidti* or *O. puxiongensi*, both of which were most frequently resolved as sister taxa. The missing data were responsible for the ambiguity.

Discussion

Phylogeny of *Oreolalax*

Oreolalax rhodostigmatus was consistently resolved as the sister of all other species in the genus. Three characters (8, 10, 18; Appendix I) separate it from other species. A BS value of 0.634 was calculated for the node excluding *O. rhodostigmatus*. The *rugosus* group of Xu et al. (1992) also appears to be monophyletic and received a relatively high BS value (=0.732). Zhao and Adler (1993) regarded *O. puxiongensis* as a synonym of *O. schmidti*. Here, the highest BS value observed from the data, BS = 0.840, shows that these two taxa are very similar. Although further detailed work is needed to determine the status of *O. puxiongensis*, because *O. multipunctatus* is resolved as the sister species of either *O. puxiongensis* or *O. schmidti*, synonymization of these latter two taxa would also require synonymization of *O. multipunctatus* if a holophyletic classification is to be maintained. Thus, we recommend recognition of all three species until far more detailed evaluations can be made.

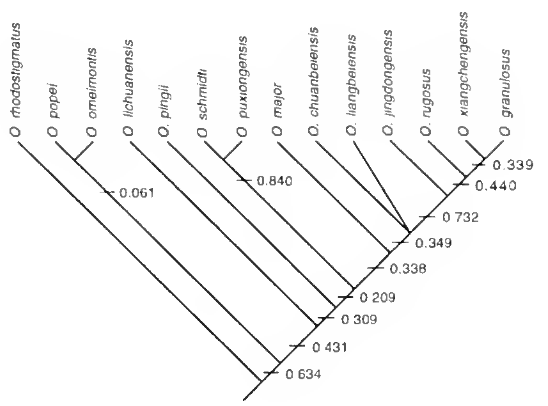

Figure 6. Phylogeny of Oreolalax as resolved by using our progressive functional outgroup analysis. One node remains unresolved. Bootstrap values are provided for each node.

Although *O. popei* and *O. omeimontis* are grouped together on our preferred tree (ure 6), the BS analysis shows a very low value of 0.061. They shared five characters (8, 10, 18, 21, 29). Optimizing these characters on the preferred tree shows that character 8, 10 and 18 are shared by all ingroup members excluding *O. rhodostigmatus*, with 1 or 2 independent reversals. Characters 21 and 29 are shared by all ingroup members with more than 2 independent reversals. These two taxa do not share any uniquely derived characters. We believe that this association should be considered tenuous because of the low BS value, and the resolution of a different set of relationships for these two taxa in our SAW evaluation (Fig. 3). More work is needed to determine the relationships of these species with the others.

The relationships of *O. chuanbeiensis*, *O. liangbeiensis* and the *rugosus* group are unresolved. There are no unambiguous characters to support any resolution of these three taxa. More characters are required for the resolution of this polytomy.

Most species of *Oreolalax* are distributed along the east edge of the Qinghai-Tibet Plateau. *Oreolalax rhodostigmatus* occurs in the far east of the Qinghai-Tibet Plateau and is almost allopatric in distribution from all other species. The *rugosus* group occurs at the highest elevations, 2100-3300m. This suggests that their common ancestor was adapted for the rigors of alpine life. The speciation within the *rugosus* group appears to be closely associated with the uplift of the Qinghai-Tibet Plateau.

Functional Outgroup Method

Our progressive functional outgroup method may prove to be a powerful method for dealing with multiple equally parsimonious trees, especially when levels of homoplasy are relatively great, and the outgroup is so distant from the in-group that mispolarization of the character states is commonplace. When divergences are great, and characters are constrained to only a few possible alternative states, homoplasy may be so rampant that there is very little resolving power to the data when a taxonomic outgroup is used to polarize character states. Selecting a closer sister group, as in the use of FOGs, may prove particularly beneficial for reducing this problem. Thus, the use of FOGs might possibly result in the defensible selection of a single most parsimonious tree when, otherwise, a suite of equally parsimonious trees would be found.

The application of consensus tree methods has not been recommended as a way of selecting among equally parsimonious solutions, although this stance has not been universally accepted (e.g., Wilkinson 1994). Our trial of this approach with the *Oreolalax* data did not demonstrate high resolving power. The strict consensus tree seeks the unambiguous nodes appearing on all MPTs. It often results in a large number of unresolved nodes. A single taxon with ambiguous relationships may cause the whole consensus tree to be a total "bush". The Adams consensus method improves this problem, but in both our case and in others, it still frequently resolves ambiguous nodes. In our case, strict and Adams consensus left 6 and 5 nodes unresolved respectively. Although the majority rule consensus method often gives a more complete solution, the percentage is arbitrary and it is doubtful that all nodes reflect phylogeny.

Successive approximations weighting (Farris 1969) often reduces the number of cladograms to be considered by restricting attention to the most consistent characters, and hence the "best" evidence (Carpenter 1988). Consequently, some ambiguous nodes that are supported by the "best" evidence may get resolved. However, the ambiguous nodes not supported by the suite of consistent characters will remain unresolved. In our trials, SAW resolved three equally parsimonious solutions. The ambiguous position of *O. popei* and *O. omeimontis* is responsible for these three trees. Character 28, which clusters these two taxa together under FOG analysis, was not included in the "best" evidence; It received a weighting value of 0 from the SAW analysis.

In our case, the high resolving power of FOG analysis results from the changing of the character state polarizations. Some symplesiomorphies which are useless in providing evidence of common ancestry became synapomorphies after re-polarization. However, we believe that the revised data result in a better solution. For example, the polarity of the states of Character 28, changes after using *O. rhodostigmatus* as the FOG. Unlike in our initial analysis, a derived state united *O. popei*, *O. omeimontis* and *O. liangbeiensis*. Similarly, after using *O. lichuanensis* as our FOG, the polarities of the states of Character 24 changed such that a synapomorphy united *O. schmidti* and *O. puxiongensis* with *O. major*.

Evolution of the Characters

Among the 29 characters used by Xu et al., 10 contributed no information to the phylogeny. Characters 7, 11, 12, 22 have autapomorphic states and hence are phylogenetically uninformative. The derived states of characters 1, 13, 20, 23, and 24 were resolved as independent "gains" (parallelism). Character 28 was interpreted to be two independent reversals. Conversely, 19 characters showed clear evolutionary trends when mapped on our preferred tree. However, although characters 2, 3, 4, 5, 6, 8, 9, 10, 14, 15, 16, 18, 19, 21, 26, and 27 evolved from state 0 to 1, characters 17, 25, 29 show a progression from state 1 to 0. These latter three characters are undoubtedly mispolarized by Xu et al. if our tree reflects the genealogical relationships of the taxa.

Acknowledgments

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Appendix I

The Characters used by Xu et al (1992)

1. Quadratojugal either long, overlapping with maxilla (O), or short, not overlapping the maxilla.
2. Spoon-like cartilage either present (0), or absent (1).
3. Columella either long (0), or reduced as a small projection (1).
4. Tympanum either present (0), or absent (1).
5. Tympanic annulus either large, diameter>1.9 mm (0), or either small, diameter<1.3 mm, or absent (1).
6. Post-otic projection of squamosal either present (0), or absent (1).
7. Ilium either short (0), or long (1).
8. Body length of males either greater than 65 mm (0), or less then 56 mm (1).
9. Opening of Eustachian tube either large (0), or small (1).
10. Tympanic status either obvious (0), or hidden (1).
11. Dorsal skin either smooth (0), or warty and granular (1).
12. Skin groove along posterior area of the dorsum either absent (0), or present (1).
13. Belly skin either smooth (0), or granular (1).
14. Colour pattern on belly either present (0), or absent (1).
15. Triangular pattern between eyes either absent (0), or present (1).
16. Toes either webbed (0), or either not webbed or only a trace (1).
17. Vocal sac either present (0), or absent (1).
18. Spines in lip margins either absent (0), or present (1).
19. Spinal patches on the chest either small (0), or large (1).
20. Spines on the chest either small (0), or large (1).
21. Nuptial spines on fingers either small (0), or large (1).
22. Spinal patches on the ventral surface at the base of the upper arm either absent (0), or present (1).
23. Spinal patches on the inner side of the lower arm either absent (0), or present (1).
24. Spinal patches on the back of the upper arm either absent (0), or present (1).
25. Linea musculinae either absent (0), or present (1).
26. Labial tooth formula of tadpole either 1:7-7/1:7-7 or more (0), or 1:6-6/1:6-6 or less (1).
27. Papillae of tadpole nostril more than one circle clear (0), or only half circle clear (1).
28. Number of eggs laid either more than 280 (0), or less than 220 (1).
29. Egg pigment. either present (0), or absent (1).

Apendix II

Coded Data set from Xu et al. (1992). A hypothetical ancestor (HA) was added for analysis.

HA	00000 00000 00000 00000 00000 0000
O. popei	10000 00111 00000 01101 10000 0001
O. chuanbeiensis	00001 00111 00010 01100 00010 1011
O. major	00000 00011 00110 01110 00000 1111
O. schmidti	10000 00111 00011 11000 10001 1111
O. omeimontis	00000 00101 00001 10100 10101 0001
O. puxiongensis	00000 00111 00111 11000 11001 1110
O. lichuanensis	00000 00101 00000 01101 10111 1111
O. rhodostigmatus	00000 01000 00000 01000 10001 0011
O. liangbeiensis	00001 00111 00010 01100 00000 1101
O. pingii	00000 00111 11010 01100 10011 1111
O. rugosus	01111 10111 00000 01100 00000 11-0
O. xiangchengensis	01111 00111 00000 01110 00000 1110
O. jingdongensis	01011 10111 00001 01101 10000 1110
O. granulosus	01111 10111 00000 01110 00010 1011

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Helminths of Tago's Brown Frog, *Rana tagoi tagoi* (Ranidae), from Japan

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Abstract. -Of 32 *Rana tagoi tagoi*, 22 (69% prevalence) harbored helminths. One cestode *Cylindrotaenia japonica* (prevalence 25%, mean intensity 3.4), three nematodes *Cosmocerca japonica* (prevalence 53%, mean intensity 3.1), *Oswaldocruzia socialis* (prevalence 3%, mean intensity 1.0), *Rhabdias nipponica* (prevalence 22%, mean intensity 2.9) and an acanthocephalan, *Acanthocephalus lucidus* (prevalence 22%, mean intensity 4.7) were found. *Rana tagoi tagoi* represents a new host record for *Cylindrotaenia japonica, Cosmocerca japonica, Oswaldocruzia socialis* and *Rhabdias nipponica.*

Key words: Rana tagoi tagoi, Ranidae, *Cylindrotaenia japonica, Cosmocerca japonica, Oswaldocruzia socialis, Rhabdias nipponica, Acanthocephalus lucidis*, Japan

Introduction

Tago's brown frog, *Rana tagoi tagoi* Okada, 1928 is known from Honshu, Shikoku, Kyushu Islands, Japan where it lives in montane regions (Maeda and Matsui, 1990). To date the only helminth known from *R. t. tagoi* is the acanthocephalan, *Acanthocephalus lucidus* Van Cleave, 1925 reported by Uchida (1975). With world-wide concern over declining amphibian populations (Heyer et al., 1994), possible negative effects of parasites on frogs has become a topic of interest; however, the helminth fauna are incompletely known or has yet to be studied in many species of amphibians. The purpose of this note is to report the results of a helminth survey of *R. t. tagoi.*

Materials and Methods

Thirty two (25 males, 7 females) *Rana tagoi tagoi* (mean snout-vent length 40.9 ± 6.2 SD, range 26-54) were examined. Specimens were collected on Honshu Island during the period June 1988-May 1995 between elevations of 160-800 m. Twenty-nine were from Kanagawa Prefecture; seventeen from Tanzawa (35°28'N, 139°10'E), eight from Hakone (35°12'N, 139°02'E), two from Hadano (35°22'N, 139°14'E) and two from Kiyokawa (36°12'N, 138°30'E). Two were from Shizuoka Prefecture; Gotemba (35°18'N, 138°56'E) and one was from Fukushima Prefecture, Hinoemata (37°02'N, 139°24'E).

The body cavity was opened ventrally and the esophagus, stomach, small intestine, large intestine, lungs and urinary bladder were slit longitudinally and examined under a dissecting microscope. The liver and body cavity were also examined for helminths. All helminths were identified utilizing a glycerol wet mount. Selected cestodes were stained with hematoxylin and mounted whole in Canada Balsam. Frogs were deposited in the herpetology collection of the Natural History Museum of Los Angeles County (LACM): Fukushima Prefecture LACM 141442; Kanagawa Prefecture 141247-141251; 141426-141440; 141443-141447; 141916; 141918-141920; Shizuoka Prefecture 141441; 141917. Helminths were deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705): *Cylindrotaenia japonica*, 85329; *Acanthocephalis lucidus*, 85333; *Cosmocerca japonica*, 85330; *Oswaldocruzia socialis*, 85332; *Rhabdias nipponica*, 85331. Terminology usage is in accordance with Margolis et al. (1982).

Results and Discussion

Twenty two of 32 (69% prevalence) frogs were infected by helminths (Table 1): 19 of 25 males (76% prevalence) and 3 of 7 females (43% prevalence). However, there was no significant difference for prevalence of infection between males and females (Chi-square statistic = 0.58, 1 df, P > 0.05). None of these parasites are unique to *R. t. tagoi.*

Cylindrotaenia japonica (Yamaguti, 1938) Jones, 1987, a parasite of the small intestine, has been reported only from anurans of the Japanese Archipelago. Although nothing is known of its life cycle, Joy-

Table 1. Helminth parasites of Tago's brown frog, Rana tagoi tagoi, from Japan.

Parasite	Prevalence (%)	Mean intensity (range)	Location
Cestoda			
Cylindrotaenia japonica	25	3.4 (1-6)	a
Nematoda			
Cosmocerca japonica	53	3.1 (1-8)	b
Oswaldocruzia socialis	3	1.0	a
Rhabdias nipponica	22	2.9 (1-8)	c
Acanthocephala			
Acanthocephalus lucidus	22	4.7 (2-8)	b

* a = small intestine, b = large intestine, c = lungs.

eux (1924) considers the life cycle of *Cylindrotaenia americana* Jewell, 1916 to be direct with infection ocurring when a contaminated fecal pellet is swallowed by a frog. Other hosts include *Hyla japonica, Rana japonica, Rana ornativentris, Rhacophorus schlegelii* and *Rhacophorus viridis* (Goldberg et al., 1994; Jones, 1987; Uchida, 1975).

Cosmocerca japonica Yamaguti, 1938, a parasite of the rectum, has been reported in amphibians from the Palearctic biogeographic realm. Hasegawa (1989) suggested a synonymy of *Cosmocerca japonica* with *C. ornata* (Dujardin, 1845) Diesing, 1861, which has been found in all biogeographic realms except the Nearctic and Australian; but further review is necessary before this synonymy can be accepted. The life cycle of *C. japonica* is not known; however, the life cycle of *Cosmocerca commutata* (Diesing, 1851) Diesing, 1861 was studied by Fotedar and Tikoo (1968). Eggs hatched in 2-4 hours. Larvae penetrated the skin of the host and migrated through the viscera to reach the lungs 3 days postinfection and the rectum 10-14 days postinfection. Other hosts include *Buergeria japonica, Bufo japonicus, Bufo melanostictus, Cynops ensicauda, Hyla japonica, Microhyla ornata, Polypedates leucomystax, Rana ishikawae, Rana japonica, Rana limnocharis, Rana narina, Rana nigromaculata, Rana ornativentris, Rana rugosa* from Japan (Goldberg et al., 1994; Hasegawa, 1989; Uchida, 1975; Yamaguti, 1938; 1954); *Bufo biporcatus, Limnonectes macrodon, Phrynoglossus laevis, Rana cancrivora, Rana limnocharis,* from the Philippines (Schmidt and Kuntz, 1969); *Bufo bufo, Bufo melanostictus* from Taiwan (Yamaguti and Mitunaga, 1943; Myers and Kuntz, 1970); *Rana limnocharis* from Okinawa (Hasegawa, 1984); *Rana kuhlii, Rana limnocharis, Rana rugulosa* from North Viet Nam (Moravec and Sey, 1985).

Oswaldocruzia socialis Morishita, 1926, a parasite of the small intestine, is apparently restricted to Japan. Travassos (1937) synonymized *O. insulae* Morishita, 1926 and *O. socialis* with *O. filiformis* (Goeze, 1782) Travassos, 1917 which has wide distribution in Europe; but further review is necessary before this synonymy can be accepted. The life cycle of *O. insulae* is not known, however Baker (1978) reported that *Oswaldocruzia pipiens* Walton, 1929, development to infective larvae occurred in fecal pellets with transmission to new hosts by skin penetration. Other hosts include *Rana japonica, Rana nigromaculata* (Uchida, 1975).

Rhabdias nipponica Yamaguti, 1935, a parasite of the lungs, is known from Japan, South China and Viet Nam. The life cycle of *Rhabdias nipponica* is not known, but Baker (1979) has studied the life cycle of *Rhabdias americanus*. Development of larvae to the infective third stage was by matricidal endotoky. Infection occured by skin penetration followed by migration through tissue to body cavity and lungs.

Adults appeared 7-9 days postinfection. Other hosts include *Rana nigromaculata*, *Rana rugosa* from Japan (Uchida, 1975); *Rana guentheri*, *Rana limnocharis*, *Rana nigromaculata* from South China (Kung and Wu, 1945; Wang et al., 1978); *Rana rugulosa* from Viet Nam (Moravec and Sey, 1985).

Acanthocephalus lucidus, a parasite of the small intestine, is apparently restricted to Japan. The life cycle of *Acanthocephalus lucidus* has not been studied, but infection is most likely acquired by consumption of an intermediate host, probably an insect (Petrochenko, 1956). Other hosts include *Bufo japonicus*, *Buergeria buergeri*, *Rana japonica*, *Rana nigromaculata*, *Rana ornativentris*, *Megalobatrachus japonicus* (Petrochenko, 1956; Uchida, 1975).

Uchida (1975) lists 15 anurans from Japan harboring on average 7.7 species of helminths; helminth diversity ranges from a minimum of 1 species in *Hoplobatrachus tigerinus* to 26 species in *Rana nigromaculata*. With 5 helminth species present, *R. t. tagoi* is near the lower end of the diversity scale for Japanese frogs. Subsequent examinations of *R. t. tagoi* will be needed before the full extent and impact of helminth parasitism in this species is known.

Acknowledgments

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A New Species Of *Leptolalax* (Anura: Megophryidae) from Borneo

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Abstract.- A new species of frog of the genus *Leptolalax* is described from high elevation in Sabah, northern Borneo. The new species is remarkable for its small size and the large size of its ova.

Key words: Borneo, Amphibia, Salientia, *Leptolalax*

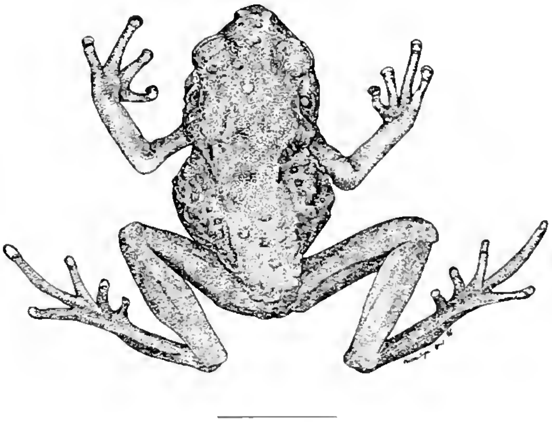

Figure 1. Dorsal view of holotype of *Leptolalax maurus*, new species. The scale line equals 10 mm.

Introduction

Sabah Parks (Sabah, Malaysia) has initiated a program monitoring populations of amphibians at three sites at differing elevations in Kinabalu Park. One of these sites is at Mesilau (1850-1950 m, 6°04'N/ 116°34'E), southeast of the peaks. At this elevation, the vegetation changes from lower montane to upper montane and the climate is temperate in Köppen's system with mean temperature near 16.5° (Kitayama, 1992).

During the course of our initial survey at this site, we collected a gravid female, which we describe below as the holotype of a new species of *Leptolalax*. On our next visit to the same site, we found an additional adult, one juvenile and two metamorphosing individuals of the same species. This is not the first *Leptolalax* to be found at montane elevations in Borneo. *Leptolalax dringi* Dubois was collected at 1800 m on Mt. Mulu, Sarawak (Dubois, 1987), and *L. dringi* and *L. pictus* Malkmus at 1230-1560 m in Sabah (Inger *et al.*, 1995). However, as will be detailed below, the Mesilau species is smaller than any other yet found in Borneo, has larger ova and smaller clutch than females of other Bornean species, and has a distinct coloration.

Material and Methods

The specimens were preserved in 10% formalin after being euthanized and transferred to 70% ethanol after four days. Comparisons with other species of *Leptolalax* were made using the collections of Field Museum (FMNH) and by reference to Dubois (1983, 1987). We use the following abbreviations: SVL, snout-vent length; T, tibia length; HW, head width; HL, head length; TYM, diameter of tympanum.

Leptolalax maurus new species

Material examined.–Holotype: Sabah Parks 2531, an adult female, collected by the authors July 1, 1995, at Mesilau Station, 1860 m, Kinabalu Park, Sabah, in floor litter of oak-chestnut forest (Fig. 1).

Paratypes: FMNH 252425-26, Sabah Parks 2305-06, one male, one juvenile, and two stage 45 metamorphic individuals.

Diagnosis.–A small species of *Leptolalax*, adult female 32 mm, male 26 mm SVL; dorsal and ventral surfaces dark, dorsally without visible pattern, belly with narrow network of small light spots; underside of hind limb dark; a superficial, round pectoral gland.

Description.–Habitus moderately stocky, width of head and body subequal. Snout obtusely pointed, rounded in profile, not projecting; nostril lateral, slightly nearer tip of snout than to eye; canthi distinct, weakly constricted; lores weakly sloping, concave; diameter of eye slightly longer than length of snout; interorbital equal to eyelid, slightly wider than internarial; tympanum visible, slightly more than half diameter of eye; no vomerine teeth. Finger tips rounded; first finger shorter than second; no subarticular tubercles, but long cornified strips under fingers; a large inner palmar tubercle, a much smaller one at base of fourth finger. Tips of toes like those of fingers; third toe longer than fifth; toes webbed at base only; subarticular tubercles replaced by long strips of cornified tissue; low, oval inner metatarsal tubercle, no outer one; heels overlapping when limbs are flexed. Back with many low, rounded tubercles, homogeneous in shape and size; sides with more elevated, round tubercles; similar but smaller tubercles on limbs; a strong angular supratympanic fold; ventral surfaces smooth; a large superficial, circular, pectoral gland on each side, gland diameter 1.8-2.5 mm.

Color in life almost black without visible pattern dorsally; limbs slightly lighter, with dark crossbars; sides black with light dots, reddish ventrolaterally in one individual; venter black or dark gray brown, with indistinct small light areas; limbs ventrally dark olive brown to black. In preservative dark purplish brown dorsally, without visible pattern; obscure crossbars on calf; sides dark brown, with small light spots (ca. size of finger tips); venter dark brown with narrow network of small light spots on belly; entire underside of hind limb dark brown.

Measurements (mm) of holotype: SVL 31.8, T 15.9, HW 10.7, HL 13.0, TYM 2.7, interorbital 3.3.

Variation.–Male paratype: SVL 26.1, T 12.3, TYM 2.2, interorbital 3.3. Male with very large testis, but no vocal sac opening visible. Newly transformed frog: SVL 20.6, T11.0, HW 7.4, HL 8.2. Metamorphosing individuals in stage 45: 20.4, 22.0, tail lengths 27.0, 18.2, respectively. The light network on the venter of the stage 45 frogs is wider than in the others, but still occupies less than 20% of the total area.

Female with 45 large, white ova in left ovary; ova 1.83-2.33 mm (13 measured).

Etymology.–*maurus*, from *mauros*, Greek, meaning dark.

Comparisons.–The new species differs from all previously known Bornean *Leptolalax* in size, skin surface, coloration, pectoral gland, and size and number of ova. The size range of females of other Bornean species is 36.1-48.3 mm (n=77) and of males 28.7-38.9 m (n=136) (Inger *et al*., 1995), compared to 31.8 (female) and 26.1 (male) in *L. maurus*. The back and sides of *L. maurus* are covered with homogeneous, round tubercles; in two of the other Bornean species [*L. pictus* and "unspotted Sarawak" (Inger *et al*., 1995)] the dorsal skin is smooth and in the two others (*L. gracilis* and *L. dringi*) the dorsal tubercles are heterogeneous in size and smaller than those on the sides.

Leptolalax maurus is the darkest of the Bornean species of the genus. It is the only species that is uniformly dark brown on the ventral surface of the head and hind limbs, and the only one in which no dark pattern is evident on some portion of the dorsal surface. It is also the only Bornean species with a conspicuous, superficial, round pectoral gland. A pectoral gland is usually present in the other species, but the skin must be cut and rolled over before the gland becomes visible on the interior surface.

Leptolalax maurus also differs from the three currently recognized species (Dubois, 1983) from Southeast Asia, *L. pelodytoides* (Boulenger), *L. heteropus* (Boulenger), and *L. bourreti* Dubois, in having a very heavily pigmented belly and in lacking distinct dorsal markings. The new species is much smaller than *L. bourreti* [SVL males 36 mm, females 42-45 (Dubois, 1983), but similar to the other two in size.

The enlarged but not yet ovulated ova of *L. maurus* are distinctly white; ova in the same stage of development are yellow in the other Bornean species and in *L. pelodytoides*. The left ovary of *L. maurus* had 45 enlarged ova, compared to 112-210 in *L. gracilis* (n=1), *dringi* (2), *pelodytoides* (1) and *pictus* (2). Mean diameter of 10 large ova in each of the last four species ranged from 1.60±0.027 to 1.78±0.050 mm; in *L. maurus* the mean of 13 ova was 2.0±0.049. The volume of ova in the left ovary (ovum volume, based on mean ovum diameter, times number of ova) for *L. gracilis*, *dringi*, *pelodytoides*, and *pictus* varied from 255.5 to 542.3 mm^3, but only 188.5 mm^3 in *L. maurus*. However, if the cube root of ovarian volume is divided by SVL of females to obtain a relative measure of ovarian volume, there is very little difference among the species; the ratio of cube root of ovarian volume to SVL varies from 0.152 to 0.179 in *L. gracilis*, *dringi*, *pelodytoides*, and *pictus* and 0.180 in *maurus*. Although relative reproductive effort measured in this manner is approximately the same in all these species, the division of the material into ova is quite different in *L. maurus*. The enlargement of ova in the high altitude species *L. maurus* is consistent with the general trend in other Bornean anurans. The montane frogs listed by Inger and Stuebing (1992) include a high proportion with enlarged ova: species of *Philautus* and *Pelophryne* with direct development and species of *Ansonia* with normal larval development. Together, species of those three groups compose 50% of the montane frog fauna of northwestern Borneo.

Acknowledgments

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Taxonomic Notes on Pakistani Snakes of the *Coluber karelini-rhodorachis-ventromaculatus* Species Complex: A New Approach to the Problem

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Abstract. -Taxonomic characters used for definition of Pakistani species of *Coluber* snakes are analyzed and discussed. New combinations of characters are used to devise a key for identification of Pakistani snakes of the genus *Coluber*. Zoogeographical distribution is discussed.

Key words: Taxonomy, *Coluber karelini-rhodorachis-ventromaculatus* species complex, Pakistan.

Introduction

The taxonomic status of Pakistani racers belonging to the genus *Coluber (C. ventromaculatus* Gray and Hardwicke 1834, *C. karelini* Brandt 1838 and *C. rhodorachis)* Jan 1865, has long remained enigmatic to herpetologists (Minton, 1966; Mertens, 1969; Khan 1982). Despite the problematic taxonomy of *C. ravergieri* in the circum-Mediterranean region (Boulenger, 1893; F. Werner, 1905; Mertens, 1952; Baran, 1976; Bannikov et al., 1977; Schatti and Agasian, 1985), it is readily differentiated from its Pakistani congeners by 21 midbody scale rows (Khan, 1982). However, *C. karelini, C. rhodorachis* and *C. ventromaculatus,* due to their dubious color variations and overlapping scale counts, have always posed taxonomic problems to the herpetologists working in Middle East and southeast Asia (Clark et al., 1969; Leviton, 1959; Leviton and S. Anderson, 1969, 1970; Minton, 1966; Mertens, 1969; Haas and Y. Werner, 1969; Khan, 1977, 1982; Latifi, 1991; Tiedemann, 1991; Leviton et al., 1992).

The present work has been undertaken to assess the validity of various morphological characters which have usually been used to define these colubrid taxa. New combinations of readily observable morphological characters are suggested for identification of these species, gathered from the material coming from different parts of Pakistan and Azad Kashmir.

Materials and Methods

For this study a total of 27 *C. karelini,* 92 *C. rhodorachis* and 142 *C. ventromaculatus,* from different parts of Pakistan and Azad Kashmir, were available. States of the following morphological characters, usually used in the taxonomic determination of these snakes, were recorded for each species: i. Measurements: total length (from anterior tip of snout to the posterior tip of tail); body or snout-vent length (from anterior tip of snout to anterior lip of anal aperture); tail length (from posterior lip of anal aperture to the tip of tail); head length (from anterior tip of snout to posterior margin of the last supralabial); head width (at the level of last supralabials across head), were recorded to the nearest 0.1 mm. ii. Snakes under 500 mm total length are taken as juveniles, up to 750 mm subadults, and above, adults. iii. Scutellation: number of scale rows at midbody and just anterior to vent were counted on both sides of the same ventral; pre- and postsuboculars lie below the level of eye; first broader than long scale in the gular region was counted as the first ventral, and the preanal scale is not counted. iv. Color pattern: For description of dorsal body pattern, formed by the deposition of sooty pigment, Fig. 11 and 1A (Peters, 1964) and Fig. 27 (Khan, 1993a) were followed. v. For hemipeneal study three *Coluber ventromaculatus* , one *C. rhodorachis* are available with fully everted hemipenes. However, for additional comparative material for these species and for *C. karelini,* the technique suggested by Pesantes (1994) was used to evert the organ of preserved specimens. Description of the organ follows Dowling and Savage (1960) and Khan (1993b).

Characteristics of Pakistani *Coluber* snakes

Long, narrow, cylindrical body with distinct elongated head, long tail with very gradual taper with a fine tip. Head with large, symmetrically arranged scales; rostral strongly hollowed underneath, a pair of internasals and prefrontals; single supraorbital and frontal, a pair of parietals, single loreal, 1-2 pre- and postoculars, 1-2 pre- and postsubocular, upper preocular in contact with frontal; 9 supralabials, 1-2 in contact with eye; frontal broad, elongated, parietals broad and elongated; temporals 2+3 or 3+3. Genials 2, posterior longer, separated from each other by small scales;

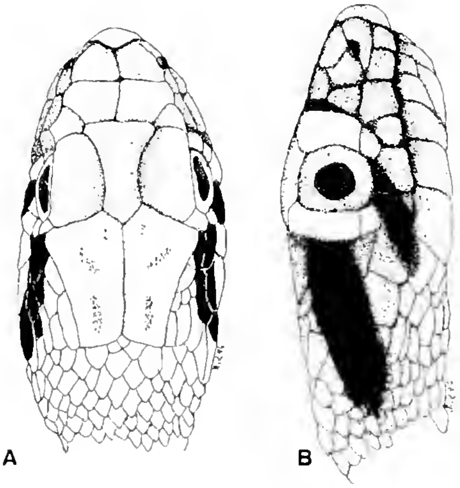

Figure 1. *Coluber karelini*. A. Dorsal head scales; B. Lateral head scales.

eyes large, with distinct round pupil. Snout projecting, distinct canthus, a pair of nasals. Body scales smooth, 19-21 at midbody, reduced to 11-13 at vent, anal divided; ventrals rounded, ranging 192-277; subcaudals paired, ranging 82-145; hemipenis is simple with single sulcus spermaticus, distal portion calyculate, proximally spinose, spines enlarged.

Evaluation of Characters used in *Coluber* taxonomy

Various morphological characters have been used in different combinations for Taxonomic determination of Pakistani *Coluber* racers. In the following section these characters are examined in the light of the data collected from present collections:

i. *Circumocular scales:* Basic circumocular scalation consists of one supraocular, one preocular and two postoculars. Usually one supralabial, the fifth, touches orbit in *C. karelini* (Fig. 1b), while two supralabials, 5th and 6th (rarely 4th and 5th) touch the orbit in both *C. rhodorachis* and *C. ventromaculatus*. Circumocular conditions are complicated by the appearance of a presubocular or a postsubocular scale preventing either 4th or 5th, rarely 6th supraocular to come in contact with orbit, so that one, two, three, or none of the supralabials comes in contact with orbit and conditions like that seen in *C. karelini* may appear in *C. rhodorachis* and *C. ventromaculatus* (Bannikov et al., 1977; Gasperetti, 1988). Rarely, presubocular and postsubocular are fragmented in 3-4 scales at loreal and postocular region.

Table 1 summarizes different circumocular states observed in the present collection: in 97% *C. karelini* 5th supralabial is in contact with orbit on both sides, 3% have 5th on one side and 5th and 6th on the other, one specimen has none in contact on one side, one on the other. More variation is observed in *C. rhodorachis* and in *C. ventromaculatus*.

Table 1. Variations in circumocular scutellation of Pakistani colubrid snakes: (1= *C. karelini*; 2= *C. rhodorachis*; 3= *C. ventromaculatus*. Note: figures with oblique represent bilateral configurations, while those in parentheses represent number of specimens of each species present in present collection).

Number of supralabials in contact with eye	1 (27)	2 (92)	3 (142)
4, 5	–	2	8
5	25	3	5
5/5, 6	2	7	3
5, 6	–	68	103
4, 5, 6	–	3	7
4, 5, 6/5, 6	–	5	5
Damaged, not included	2	4	11

ii. *Number of ventrals and subcaudals*: Ventral and subcaudal counts overlap in these snakes; however, *C. rhodorachis* is recognized due to its high subcaudal counts (139-144), well above range of *C. karelini* and *C. ventromaculatus*. To make ventral and subcaudal counts taxonomically more meaningful, Mertens (1969) and Leviton (1986) computed ventrals together with subcaudals to single out *C. rhodorachis*, where low ventral counts for this species may overlap high counts for the other two species (Table 2).

iii. *Number of dorsals anterior to vent*: Nineteen midbody scale rows, in *C. karelini* and *C. ventromaculatus*, are reduced to 13 just anterior to vent and 10-13 in *C. rhodorachis*. A clear distinction between these taxa, on this basis, is not possible.

iv. *Loreal scale*: Shape of loreal scale has been considered a taxonomically important character (Smith, 1943; Khalaf, 1959). In *C. karelini* the loreal scale is almost squarish to triangular (Fig.1b), while in *C. rhodorachis* and *C. ventromaculatus* it is usually longer than high, rarely squarish.

v. *Hemipenial morphology*: Typically, the hemipenis is a simple single-lobed cylindrical organ, with a

Table 2. Range of ventral (V) and subcaudal (Scd) counts in *Coluber* species in present collection.

Taxon	V	Scd	V+Scd
C. karelini	192-207	90-11	282-317
C. rhodorachis	205-277	139-144	344-421
C. ventromaculatus	195-220	82-119	277-339

Table 3. Distribution of sex in a collection of *C. karelini*, *C. rhodorachis*, and *C. ventromaculatus* from Pakistan.

Sex	*C. karelini*	*C. rhodorachis*	*C. ventromaculatus*
Sample size	27	92	142
Males	15	73	95
Females	6	13	32
Undetermined:			
Juveniles	3	4	5
Damaged	3	2	10

median sulcus spermaticus. Distally, the organ is calyculated with deeply scalloped cups fringed with spines, while the proximal portion is spinose with several rows of large proximally curved spines extending to the organ's base, with several transverse rows of much smaller scales at the middle. In *C. karelini* the calyculated part is more extended, and cups are much longer than broad, more deeply scalloped, and are fringed with much longer spines. The proximal spiny half of the organ merges abruptly into the distal calyculated half. On the other hand, cups in *C. rhodorachis* and *C. ventromaculatus* are shallower, squarish, fringed with smaller spines and the proximal spiny portion gradually merges with the scalloped distal part through spines, which gradually decrease in size.

Males predominate in our collections of these snakes from Pakistan (Table 3).

vi. *Extension of rostral scale*: The dorsal part of the rostral scale is more acutely pointed behind and raised in *C. ventromaculatus*, and extends between internasal scales to almost 1/4 of the internasal suture, while in *C. karelini* and *C. rhodorachis* it is not raised and is broadly rounded off, just touching the internasal suture (Fig. 1a).

vii. *Number of temporals*: Usually the temporal formula for these snakes is 2+3+3, however, 1+2+3, 2+2+3 and 1+3+3 temporal counts unilaterally or bilaterally are recorded in all the species.

viii. *Dorsal body pattern*: There is no marked difference between adult and juvenile patterns in *C. karelini* and *C. ventromaculatus* except size of spots and blotches; however, adult/juvenile differences are quite marked in *C. rhodorachis*.

The head of *C. karelini* is relatively light in color, with slight darkening of supralabials and internasals, while the head of *C. rhodorachis* is more melanistic and dark mottling is not discernible. The head of *C. ventromaculatus* is lighter with distinct dark-brown mottlings at the supralabials, frontal and parietals. The suboculo-labial and a postoculo-temporal stripe is vividly marked in *C. karelini* (Fig. 1A, B), hardly discernible in *C. rhodorachis* and well marked in *C. ventromaculatus*.

Grayish, pale-gray, buff, sandy, pale, reddish-brown, brownish and greenish body hues have been reported for these snakes by different herpetologists. The basic body color is due to the deposition of minute dots of different colors, to which additional sooty-black pigment is deposited in three specific patterns (Khan, 1993a).

In *C. karelini* the sooty pigment is uniformly deposited on the whole scale, resulting in the vivid dorsal pattern in this snake. It consists of a median

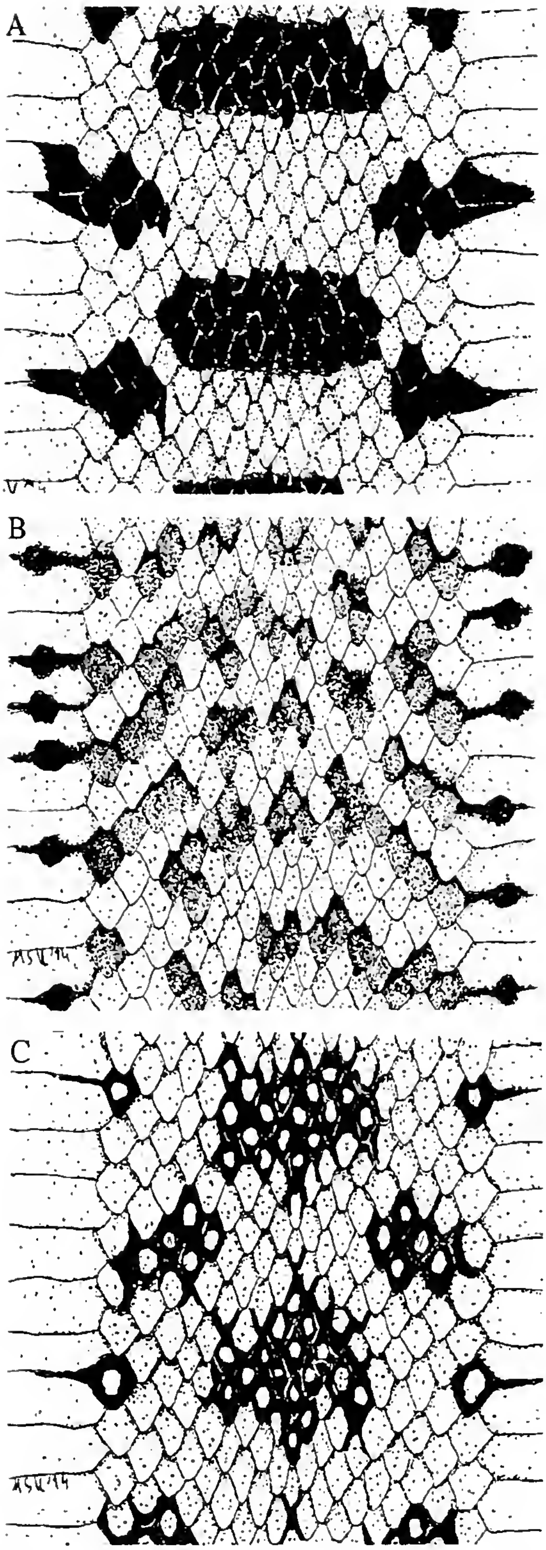

Figure 2. Pigmentation of dorsal pattern. A. *Coluber karelini*; B. *Coluber rhodorachis*; C. *Coluber ventromaculatus*

Figure 3. *Coluber karelini*

Figure 4. *Coluber rhodorachis*

Figure 5. *Coluber ventromaculatus*

row of vivid sooty-black transverse bars extending from nape to base of tail. In the anterior half of the body, the bars are 2-3 scales thick, narrower than interspaces, occupying 10-11 median rows of dorsals, alternating with a transversely enlarged lateral row of spots, the bases of which touch tips of adjacent ventrals (Fig.2A). Ventrum is spotless ivory.

In *C. ventromaculatus* the fine dark brown dots are uniformly deposited on the scales, more densely on scales of dorsal pattern while sooty pigment is rare. A median row of squarish or rectangular blotches or sad-

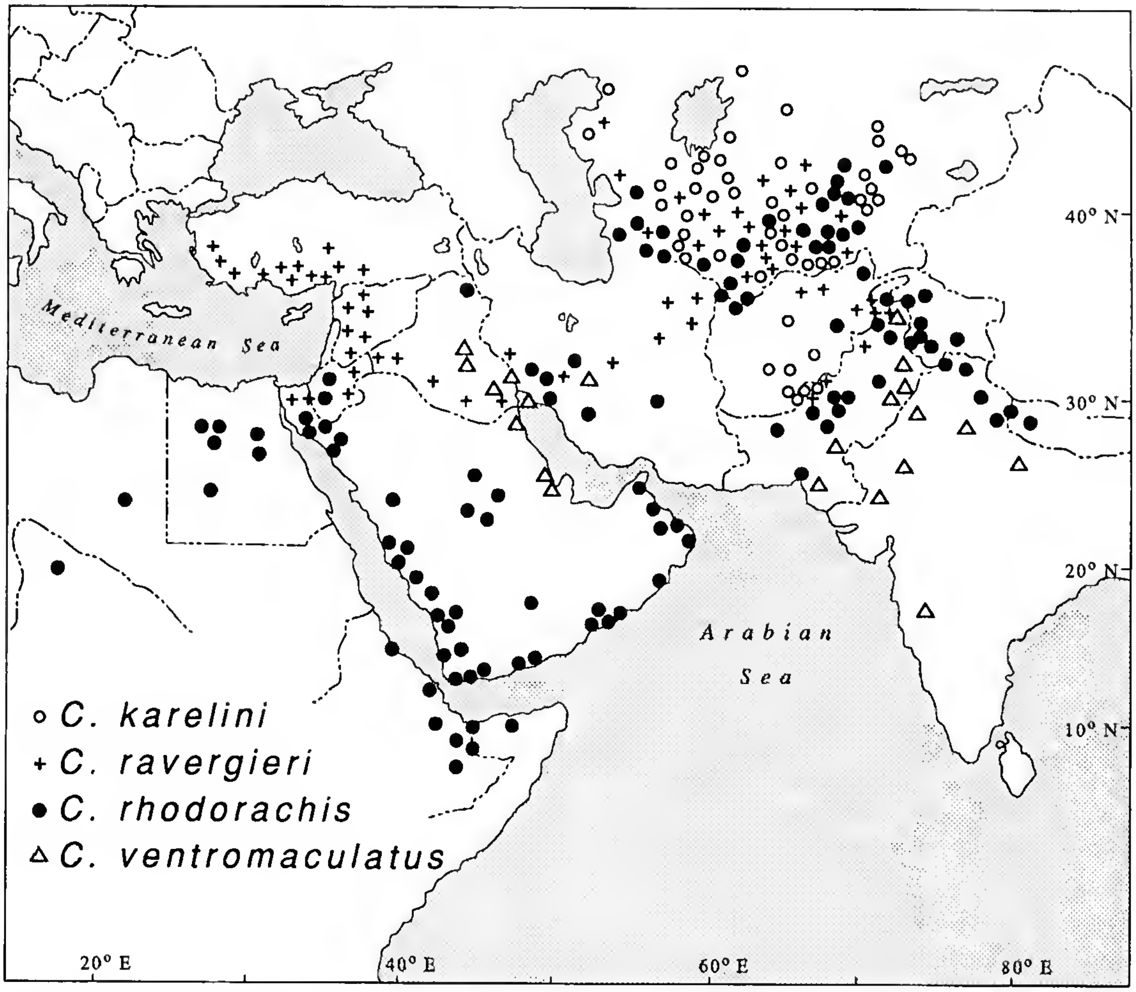

Figure 6. Geographic distribution of *Coluber ravergieri* (+), *Coluber karelini* (o), *Coluber rhodorachis* (O), *Coluber ventromaculatus* ()

dles is characteristic of this species. The blotches are broader than interspaces, occupying 8-9 median dorsal scale rows, alternating with a pair of lateral rows of spots, the outermost row is just of dark specks which occasionally touch edges of corresponding ventrals. Here the sooty pigment is deposited on the periphery of the scales, leaving their centers clear, resulting in a dull pattern (Fig. 2C). A distinct 6-9-scale long, 2-4-scale thick nuchal blotch or stripe is characteristic of this species, this mark generally flanked by a large blotch on temporals. In specimens from the Middle East, the nuchal stripe is long and thin, occupying half scales of the median dorsal pair of scales. Ventrum is ivory white, with occasional lateral spots on ventrals.

In juvenile *C. rhodorachis*, the anterior half of the body is lighter with distinct 4-5 alternating rows of dark irregular blotches or spots, replaced in the posterior, darker half by a mosaic of close-set vertical narrow, dark streaks. The streaked pattern is due to a concentration of pigment between adjacent rows of scales, creating a light/dark zigzag mosaic pattern (Fig. 2B), ventrum melanistic, due to deposition of pigment between ventrals.

Adult *C. rhodorachis* are more melanistic anteriorly, while the posterior half, which appeared darker in juveniles, now appears lighter. Juvenile spotted pattern is either lost altogether in darker adult specimens as is usual in snakes from Kashmir (Khan, unpublished data; Murthy and Sherma, 1976; 1979), or is replaced by fine light/dark streaked mosaic pattern as in snakes from Baluchistan (Mertens, 1969,Fig. 17). Ventrals, in adults, are ivory, except for occasional lateral spottings.

ix. *Geographical distribution* (Fig. 6): Racers are nocturnal, alert and shy snakes. They generally prefer open semidesert country with sparse grass and scrubby vegetation. They are widely distributed from Transcaspia to Transcaucasia in the north, to the African Sahara in the west, extending in the east to Kashmir and Nepal, and descending through the Indo-Gangetic plains into the Indian peninsula in the south.

Coluber ravergieri is a wide-ranging Central Asian species, extending from the Turanian Plateau to the Anatolian highlands in the west, through Turkey, Israel, Jordan, northern Egypt, Iraq, Iran, and Afghanistan. It reaches the western border of Pakistan at its eastern limit of distribution.

Coluber karelini is widely distributed in the Middle East, from the Turanian Plateau to the Kazakh uplands in the north, entering Afghanistan, and extending south to the low hills of the Quetta-Pishin area in Baluchistan (Khan, 1980, 1987).

Coluber rhodorachis is the most wide-ranging Saharo-Sindian racer, extending from Algeria to the western and northwestern highlands of Pakistan through Egypt, Ethiopia, Arabian Peninsula, Iraq, Kuwait, Iran, and extending northwards to the Aralo-Caspian region and Afghanistan. In Pakistan it is widely distributed in Baluchistan to the Makran coast, extending through Waziristan into the Siwaliks in Kashmir, Utter Pardesh, India to Nepal.

Coluber ventromaculatus is primarily an Indian species. It is widely distributed in the Indo-Gangetic plains and does not extend west of the Indus. I regard all reports of this snake from Iran and Iraq as pertaining to local races of *C. rhodorachis* with low ventral and subcaudal counts.

Coluber karelini, *C. ravergieri*, and *C. rhodorachis* are sympatric in most of their northern Caucaso-Turanian and Afghanistan range. However, in the Saharo-Sindian belt *C. ravergieri* is primarily a northern species, while *C. rhodorachis* is a southern form extending to northern Somalia. In Pakistan *C. karelini* is sympatric with *C. ravergieri* and *C. rhodorachis* in western Baluchistan, while *C. ventromaculatus* is in sympatry with *C. rhodorachis* in northern, northwestern and coastal foothills (Fig. 6).

Diagnoses of Pakistani species of *Coluber*

Coluber ravergieri Ménétriés, 1832

Diagnosis:

i. Midbody scale rows 21, reduction to 15 just anterior to vent.

ii. Dorsum buff or grayish with a dorsal series of dark rhomboidal spots or narrow cross-bars alternating with a series of smaller spots on sides.

iii. Temporals 3+3.

iv. Ventrals 197-234, subcaudals 82-101.

Distribution in Pakistan (Figure 6): Central Asian; reaches western Baluchistan and northwestern hills in N.W.F.P., collected at 3,000 to 5,000 m elevation.

Coluber karelini Brandt, 1838 (Figures 2A, 3)

Diagnosis:

i. Midbody scale rows 19, reduction to 12-13 just anterior to vent.

ii. Vivid sooty pigment is uniformly deposited on scales of the dorsal pattern (Fig. 2A).

iii. Dorsal pattern vivid, consisting of a median row of black crossbars, narrower than interspaces, alternating with a lateral row of spots touching ventrals.

iv. Vivid oculo-labial and oculo-temporal stripes always present.

v. Almost always 5th (rarely 6th or 5th, 6th, or none) supralabial in contact with orbit.

vi. Ventrals 192-207, subcaudals 90-110.

Distribution in Pakistan (Fig. 6): From Transcaspia to low hills of Quetta-Peshin area, at an elevation of 1600-1840 m; does not extend eastward into Sind and Punjab.

Remarks: Often *C. rhodorachis* is confused with this taxon due to occasional occurrence of *C. rhodorachis* with one supralabial in orbit and dorsal row of lighter cross bars. Specimens are illustrated by Gasperetti (1988, Fig. 29) from Afghanistan and Nushki (Baluchistan); specimens from this region have neither dorsal pattern nor orbito-labial and temporal stripes as vivid as observed in *C. karelini* from Quetta-Peshin, Baluchistan. Mertens (1969) erected his *C. karelini mintonorum* on similar *C. rhodorachis* from the Baluchistan highland. In southern Turkmenistan, *C. karelini* is known to hybridize with *C. rhodorachis* (Bannikov et al., 1977).

Coluber rhodorachis Jan, 1865 (Figures 2B, 4)

Diagnosis:

i. Midbody scale counts 19, reduced to 11-13 at the level of vent.

ii. Colored dots are uniformly deposited on dorsal scales, while the dorsal pattern is formed by concentration of colored dots, however, melanicity of older snakes is due to additional deposition of sooty pigment (Fig. 2B).

iii. Juvenile pattern is of spots on anterior part of body, unicolor or streaked posteriorly; venter melanistic. Adults become melanistic anteriorly, losing spots, sometimes having fine, streaked pattern anteriorly and are unicolor posteriorly. Venter ivory, with sides of ventrals darkly smudged.

iv. Usually two, 5th and 6th (rarely 4th and 5th or 5th or three, 4th, 5th, and 6th) supralabials touching orbit.

v. Ventrals 205-277, subcaudals 139-144.

vi. Distinct oculo-labial stripe, indistinct oculo-temporal stripe.

Distribution in Pakistan (Figure 6): Widely distributed in Baluchistan, western and northern sub-Himalayan (N.W.F.P.) highland and inland low ranges (Punjab and Sind). From sea level (along Makran coast) to about 2300 m. It does not extend onto plains.

Remarks: Unaware of Jan's (1865) erection of the nominal taxon, J. Anderson (1871) described *Zamnis ladacensis* from Ladakh, Baltistan. Later, he (1895) compared *rhodorachis* with *ladacensis* and found them identical. Despite proven conspecificity, a *rhodorachis* with a median dorsal pinkish-red (Nikolskii, 1916), drab (Corkill and Cochran, 1965), light orange to vermilion (Minton, 1966), red (Mertens, 1969) vertebral line has been regarded as *ladacensis*. The so-called "colored vertebral line" is discernible only in living snakes, as it is soon lost on preservation, especially in formalin. This is why the validity of *ladacensis* as a separate taxon has frequently been questioned (Mertens, 1956; Kramer and Schnurrenberger, 1963; Leviton and S. Anderson, 1961; Kral, 1969; Ataev, 1985).

Coluber rhodorachis from southern Israel (F. Werner, 1896, Fig. 2A, B) has more close-set (2 scales wide) transverse stripes which are much broader than interspaces. Leviton et al., (1992, Plate 15) show two color morphs of *C. rhodorachis* from the Arabian peninsula: Fig. C, from Tabuk Emirate, anterior half of body spotted, posterior unicolor; Fig. D, from Taif, Makkah Emirate, is unicolor melanistic, while Fig. E, from Khuzistan Province, Iran, is a banded form, the bands broader than interspaces. Latifi (1991, Plate 16) shows two more color morphs from Iran: Fig. 41 unicolor and Fig. 42 spotted, the spots are more like broken transverse bands. *C. rhodorachis* is known to exhibit high variability of color and pattern throughout its range (Y. Werner, 1971).

Coluber ventromaculatus Gray and Hardwicke, 1834 (Figures 2C, 5)

Diagnosis:

i. Midbody scale rows 19, reduced to 13 at level of vent.

ii. The sooty pigment is confined to each scale's periphery in dorsal body pattern (Fig. 2C).

iii. Dorsal pattern consists of a median row of rhombs or saddles, broader than interspaces, alternating with a lateral row of spots, usually touching ventrals.

iv. Two supralabials, 5th and 6th or 4th and 5th, touch orbit.

v. Ventrals 195-220, subcaudals 82-119.

vi. Loreal scale longer than high.

Distribution in Pakistan: Plains of Punjab and Sind; rarely extends above 300 m elevation. (Fig. 6).

Remarks: This taxon is based on Plate 80, Fig. 1, a, b of Gray and Hardwicke (1834), with only the inscription, "spotted bellied snake *Coluber ventromaculatus*"; no description or type locality is given. The figured snake has approximately 220 ventrals, 70 subcaudals, with a median row of more than 60, 1-2-scale-wide narrow cross bands, replaced on tail by narrow transverse streaks formed of dark edges of lateral scales, distinct orbito-labial and temporal stripes. Figure 1a shows an irregular cross band between the orbits and a few spots on temporals and a distinct median dorsal one-scale-narrow nuchal streak. The lower jaw is shown distinctly countersunk, abnormal for this species.

Schmidt (1939) restricted the type locality to Bengal, since, according to Smith (1931), Hardwicke mostly collected from the region. A comparison with Pakistani snakes of this taxon shows differences in dorsal pattern, which usually consists of 3-4-scale-wide diamonds or saddles, obscure oculo-temporal bar, 2-4-scale-wide nuchal streak always flanked by larger temporal blotches obscuring oculo-temporal streak; pigment is peripherally deposited on scales, head with indistinct dark mottling. However, a pair of snakes from southeastern Thar Pakar, Sind, has a single scale-wide uninterrupted median nuchal streak, running to the midbody, passing through dorsal saddles, while snakes from Punjab and most of Sind have a short, 2-4-scale-wide and 5-6-scale-long streak or blotch, which seldom extends between saddles.

Leviton et al., (1992, Pl. 15) illustrate two snakes as *C. ventromaculatus*: Fig. F, from Sabiya Peninsula, near Kuwait City, with a long narrow nuchal streak and transverse bands, broader than interspaces, and a row of lateral spots, while Fig. H, from Ghizri, Karachi, with indistinct spottings on anterior half of body, is just like snakes mostly from Baluchistan.

Coluber ventromaculatus and *C. rhodorachis* sometimes indistinguishably intergrade into each other in appearance, scale counts and dorsal body pattern. For a long time, Russian herpetologists confused *C. rhodorachis* with *C. ventromaculatus* (Nikolskii, 1916; Terentev and Chernov, 1949; Leviton, 1959; Leviton and S. Anderson, 1970), and still this confusion exists (Baran, 1982). I am inclined to believe that all *C. ventromaculatus* reported from west of the Indus (Fig. 6) are actually color morphs of *C. rhodorachis*, and *C. ventromaculatus* does not extend westward beyond the Indus. Reports of this species from Chitral, Dir and Swat (McMahon, 1901a,b), actually pertain to *C. rhodorachis*. Mostly, the confusion between these taxa is created by dorsal pattern figured in the type, Fig. 1, Plate 80 (Gray and Hardwicki, Vol. II, 1834). Famous Indian ophiologist Wall (1923) found no option but to unite *C. ventromaculatus* with *C. rhodorachis* to settle this taxonomic tangle.

Key to Pakistani Snakes of the Genus *Coluber*

A satisfactory key for identification of Pakistani *Coluber* has long been needed. The following key is based on diagnostic characteristics gathered from the present collection, satisfactorily helping in diagnosis of these taxa (Khan 1993):

1a. Midbody scale rows 21; collected from Chitral and northern Baluchistan ....*C. ravergieri*

1b. Midbody scale rows 19 2

2a. Subcaudals 125-144; unicolor, spotty, or with close-set transverse striations; sooty pigment deposited between scales, main dorsal pattern formed by concentration of tiny dots; collected from western and northern highland and Salt Range, Punjab ....*C. rhodorachis*

2b. Subcaudals 80-120; dorsal pattern of saddles, diamonds, or transverse bars 3

3a. One (5th, rarely 6th, or none) supralabial in contact with orbit; dorsal pattern of vivid black transverse bars, narrower than interspaces; sooty pigment deposited uniformly on scales; collected from western Baluchistan...*C. karelini*

3b. Two (5th and 6th) supralabials in contact with orbit; dorsal pattern a median row of saddles or diamonds, broader than interspaces; sooty pigment deposited on periphery of scales; collected from Punjab and Sind plains........................*C. ventromaculatus*

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Appendix I

Snakes for this study were collected from within a radius of 5-10 km around the following localities in Pakistan and Azad Kashmir. Figures in parentheses indicate the number of snakes collected from each locality.

Coluber ravergieri: Baluchistan: Boostan (1); Shadezai (2).

Coluber karelini: Baluchistan: Punj Pai (4); Quetta (4); Peshin (6); Boostan (3); Chaman (4); Loi Banda, Zob (4); Muslim Bazar, Zob (2).

Coluber rhodorachis: Baluchistan: Punjpai (2); Quetta (3); Peshin (2); Boostan (1); Chaman (2); Loi Banda, Zob (1); Muslim Bazar, Zob (1); Khuzdar (3); Karna, Khuzdar (2); Waddh, Khuzdar (3); Arnachh, Khuzdar (1); Naal, Khuzdar (2); Nushki (1); Kalat (1); Mastung (5).

Northwestern Frontier Province: Wana (1); Tank (1); Bannu (1); Kohat (1); Nowshera (3); Peshawer (4); Mardan (2); Manshera (2); Dadar (1); Abbottabad (2); Ghari Habibullah (2); Swat (2); Kalam (2).

Punjab: Rohtas Fort (2); Islamabad (2); Chattar (2); Attock (1); Pir peahai (2); Pind Dadan Khan (2); Dandot (1); Khewara (2); Choa Saidan Shah (2).

Sind: Chauki (1); Band Murad Khan (1); Karachi (2); Thatta (1).

Azad Kashmir: Mirpur (1); Bhimbar (2); Dulaih Jattan (1); Kotli (3); Goi Madan (8); Aram Bari (2); Palandri (1), Punch (1); Bagh (1); Muzaffarabad (3).

Coluber ventromaculatus: Punjab: Jhelum (2); Lala Musa (1); Gujrat (2); Wazirabad (1); Sialkot (3); Gujranwala (1); Lalian (3); Rabwah (25); Chiniot (14); Sargodha (4); Mianwali (5); Khushab (10); Nurpur (12); Bhakkar (4); Leiah (3); Toba Tek Singh (2); Multan (5); Dera Ghazi Khan (6); Rajanpur (3); Bahawalnagar (3); Fort Marot (2); Rahimyar Khan (4);

Sind: Sukkur (2); Sehwan (3); Larkaa (2); Nawab Shah (3); Dadu (3); Hyderabad (1); Mithi (2); Diplo (3).

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A New skink from the Thal Desert of Pakistan

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Abstract. - A new skink belonging to the genus *Eumeces* is morphologically described and compared with its Pakistani congeners.

Key words: Eumeces indothalensis new species, description, Sauria, Scincidae, *Eumeces*

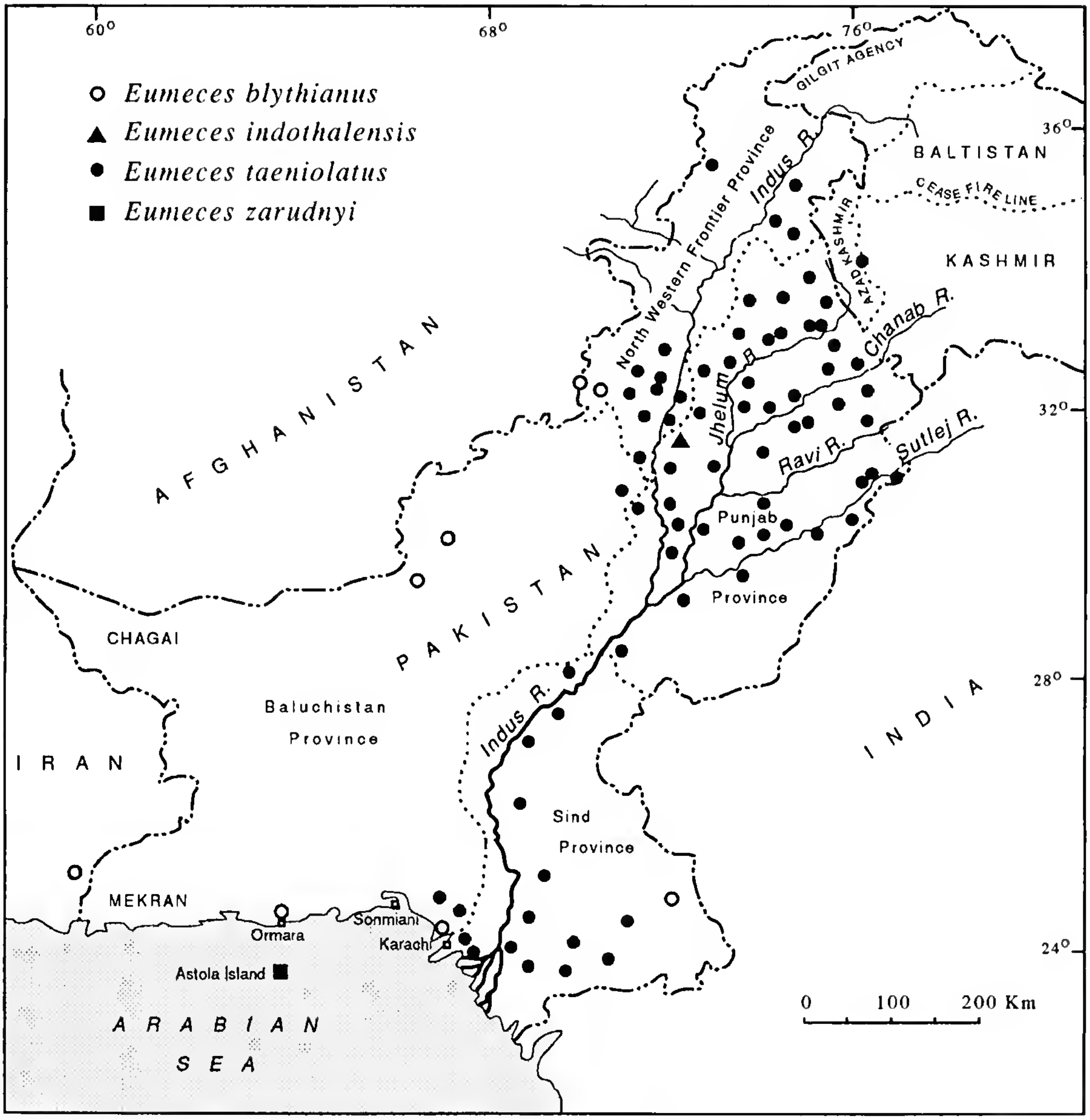

Figure1. The distribution of lizards of the genus *Eumeces* in Pakistan

Figure 2A (top) and B (bottom). *Eumeces indothalensis* new species.

Introduction

In early summer, 1984, the senior author picked up a pair of eviscerated skinks with a vivid dorsal striped pattern from a heap of *E. taeniolatus* skinks. Mr. Nazar Muhammad, an animal and plant collector for local Hakims (physicians), was eviscerating almost a sackful of living mass of writhing and struggling *Eumeces taeniolatus* skinks. He had collected the animals from the roots of common reed-bush, *Sachharum moonja*, close to village Bar Ganga, 9 km SW of Bakkhar, District Mianwali, western Punjab, Pakistan. The eviscerated lizards were to be sun-dried and sold in the market as reg mahi at Rs. 500-800 per 500 gram. Dried skinks are in great demand since the stuff is used in several aphrodisiac preparations (Khan, 1991, in press).

Laboratory examination of the striped pair of skinks proved that they belong to a new species, which is being described here.

Abbreviations used: BMNH=British Museum (Natural History), London; MCZ=Museum of Comparative Zoology, Harvard University, Cambridge, USA; MSK=Herp Laboratory, 15/6 Darul Saddar North, Rabwah 35460, Pakistan.

Taxonomic Considerations

The cosmopolitan genus *Eumeces* is represented by three species in Pakistan: *E. taeniolatus* (Blyth, 1854), *E. blythianus* (J. Anderson, 1871) and *E. zarudnyi* Nikolsky, 1899 (Minton, 1966; Mertens, 1969; Khan and Mirza, 1977) (Fig. 1). Taylor (1935) revised the genus *Eumeces* distinguishing it into several species groups: placing *E. taeniolatus* in the Taeniolatus Group, which is characterized by the presence of a postnasal, frontal in contact with interparietal, a single row of median dorsal much widened scales, dorsum golden yellowish with light and dark flecks which extend on limbs and tail. While both *E. zarudnyi* and *E. blythianus* are included in the *schneiderii* group, which has no postnasal scale, frontal is not in contact with interparietals, has a pair of median dorsal row of wider scales on dorsum with striped or unicolour pattern. However, Mertens (1946) gives *E. zarudnyi* and *E. blythianus* subspecies status of the widely distributed Saharo-Sindhian *E. schneiderii*. The new species has strong affinities with *E. schneiderii*.

Eumeces indothalensis, sp. nov.

Holotype: BMNH 1990.6 (MSK 0423.85, Fig. 2, A), a young male,from under roots of a common reed plant, *Sachharum moonja*, near village Bar Ginga, 9 Km SW of Bakkar, midwestern Punjab, Pakistan, 32°.50' N, 71° E, along west bank of Indus River, elevation 75 m, Nazar Muhammad collector, 16 July, 1984.

Paratype: (1): MSK 0422.85, (Fig. 2, B), an adult male, data as holotype, except 17 July, 1984.

Diagnosis: Medium sized skink, with dorsal pattern of 5-7 dark brown stripes separated by alternating light narrower stripes, extending on to the tail, no scattered scales of different colour on the body and limbs; nasal scale resting on first supralabial; nasal suture horizontal; no postnasal; interparietal about half the size of frontal and is of the same shape; two azygos postmentals; 52-56 scales in paired middorsal row of wider scales; posterior loreal and presuboculars longer than deep; no intercalary scales between subdigital lamellae.

Description of holotype: Rostral as high as broad,triangular, its part visible from above distinctly narrower than frontonasal, broadly truncate posteriorly. Supranasals lateral, about thrice as long as broad, reaching mesially to form a suture above nasals, the length of which equals the breadth of the rostral visible from above. Frontonasal transverse, much smaller than prefrontals, extend considerably forward between supranasals, laterally contacting anterior loreal. Prefrontals two, hexagonal, forming a median suture, contacting on sides with both loreals and first supraciliary. Frontal as long as its distance from rostral tip, abruptly truncated to a median point at anterior and posterior end, its length about twice its greatest breadth, in contact with three supraorbitals. Frontoparietals hexagonal, forming a median suture which is in line with that of prefrontals.

Interprietal longer than broad, about half the length of frontal and of the same shape, much longer than frontoparietals, abruptly truncated at both ends, posteriorly bordered by first pair of nuchals. Parietal,

Table 1. Pholidosic counts and measurements of the type series of the new species *Eumeces indothalensis* (br=broken).

Character	Paratype (MSK 022.85)	Holotype (BMNH 1990.5)
Supralabials	8	8
Infralabials	7	6
Postmentals	2	2
Chin shield	2	2
Preauricular lobes	3/4	3/3
Scales around:		
neck	32	33
axilla	42	41
midabdomen	27	26
groin	30	29
upper arm	16	17
fore arm	13	14
femur	14	14
thigh	22	22
tail base	22	24
Scales from:		
arm pit to groin	56	51
parietal to level of vent	56	52
postmental to vent	63	60
Subdigital lamellae:		
I finger	7	7
II	10	11
III	10	11
IV	11	9
V	7	7
I toe	7	7
II	10	9
III	12	13
IV	16	16
V	12	11
Measurements:		
Snout-vent length	82	57
Caudal length	17 br	40 br
axilla to groin	45	30
Head length	17	13

longer than broad, produced anterolaterally to contact the fourth postocular. A single pair of much broad nuchals, meeting at the posterior pointed tip of interparietal, an azygos nuchal on left side. Nasal slightly longer than broad, lies exactly on first supralabial not touching second, nasal suture horizontal, passing above naris, meeting rostral at its midlateral side, lower nasal larger bears major part of postero-lateral naris which lies posterior to nasorostral suture. Anterior loreal rectangular, oblique, about thrice as long as broad, higher than posterior, touching prefrontal, posterior loreal longer than high narrowing posteriorly to come in contact broad, forms a continuous subocular series with 8 postsuboculars, fifth is broadest, seventh longest; second presubocular longer than broad, smaller than anterior. A distinct small triangular preocular with two posterior smaller ones form a series with several more or less longer scales extending on to the posterior of eye, separating supraciliaries from pelpebral scales.

A series of 7 supraciliaries, first largest, a little smaller than first supraocular, extending on to head top to contact with prefrontal, second longest, while seventh about as high as first but half of its size. A pair of small postoculars and three oblique rows of granular scales touching lower palpebrals. Supraoculars 4, first three in contact with frontal, parietal separates fourth from upper secondary temporal. A single primary temporal, quadrangular, oblique; secondary temporals two, upper as broad as parietal, lower vertical, produced anteriorly to touch primary temporal. Two tertiary temporals, upper smaller, lower vertical, about twice as long as broad.

Eight supralabials, first five anterior to eye, sixth subocular about twice as long as high, first smallest, subtriangular, narrower along oral orifice, 7th and 8th subequal and largest, 8th supralabial separated from ear by four scales occupying a space equaling the width of 8th supralabial. A slightly distinct preocular from pelpebral scales. Ear opening vertical, oval, preauricular lobes 3/3, upper two broad reaching to the middle of the auditory meatus, third very small. Mental scale broader than rostral. A pair of azygos postmentals, first as broad and as long as mental, second about twice broader than first, mesially produced backwards between first pair of chin shields; chin shields three pairs, first in contact, second separated from each other by a scale while third by three scales. Infralabials seven, 7th largest.

Body scales smooth, polished, imbricate, regular, arranged in parallel longitudinal rows; scales of median dorsal two rows 3-4 times broader than long, 52, from parietal to the level of vent. All ventrals similar except abdominals which are slightly larger; midventrals 60, from postmental to the level of vent; 33 around neck, axilla 41; mid-abdomen 26, around groin 29 and 51 from armpit to groin.

Median dorsal pair of enlarged scales extends on the tail dorsum. At base, the tail squarish in cross section, becoming round at middle, with a very gradual taper to its pointed tip. A median ventral series of transversely enlarged subcaudals, 33 in holotype, as tail is broken. A pair of large median preanal scale surrounded anterolaterally by 8 smaller scales, overlapped later ally by the median large scales; a distinct tubercular large scale on each side of the anal slit; four postanal transverse rows of smaller scales, with a shallow transverse postanal pit; 22 scales round the tail base just posterior to the lateral anal tubercular scale.

Limbs short, anterior when stretched forward claws reaching to eye, posterior reaching to the level of mid-abdomen; when thighs are bent at right angle to the body, toes freely overlap. Limbs with smooth cycloid scales in parallel longitudinal rows, 17 at mid-upper arm, 14 mid-fore arm, mid-thigh 22 and 14 rows scales, no intercalary scales. Claws strong with a basal solid part and long sharp broader tip.

Color (in formalin): Seven vivid dark brown longitudinal stripes on body: a single median dorsal starts from behind inter parietal and extends to the level of vent; second dorsal, paired, from behind parietals to the level of vent, join each other at the level of vent, do not extend on tail; third pair, from behind eye extends laterally to groin than along lateroventral side of tail; fourth pair from behind ear above shoulder to groin. The dark brown stripes separated from each other by narrower lighter stripes, making the pattern distinct. Head uniform brownish, lips, chin and ventrum light yellowish. Measurements (in mm): Snout vent length (SVL) 57, tail length (TL) 40 (broken), snout to eye 4, snout to ear 13 snout to fore limb 21, axilla to groin 30, head length 13, head breadth 9.

Variation: Table 1 summarizes pholidosic and measurement variations in the type series. Both specimen have broken tails, MSK 0422.84 after 11th subcaudal while holotype after 33rd. Snout region of MSK 0422.84 is injured, not allowing detailed morphological study. A part differences in snout-vent length and some minor differences in scale counts the type series is consistent in other pholidosic characteristics, however, MSK 0422.84 has 9 stripes on dorsum, while there are seven in holotype.

Head uniform brownish in both specimens, however, supralabials and preauricular lobules are with brownish specks in the paratype.

Etymology: The name *indothalensis* refers to the part of the Thal Desert lying on the western bank of Indus River, northwestern Punjab, Pakistan, from where the new species was collected.

Comparison: According to the collector, Mr. Nazar Muhammad, *Eumeces taeniolatus* is sympatric with the new species in the type locality and is much more common. *E. taeniolatus* differs from the new species in having a postnasal, single row of broadened median dorsals, frontal in contact with interparietal, dorsum pale grey to bronze, speckled with creamy specks, three dark brown stripes on dorsum with pale specks, tail and limbs similarly speckled. On the other hand absence of postnasal scale, median dorsal double row of broadened scales, a pair of azygos postmentals and separation of frontal from interparietal warrant inclusion of the new species in the *Schneiderii* Group (Taylor, 1935).

Table 2. Comparison of pholidosic and measurement data of *Eumeces indothalensis* new species with its congeners; br=broken. (Data except of type series and *E.zarudnyi* from Taylor, 1935. Data for *E. zarudnyi* partially through courtesy Dr. Rosaldo [per. comm.] for material in Museum of Comparative Zoology collected by Loveridge [1959] from Balochistan).

Character	*E. indothalensis*	*E. schneideri*	*E. blythianus*	*E.zarudnyi*	*E. pavimentatus*	*E. princeps*
Postmental	2	2	1	2	2	2
Infralabials	6-7	8	6-7		7	5-6
Supraciliaries	7	6	7-8		6	7
Preauricular lobes	3-4	3	4	5-6	4	4
Nuchals	1-1		3-3			
Scale rows at:						
Neck	32-33	27			27	28
Chest (Axillary)	41-42	30				34
Mid-abdomen	26-27	24	30	26	24	26
Groin	29-30					
Base of Tail	22-24				19	20
Mid upper-arm	16-17					
Mid fore-arm	13-14				17	
Mid thigh	22					
Mid femur	14					
Scale counts:						
Median dorsals	52-56	66	60	57		64
Median ventrals	60-63					
Axilla to groin	51-56					
Preanals	9				8	
Subdigital lamellae						
I finger	6-7	6			6	5
II	9	9			9	8
III	10-11	10			11	10
IV	11	12			10	12
V	7	8			7	6
I toe	6-7	5			6	5
II	9-10	10			9	8
III	13	13			9	10
IV	16-17	16			16	14
V	11-12	10			9	9
Measurements						
snout-vent	55-60	90	111	115	79-136	125
Tail	94-259	150	236	112	148	193br
Axilla to groin	30-45	65-81				
Head length	13-17	18-23	15		19-21	18.2
Head width	9-11	16-23		20	16-17	15

Table 2 summarizes comparison of the new species, *E. indothalensis* with its congeners of the *Schneiderii* Group: *E. blythianus* (Anderson) known from Punjab, differs from the new species in having a single postmental, 30 scales round midbody, 50-60 scales from occiput to above anus, 3 pairs of nuchals. Taylor (1935, Plate 6) illustrates *E. blythianus* (BMNH 98.7.12.1) from Afridi country (Waziristan, southern borderline of N.W.F.P. with Afghanistan, similarly Finn (1898) has also reported it from the area. Taylor's photograph shows dorsal pattern of longitudinal stripes on olive-brown dorsum separated by narrower light stripes exactly matching with the dorsal pattern of the new species (Fig. 2,A,B). A similar striped young *E. blythianus* from Karachi (Minton, 1966, plate 19, 2), is reported to have unicolour pink adult phase (Fig. 2). Mertens (1969) reports similar lizards from Astola Island off the Karachi coast. A pinkish unicolour skink has been reported from Sheikh Manda near Quetta, Balochistan by Khan and Ahmed (1987). *E. princeps* also has a striped adult pattern, however, its juveniles are patternless (Mertens, 1969).

The second species, *E. zarudnyi*, nikolsky, from southwestern Iran and southern Balochistan (Loveridge, 1959), differs from the new species in having 5-6 preauricular lobules, wider head, and uniform grey dorsum. While the wide ranging Saharo-Sindhian skink *E. schneiderii* which is known from Mekran to Waziristan, differs from *E. indothalensis* in having 66 scales in the mid dorsal row, 24 scales around midbody, subocular as wide as high, dorsum brown or olive, median dorsal rows shaded dark with light spots, a very dim dorsolateral line and spotted hind limbs.

The new species, *Eumeces indothalensis*, is unique among Pakistani eumecid lizards in having the nasal scale resting exactly on the first supralabial which is triangular and does not touch second labial; horizontal nasal suture which passes above nostril, the nostril lies posterior to rostral-labial suture; dorsal part of rostral much narrower than frontonasal; subocular longer than broad, its ocular side longer than labial side; second loreal longer than broad; presubocular much longer than broad; interparietal as long as parietals, exactly of the shape of frontal but half of its size; three preauricular lobules, upper two much broader than long, third much smaller; 1-2 pairs of nuchals with an additional azygos nuchal; no intercalary scales between subdigital lamellae; dorsum with seven dark brown stripes, which increase to nine in adult (paratype) rather to disappear and become unicolour as in *E. blythianus* (Minton, 1966).

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Taxonomic Review of the Megophryid Frogs (Anura: Pelobatoidea)

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Abstract.- The family Pelobatidae has recently undergone notable reorganization. Once composed of two subfamilies, Pelobatinae and Megophryinae, it now consists of only the former. The family Megophryidae has recently been elevated to represent Asian members once in the family Pelobatidae; megophryids are diagnosed by three synapomorphies.

A phylogenetic analysis of the Archeaobatrachia by Cannatella (1985) included three species from two genera within Megophryidae. Paraphyly in the genus *Megophrys* was supported by one character, the articulation of the urosacrum. A re-analysis of Cannatella's (1985) data indicated that alternative patterns of the relationships among megophryids were plausible and that the homology of the urosacral articulation should be examined in more detail.

Key words: Amphibia, Anura, Pelobatoidea, Megophryidae, taxonomy

Introduction

The classification of anurans has been a matter of much recent debate. Several different opinions exist about their relationships (see Ford and Cannatella, 1993 for a review of the recent work on anuran relationships), and no fewer than three different taxonomies are currently in use (Duellman and Trueb, 1986; Dubois 1985, 1986; Ford and Cannatella, 1993). Previous classifications (prior to Duellman, 1975) have been based on a single complex of characters. As a result, when alternative character schemes were derived, earlier classifications were found to be incongruent.

The source of the incongruities have been the choice of characters used to construct each classification (Noble [1922, 1931] vertebral centrum, pectoral girdle, thigh musculature, and dentition; Griffiths [1963] hyolaryngeal structures, skull and limb morphology, and reproduction and development, vertebral column; Hecht [1963] and Starrett [1973] tadpole types). Each classification directly reflected the characters used in the particular study. For example, the classification proposed by Hecht (1963) in which Orton's (1957) larval characters were used to construct a classification that differed markedly from one developed the same year based on adult morphology (Griffiths, 1963). The history of these characters and their role in the classification of anurans is reviewed in the works of Lynch (1973) and Duellman (1975).

Noble (1922), reflected on the problems involved with constructing a classification based on either a single character or a complex of characters. However, the trend continued until Tihen (1965) and Inger (1967) provided classifications based on multiple characters. Subsequently, others have adopted a similar approach to the classification of anurans (Kluge and Farris, 1969; Lynch, 1973; Duellman, 1975; Laurent, 1979; Dubois, 1986). More recently, Ford (1989, 1993) undertook an analysis of the Neobatrachia, in an attempt to identify the phylogenetic position of Dendrobatidae among all anurans. Similarly, Cannatella (1985) generated a phylogeny for the Archaeobatrachia. Both of these thorough phylogenetic analyses culminated in a phylogeny for all major groups of frogs (Ford and Cannatella, 1993). They have applied contemporary techniques to generate a taxonomy reflecting natural groupings (de Queiroz and Gauthier, 1992), i.e., evolutionary history.

Anuran classification has progressed since Reig (1958) divided the Anura into four suborders: Amphicoela, Aglossa, Archaeobatrachia, and Neobatrachia. Based on the analysis of Ford and Cannatella (1993), the Amphicoela and Archaeobatrachia are artificial groupings. However, Neobatrachia and Aglossa reflect natural groupings (the latter now called Pipoidea). They confirmed Lynch's (1973) observation that members of Pelobatidae represent a transitional group between the basal anurans and

Table 1. Characters that support the family Pelobatidae (Duellman and Trueb, 1986), superfamily Pelobatoidea (Ford and Cannetella, 1992) which includes pelobatines and megophryines and the genus *Pelodytes*.

ossified intervertebral discs present
procoelous centrum
presacrals I and II not fused
atlantal cotyles of Presacral I closely juxtaposed
ribs absent
sacral diapophysis greatly expanded
sacrum fused to coccyx (moncondylar articulation with the coccyx in megophryine and some eopelobatines)
transverse processes on the proximal part of the coccyx (often incorporated into the sacral diapophysis)
pectoral girdle arciferal
cartilaginous omosternum
osseous sternum
scapula not overlain by the clavicle
parahyoid absent
cricoid ring incomplete dorsally
astragalus and calcanium are fused only proximally and distally
two tarsalia
m. sartorius is not discrete from the *m. semitendinosus* and the end of the latter inserts ventral to the *m. gracilis*
m. glutaeus magnus has an accessory tendon
m. adductor magnus lacks an accessory head
pupil vertical
amplexus is inguinal
type IV larvae
trigeminal and facial ganglia are fused
diploid number of chromosomes is 26 (24 in *Leptolalax pelodytoides*)

Neobatrachia; this implies that they possess an intermediate number of primitive character states.

Cannatella (1985) found that the family Pelobatidae, composed of two subfamilies, Megophryinae and Pelobatinae, represented an artificial grouping, and that each subfamily must be elevated to familial status to remove the conflict. Currently the two families are placed in a superfamily, Mesobatrachia (Cannatella, 1985), and is composed of pelobatoids (Pelobatidae, Pelodytidae, and Megophryidae) and pipoids (Rhinophrynidae and Pipidae).

To date, the evolutionary relationships of the Mesobatrachia have been addressed only in the phylogenetic analysis of Cannatella (1985, Ford and Cannatella, 1993). Within the Mesobatrachia, the relationships of Pelobatidae (*Scaphiopus* and *Spea*) have been partially resolved by Cannatella (1985). However, within the Megophryidae, only genealogical relationships of *Scutiger* (Yea et al., 1992), and *Scutiger* with *Oreolalax* (Yang and He, 1980) has been examined. In Cannatella's (1985) analysis of the Archaeobatrachia (hereafter referred to as DCC for ease of discussion), conclusions were made regarding the relationships of two genera of Megophryidae, *Megophrys* and *Leptobrachium*. However, there were errors in the coding of the characters in DCC's analysis that have serious implications on the composition of the family. Consequently, herein, I will review the taxonomic history of the family Megophryidae, and provide a re-analysis of Cannatella's data relevant to Pelobatoidea (Pelodytidae, Pelobatidae, Megophryidae). I conclude, by discussing the need for a phylogenetic classification that includes all the genera of Megophryidae.

Taxonomic History of Megophryidae

The first megophryid, *Megophrys montana*, was described by Kuhl and Van Hasselt (1822). Only four species of megophryids were known at the time of Boulenger's (1882) comprehensive account of known amphibians. Since then, 78 additional species have been described, and undoubtably more will be added as southeast Asia is more thoroughly investigated.

The first efforts to classify anurans was Cope (1865). He grouped taxa on the condition of the pectoral girdle and the vertebral column. In the taxonomic practices of the past, grouping of organisms were based on similarity, often creating polyphyletic assemblages of taxa. The family Asterophrydidae Günther 1859, a polyphyletic group, was the first family that included a megophryid. Members of this family included three genera of megophryids

(*Megalophrys*, *Xenophrys*, and *Leptobrachium*), as well as a microhylid, and a myobatrachid.

Noble (1922, 1931) provided groupings based on multiple characters of the adult morphology; megophryids were placed in the suborder Anomocoela, family Pelobatidae. In these works, the family Pelobatidae included three subfamilies: Megophryinae (*Megophrys*, *Leptobrachium*, *Nesobia*, *Scutiger*, *Aelurophryne*, *Leptobrachella*), Pelobatinae (*Scaphiopus*, *Spea*, *Pelobates*, *Pelodytes*), and Sooglossinae (*Nesomantis* and *Sooglossus*). Noble (1926) believed that the Sooglossinae possessed all the evolutionary significant pelobatid characteristics (maxillary teeth, arciferal pectoral girdle, procoelous vertebrae, a single coccygeal condyle, and the particular arrangement of the pectoral muscles). However, it showed a different arrangement of the thigh musculature thought to be derived with respect to Asian pelobatids. Not satisfied with the characters used by Noble, Griffiths (1959) removed Sooglossinae from the family Pelobatidae and placed it in its own family, Sooglossidae.

The classification of the Pelobatidae (viz. Pelobatinae, Megophryinae, and Pelodytinae) was maintained for nearly 40 years. Lynch (1973) removed *Pelodytes* from the family Pelobatidae, and erected a new family for this one genus (Pelodytidae) on the basis of limb characteristics that were derived independently from those of pelobatids.

Duellman and Trueb (1986) provided a phylogenetic tree that placed megophryids within Pelobatidae, as the sister group to Pelodytidae (see Table 1 for a list of synapomorphies uniting Pelodytidae and Pelobatidae). This arrangement has been the convention since Lynch's (1973) work.

Cannatella (1985) performed a phylogenetic analysis of the Archaeobatrachia and found that Pelobatidae (Megophryinae and Pelobatinae) was paraphyletic with respect to Pelodytidae and thus removed megophryids from Pelobatidae and erected a new family, Megophryidae. Despite a recent effort to disseminate this information (Ford and Cannatella, 1993), with the exception of Trueb (1991) and Fu et al., (submitted), the application has not received wide acceptance. Recent taxonomic accounts have grouped megophryids as a subfamily of Pelobatidae (Dubois, 1986; Duellman, 1993; Fang, 1985; Yea, et al., 1992; Fei and Yea, 1990, 1983; Frost, 1985; Guan-Fu, et al., 1993; Inger and Stuebing, 1991; Huang, 1985; Kuo, 1985; Wu, et al., 1993; Zhao and Adler, 1993; and others).

Taxonomic History of the Genera

The generic taxonomy of Megophryidae suffers from a convoluted history and temporal instability of its genera. The first generic name was proposed for the type species, *Megophrys montana* Kuhl and van Hasselt 1822. Shortly thereafter, Wagler (1830) published the generic name as *Megalophrys* for the genus *Megophrys*. This spelling continued for a century, and appeared as the original generic name for seven species in monographic reviews of anuran taxonomy (Boulenger, 1908; van Kampen, 1923). In his review of reptiles and amphibians of the Malay Peninsula, Smith (1930) corrected this unjustified emendation but without comment to the previous error.

From this single genus, *Megophrys* (*Megalophrys*), Boulenger (1882) recognized three forms on the basis of the presence or absence of vomerine teeth and the type of vertebrae (procoelous or opisthocoelous). He split the group into three genera: *Xenophrys* (Günther, 1865), *Megalophrys* (Wagler, 1830), and *Leptobrachium* Tschudi, 1838. Boulenger (1908) later regrouped all three into the genus *Megophrys* because the characters that he previously had used to separate them varied intergenerically and were not useful for distinguishing the genera.

Ceratophrys Gravenhorst, 1829, was used to describe another form of *Megophrys montana*. *Ceratophrys*, a genus of large-headed leptodactylid, occurs exclusively in South America and bears only a superficial resemblance to *Megophrys*. Other junior synonyms of *Megophrys* are *Ixalus* (Anderson, 1871), once a genus of Rhacophoridae. The description of the species was based on juvenile material of *Megophrys lateralis* (Boulenger, 1908); Gorham (1966) considered this species a *nomen dubium*. Beddard (1907) placed *Megophrys montana* in a monotypic genus, *Pelobatrachus*. However, he did not provide any unique characters to distinguish it from the other known megophryid genera (*Xenophrys*, *Megalophrys*, *Leptobrachium*). Therefore, it was returned to *Megophrys* (Boulenger, 1908). *Brachytarsophrys* and *Atympanophrys*, were described by Tian and Hu (1983). The latter, *Atympanophrys*, (Greek [atympano = without tympanum]), was a monotypic genus described from a specimen of *Megophrys shapingenesis* in which the authors report that all structures associated with the middle ear (stapes, tympanic annulus) were absent. *Brachytarsophrys* was thought to be distinct because of its peculiar shaped head and high neural spines of the vertebrae. Dubois (1986) reviewed the three genera, *Megophrys*, *Brachytarsophrys*, and *Atympanophrys*. He concluded that the three different evolutionary states that Tian and Hu

(1983) referred to were neither sufficient nor important enough to deserve generic ranking and thus made them subgenera of *Megophrys*. A later investigation of the type series of *Atympanophrys* revealed that all structures of the middle ear were present and that the absence of the middle ear in one specimen (SM00042) was a result of improper handling of the type (Fei et al., 1991, p. 4). The genus *Atympanophrys* was considered a junior synonym of *Megophrys* (Fei et al., 1991). *Brachytarsophrys* is still recognized as a subgenus of *Megophrys* (Duellman, 1993).

Boulenger (1887, p. 405) reported that *Scutiger* Theobald, 1868 (Chinese megophryids), as a genus of Amphibia, is preoccupied by an earlier name, *Scutigera* Latreille, 1802, for a genus of centipede. As a result, Boulenger erected a new generic name, *Cophophryne*, for these forms. He also pointed out that many of the characters of *Cophophryne* appear to be intermediate between pelobatids and bufonids (viz. absence of maxillary teeth, expanded sacral diapophyses). Because of these characteristics, it was considered a member of the family Bufonidae.

Boulenger (1919) erected *Aelurophryne* for a single species, *A. mammata* (= *Bufo mammata* Günther, 1896) that could be distinguished from *Cophophryne* by the absence of a posteriorly-notched tongue. These two genera (*Aelurophryne* and *Cophophryne*) could be distinguished from bufonids by the presence of vertical pupils (a character found in many pelobatids). Thus, Boulenger (1919) placed these two genera in the Pelobatidae. Procter (1922) followed Boulenger's (1919) familial arrangement. However, he considered *Cophophryne* and *Aelurophryne* to be congeneric, and place *Cophophryne* as a junior synonym of *Aelurophryne*.

Noble (1931) recognized both *Scutiger* Theobald (= *Cophophryne* Boulenger) and *Aelurophryne* (Boulenger, 1919). He distinguished the two by the presence of short maxillary teeth in *Scutiger* and the absence of dentition in *Aelurophryne*. Pope and Boring (1940) and Liu (1950) also recognized *Aelurophryne* in their surveys of Chinese amphibians. Liu (1950) further characterized the two genera by the presence of a tympanum and a small opening for the eustachian tube in *Aelurophryne*, and the absence of these characters in *Scutiger*. After having re-examined four species fastigiate described by Liu (1950), Myers and Leviton (1962) argued that *Scutiger* and *Aelurophryne* could not be distinguished in the way of Liu, Pope and Boring, and Noble had proposed. They found that three of the four *Scutiger* forms possessed a combination of characteristics that were supposed to be present in either *Scutiger* or *Aelurophryne* (e.g., presence of a deeply notched tongue, teeth, a tympanum which was concealed under the skin, and a distinct openings for the eustachian tubes). Consequently, Myers and Leviton (1962) adopted Procter's (1922) taxonomy, but because *Scutiger* preceded *Aelurophryne*, all Himalayan megophryids were placed in *Scutiger*.

Ophryophryne, a genus described by Boulenger (1903), was originally placed in the Bufonidae because it possessed similar external characteristics (horizontal pupil and an edentate maxilla). Boulenger (1903) suggested that *Ophryophryne* was the evolutionary link between the pelobatids and bufonids. However, Noble (1926) examined the thigh musculature of two species of *Ophryophryne* and concluded that they were diminutive *Megophrys*. *Ophryophryne* remained a distinct genus, because most of the variation between *Megophrys* and *Ophryophryne* is in the head region. Dubois (1980) stated that ". . . the strong resemblance between *Megophrys* and *Ophryophryne* (to the point that it is probably impossible to determine to which group one would place the specimen without the head!) indicates that they probably do not merit the status of distinct genera"[1]. In this work, Dubois relegated *Ophryophryne* to the status of subgenus of *Megophrys*. Dubois (1986) re-examined his earlier comparisons (Dubois, 1980) and considered the differences to be distinctly different, thus returning generic status to *Ophryophryne*.

Liu (1950) placed some species of *Leptobrachium* in a new genus, *Vibrissaphora*, to represent a small group that possessed keritanized nuptial excrescences along the margin of the maxilla. Liu et al. (1973) examined members of *Vibrissaphora* and *Leptobrachium hasseltii* and found that the only difference between the two genera was the presence of the maxillary spine in *Vibrissaphora*. This character did not seem significant enough to warrant two separate genera. Therefore, *Vibrissaphora* was returned to *Leptobrachium* (Dubois, 1980). Some authors still recognize *Vibrissaphora* as a distinct genus (Zhao and Adler, 1993).

Nesobia (van Kampen, 1923) was a name given to small species that possess horizontal pupils and inhabit Natuna Island. The taxonomic status of this genus was not questioned by Dubois (1980) because material was not available for examination. However, because the name *Nesobia* was preoccupied, a genus of molluscs, a new name was applied to this group (*Leptobrachella* Smith 1925).

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[1] English translation of the original text in French.

Table 2. Genera of Megophryidae and their known synapomorphies.

Leptobrachella (Borneo and the Bunguran [=Natuna] Islands)
very reduced sternum
pointed expansion at tips of digits
ventral skin of digits sharply delimited
no denticles on larval oral disc
nuptial excrescences absent
*vertical pupil

Leptobrachium (Southern China to the Philippines, Indochina, and Sunda Is. to Bali)
*vomerine teeth absent
snout not extending beyond lower jaw
tongue strongly notched posteriorly
two well developed metacarpal tubercles
vertebrae proceolous
omosternum cartilaginous
sternum with a bony style
*horizontal pupil

Leptolalax (Burma and southern China through Thailand and Vietnam to Malaya and Borneo)
(no unique synapomorphies)

Ophryophryne (northern Vietnam and southern China)
*maxillary teeth absent
horizontal pupil
*vomerine teeth absent

Megophrys (southern, eastern, and southeastern Asia)
tadpole with funnel-shaped oral disc
larvae with median anal tube
*vertical pupil

Scutiger (high altitudes of southwestern China, northern Burma, Mepal, and northern India)
*maxillary teeth reduced or absent
rough skin
tympanum obscured
*vertical pupil

* character is not unique to the genus

Hu et al., erected *Carpophrys* (Sichuan Institute of Biology, 1977) as a generic name for a single species, *Leptobrachium oshanensis*. In a draft of the second edition (1977) of the Chinese amphibians (Liu, et al., 1966), Liu described three species of *Leptobrachium* that were distinct in which he placed them in a new genus, *Carpophrys*.

In this document Liu included a diagnosis of *Carpophrys* and the type species for the genus (*Leptobrachium pelodytoides*). This draft was distributed among Chinese colleagues and has been cited in several Chinese publications (after 1977), (personal communication, Jinzhong Fu, 1995). Dubois (1980) reviewed the status of *Leptobrachium* and agreed with Liu that three species (*L. gracile*, *L. pelodytoides*, and *L. oshanensis*[2]) were distinct from other species of *Leptobrachium* based on the position of the axillary glands, appearance of the skin on the dorsum, unpigmented eggs, and other relative proportions of the body. He thought these three species were likely to be closely related to the larger subset of *Leptobrachium*, but distinct. Dubois (1981) pointed out that the genus name *Carpophrys* was not valid because the original description was published anonymously and the type species for the genus was not designated (following Art. 13b, Art. 14, International Code of Zoological Nomenclature, 1985). Thus, he created two subgenera for the groups—*Leptolalax* for the three species, and *Leptobrachium* for the larger subset (in the genus *Leptobrachium*). Later, Dubois (1983) elevated Leptolalax to generic status. Fei and Ye (1992) investigated the validity of the two generic names, *Carpophrys* and *Leptolalax*, and concluded that although a description of the genus existed and a type species was designated, *Leptolalax* is valid because *Carpophrys* was not published in an official publication (Art. 8a.1, International Code of Zoological Nomenclature, 1985).

Currently, the family Megophryidae consists of 83 species divided into six genera (*Leptobrachella*, *Leptobrachium*, *Leptolalax*, *Ophryophryne*, *Megophrys*, and *Scutiger*). Each genus is supported by a set of unique synapomorphies (Table 2) except for *Leptolalax*. My investigation into the literature has provided no unique synapomorphies for *Leptolalax*. An addi-

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[2] Dubois (1980) used the specific epithet *oshanense* because as he noted (B.G. 476 in a footnote) that the original genus name, *Leptobrachium*, is neuter in gender, and must be amended to agree with *Leptolalax*.

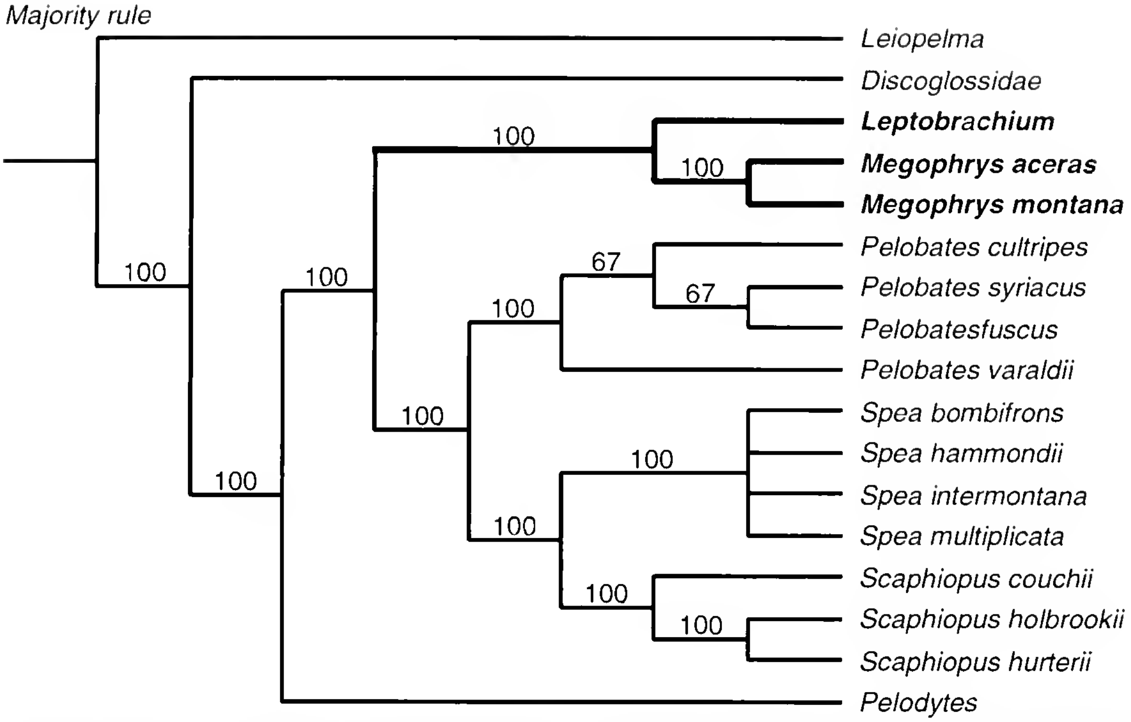

Figure 1. Majority rule consensus tree depicting the relationships of Pelobatoidea. In this phylogeny, *Megophrys* is monophyletic and multiple trees result from the ambiguous relationships of *Pelobates.* The clade, Megophryidae is bolded.

tional genus, *Oreolalax*, erected by Myers and Leviton (1962) to represent Chinese *Scutiger*-like forms that possess maxillary teeth. Recently, Fei and Ye (1989) provided additional evidence to distinguish *Oreolalax* from *Scutiger*, and this motion has been followed by some authors (Fu and Murphy, in press; Wu et al., 1993; Guan-Fu et al., 1993; Fei and Yea, 1990). Other sources do not recognize the genus *Oreolalax* (Dubois, 1979, 1986; Duellman, 1993; Frost, 1985).

Evidence of Monophyly and Outgroup Taxa

The association of megophryids with pelobatids and *Pelodytes* (= Pelobatoidea of Cannatella, 1985) has gone largely unchallenged through the history of anuran taxonomy. Previously recognized as Pelobatidae (authors prior to 1973) or Pelobatidae plus Pelodytidae (Lynch, 1973), the group is supported by several synapomorphies (Table 1).

Although DCC was fairly confident about the definitive synapomorphies of the Pelobatoidea, the monophyletic nature of megophryids does not remain incontestable. The results published in his thesis list ten synapomorphies for the group; four are reversals to the plesiomorphic condition, four represent convergences with other anuran groups, and two were considered to be uniquely derived: loss of most of the hyale of the hyoid and an ossified episternum. For unknown reasons, the latter character was not included as a synapomorphy by Ford and Cannatella (1993).

Among the 83 species of megophryids, DCC included only three species from two of the six genera. He reported that "relationships within the megophyrines are poorly defined . . . because few taxa were available to study" (p 275). He went on to say that his results suggest that *Megophrys* was paraphyletic with the single species of *Leptobrachium* used in his analysis; this was defined by a single character (the articulation of the sacrum and the coccyx). The character was said to be a reversal to the plesiomorphic condition in one species of *Megophrys*. Coding of this character is ambiguous at best, the character state is probably not homologous to the primitive condition found in discoglossids and *Ascaphus*. Cannatella alluded to this problem in his section on character analysis (p. 127).

Because the results of DCC's analysis have brought into question the monophyly of *Megophrys*, I re-investigated the issue.

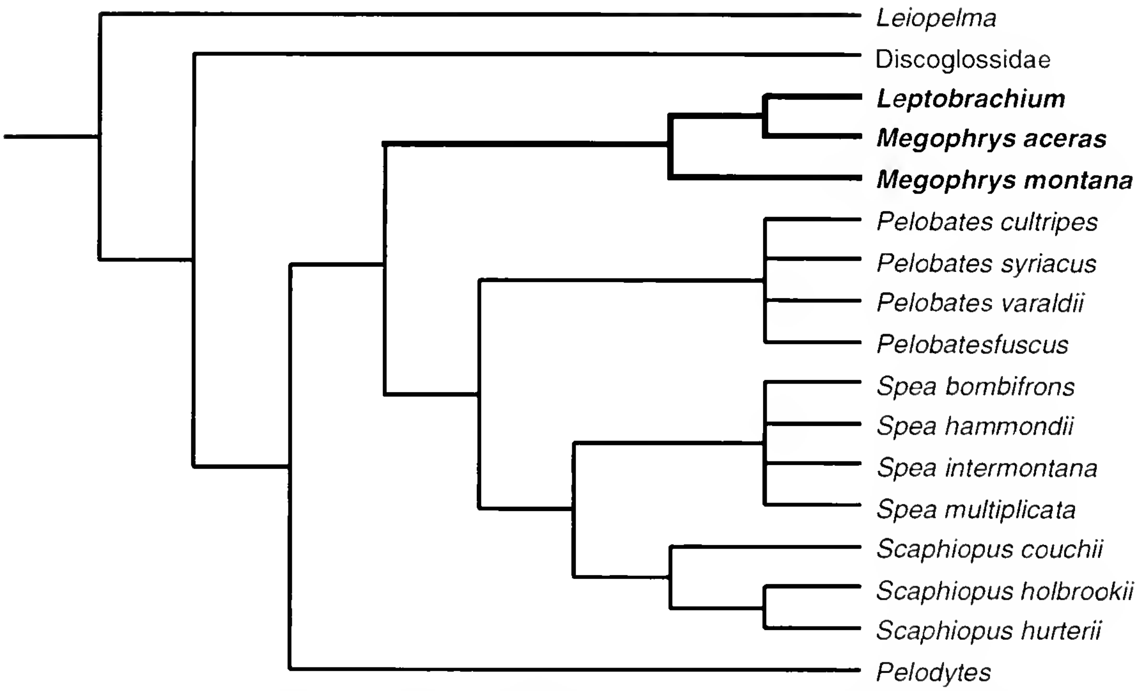

Figure 2. Phylogeny of Pelobatoidea. The relationships ol *Pelobates* is unresolved. The character UROSACRM when evaluated as ordered with its original four states (Cannatella, 1985) constrains *Megophrys* to be paraphyletic with *Leptobrachium*. The clade, Megophryidae is bolded.

Materials and Methods

I examined the data set of Cannatella (1985) in order to understand the evolution of the morphological character within pelobatoids. My evaluation of the taxa in the clade Pelobatoidea (viz. *Leptobrachium, Megophrys, Pelobates, Pelodytes, Scaphiopus,* and *Spea*) included 43 of 181 characters for 17 of 42 taxa of archaeobatrachians. Two characters associated with the stapes: COLUMEL1 (0, absent; 1, present; 2, greatly elongated) and COLUMEL2 (0, normal size; 1, reduced) were combined to removed inapplicable character states. The character COLUMEL was coded as follows (0, absent; 1, present, normal, extending entire length of ear cavity; 2, greatly elongated; 3, reduced). Uninformative characters at this level of the analysis were removed; of the 181 characters, 137 characters were not informative in the analysis of Pelobatoidea (Appendix 1). Phylogenetic analyses were performed using Swofford's (1993) Phylogenetic Analysis Using Parsimony program (PAUP). A heuristic search was performed using simple stepwise addition only minimal trees were retained and trees were constructed using branch swapping option of tree bisection-reconnection, steepest descent, and holding all most parsimonious trees. Characters were ordered and polarized by outgroup comparison (Watrous and Wheeler, 1981) using the outgroup *Discoglossus*, the sister species of the clade Pelobatoidea, and *Leiopelma* as a secondary outgroup.

Results

Three most parsimonious trees (MPTs) were resolved when the data were run as unordered (65 steps; CI = .723; RI = .860; Fig. 1). In all cases, *Megophrys* was monophyletic, with *Leptobrachium* as its sister group. Differences among the MPTs occurred within the clade of *Pelobates*. Character states for *Pelobates* were invariant, except for the COLUMELLA and the CRICOID, both of which were autapomorphic for *P. veraldii* and *P. fuscus*, respectively. These autoapomorphies were responsible for the differing topologies among *Pelobates*. When all the characters were treated as ordered, as in the DCC analysis, six MPTs were resolved, each 73 steps long (CI = .699; RI = .850). Three of trees were identical to those in the unordered analysis (Fig. 1). Among the other three topologies, *Megophrys* is paraphyletic with *Leptobrachium*, and the relationships of Pelobates were not resolved (Fig. 2).

One character used by DCC was the articulation of the sacrum and the coccyx (UROSACRM). DCC had doubts about the polarity and homology of this character. Although similar in configuration, he questioned whether the condition in *Megophrys montana* was homologous to that of *Leiopelma*. Cannatella coded this character as homologous, but with reservation. When the character was either left unordered or removed completely from the analysis, *Megophrys* was resolved as a monophyletic group and the resulting three topologies were identical to those Fig. 1.

If the articulation of the sacrum in *Megophrys montana* is not homologous to that of *Leiopelma*, and different from that seen in *Megophrys aceras*, then 5 character states are required to describe the variation in UROSACRM, rather than the original 4 states as in DCC. When UROSACRM was coded as five ordered or unordered character states (Appendix 1) the analysis resulted in three trees identical to those of the previous unordered analysis of the original data set (ordered = 73 steps; CI = .712; RI = .854; unordered = 66 steps; CI = .727; RI = .859).

Discussion

DCC's phylogeny depicts the two species of *Megophrys* as paraphyletic with respect to *Leptobrachium*. However, my re-analysis demonstrates that there is an alternative arrangement in which *Megophrys* is monophyletic. The condition of the UROSACRUM (e.g., syncondrotic or synovial, monocondylar or bicondylar) has been used as a diagnostic character for some groups of anurans (Nicholls, 1916; Griffiths, 1963; Lynch, 1973; Cannatella, 1985; Ford, 1989) and avoided by others (Duellman and Trueb, 1986). Noble (1922) cautioned against its utility as a diagnostic character for pelobatids (Megophryidae, Pelobatidae, and Pelodytidae). Furthermore, within the Megophryidae, specifically *Megophrys*, there has been several reports of variation in the urosacral fusion (Kluge, 1966). Thus, because UROSACRM has the ability to make *Megophrys* paraphyletic, the articulation of the coccyx to the sacrum must be examined more closely to determine its true homology.

Wiens (1989) illustrated the difference in development between a fused bicondylar articulation and one that is not fused, and suggested that these arrangements may have arisen via several different developmental pathways. What appears to be two different conditions in the Megophryidae—sacrum and urostyle separate; joint synchondrotic in *Megophrys montana* and *Leptobrachium hasseltii*; sacral fusion in *Megophrys aceras*— may have been formed from two very similar developmental pathways. Ontogenetic studies of the formation of the sacrum and the coccyx may reveal homologous states that would not be identified by examining just the adult condition.

The systematics of megophryids is poorly understood. Our ideas of the relationships within the family have not changed much since Noble's (1926) evolutionary hypothesis. Without a comprehensive phylogenetic hypothesis from which we can base a classification, the resulting taxonomy will likely prove to be unstable; it may include paraphyletic groupings. Although Dubois (1980) constructed a classification to serve as a starting point for future studies, his conservative scheme is not based on a phylogeny, but primarily on phenetic clusterings without regard for evolution of the characters.

To understand the relationships between the genera of Megophryidae, and the placement of megophryids within the pelobatoids, a thorough phylogenetic analysis of the family is necessary. This analysis should be performed in a similar manner as Cannatella's (1985) study, and the classification should be derived directly from the phylogeny (Wiley, 1981). Employing a phylogenetic classification would ensure that the taxonomy was consistent, functional, and maximized information content. In this way, the knowledge that is gained from this interesting group of frogs will produce a useful classification that clearly reflects the evolutionary paths of each species.

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Appendix I

Data matrix of characters from Cannatella (1985) to include only Pelobatoidae and the outgroup taxa, Leiopelma and Discoglossus. (A) Leiopelma, (B) Discoglossus pictus, (C) Leptobrachium, (D) Megophrys aceras, (E) M. montana, (F) Pelobates cultripes, (G) P. syriacus, (H) P. varaldii, (I) P. fuscus, (J) Spea bomifrons, (K) S. hammondii, (L) S. intermontana, (M) S. multiplicata, (N) Scaphiopus couchii, (O) S. holbrookii, (P) S. hurterii, (Q) Pelodaytes punctatus. See original work (Cannatella, 1985) for character coding.

characters	**taxa**																
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
ADDLONG	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1
ALHYOID1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
ALHYOID3	0	0	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1
ANALGLND	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
COLUMEL	0	1	1	1	1	?	3	1	3	1	1	1	1	1	1	1	1
CRICOID	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
DEPRMAN2	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
EPIPUBIS	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
EXOSTOS	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0
FPFONT	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0
FPFUSION	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
FREERIBS	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
GRACMIN3	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
GRACMIN4	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
HUMHEAD	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
HYALE	0	0	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
HYOGLSN2	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
ISCHCUTA	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
LENSCAP	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
NASAL2	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
PARAHYD1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
PECTGLND	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
PIRIFORM	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	0	0
PREACET	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
PREZON2	0	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
QUADRAT1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
SARTSEM3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
SEPNAS	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	2	0
SPADTUB1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0
SPADTUB2	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
STERNOSS	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
STERNSH	1	1	?	?	?	?	?	?	?	0	0	0	0	0	0	0	?
SUPFLFP	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
TORSION	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TPRODIRP	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
TYPE4TAD	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

(Continued)

characters	taxa																
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
UROSACRM	0	2	0	3	4[a]	3	3	3	3	3	3	3	3	3	3	3	1
VOCSAC	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1
VOMER3	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
VOMER4	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
ZYPROSQ3	0	1	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0

a. UROSACRM is coded as 0 in Cannatella (1985).

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A Brief Herpetological Excursion To Wai Ling Ding, Wanshan Islands, South China Sea

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Abstract. - Two frogs and three lizards are recorded from Wai Ling Ding, one of the larger Wanshan Islands southwest of Hong Kong, in Guangdong Province, China (the number of additional unpublished records for islands within Hong Kong Territory for both frogs in parentheses): *Kaloula p. pulchra (7), Rhacophorus leucomystax or "Polypedates megacephalus" (7), Hemidactylus bowringi, Eumeces quadrilineatus,* and *Scincella modesta.* Ours is the first record for *S. modesta* in Guangdong Province; ontogenetic and elevational data are presented for this species.

Key words: Biogeography, Wanshan, Hong Kong, Anura, *Kaloula, Rhacophorus, Polypedates,* Squamata, *Hemidactylus, Eumeces, Scincella modesta.*

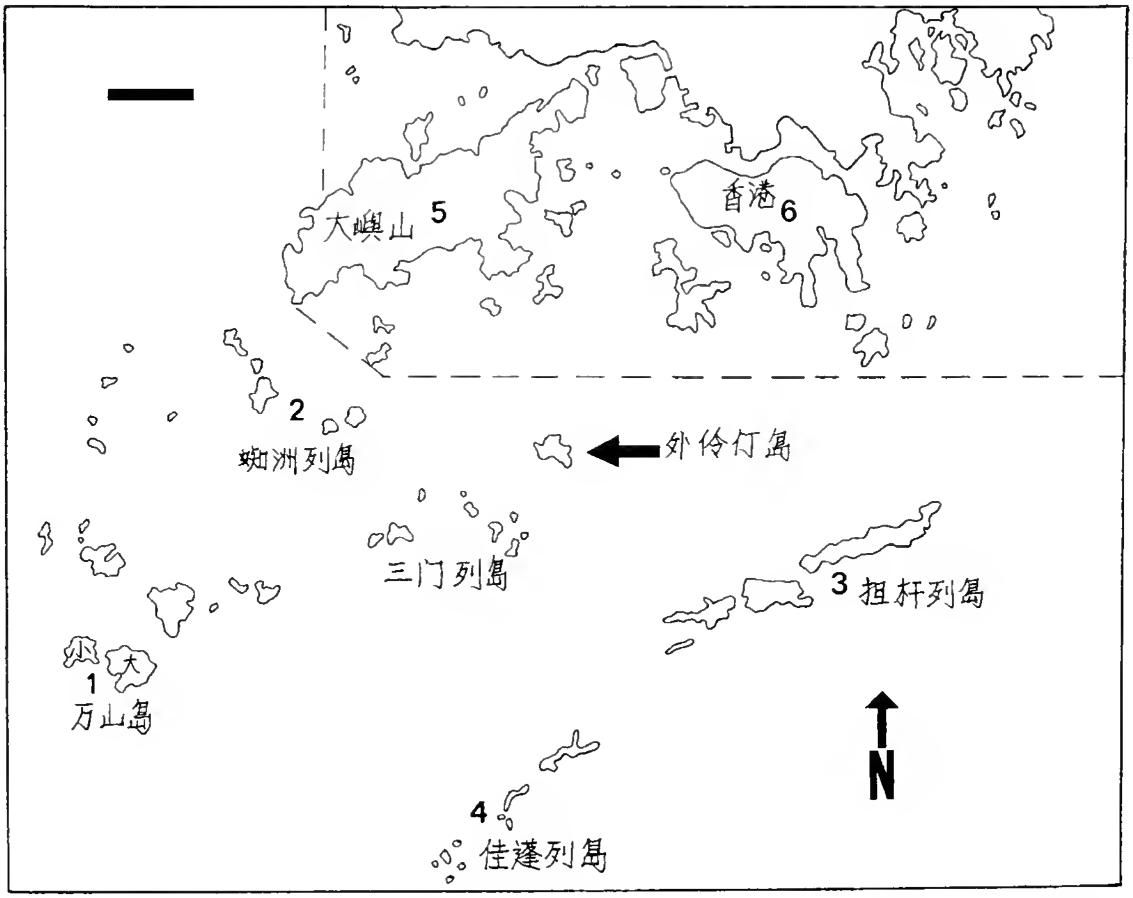

Figure 1. The Wanshan Islands and adjacent portions of Hong Kong Territory. 1, Da and Xiao Wanshan (the "Ladrones"); 2, Zhizhou; 3, Dangan; 4, Jiapeng; 5, Lantau (Tai Yue Shan); and 6, Hong Kong Island. Arrow indicates Wai Ling Ding. Dashed line indicates part of the southern and western border of Hong Kong Territory. Bar, top left, is 5 km.

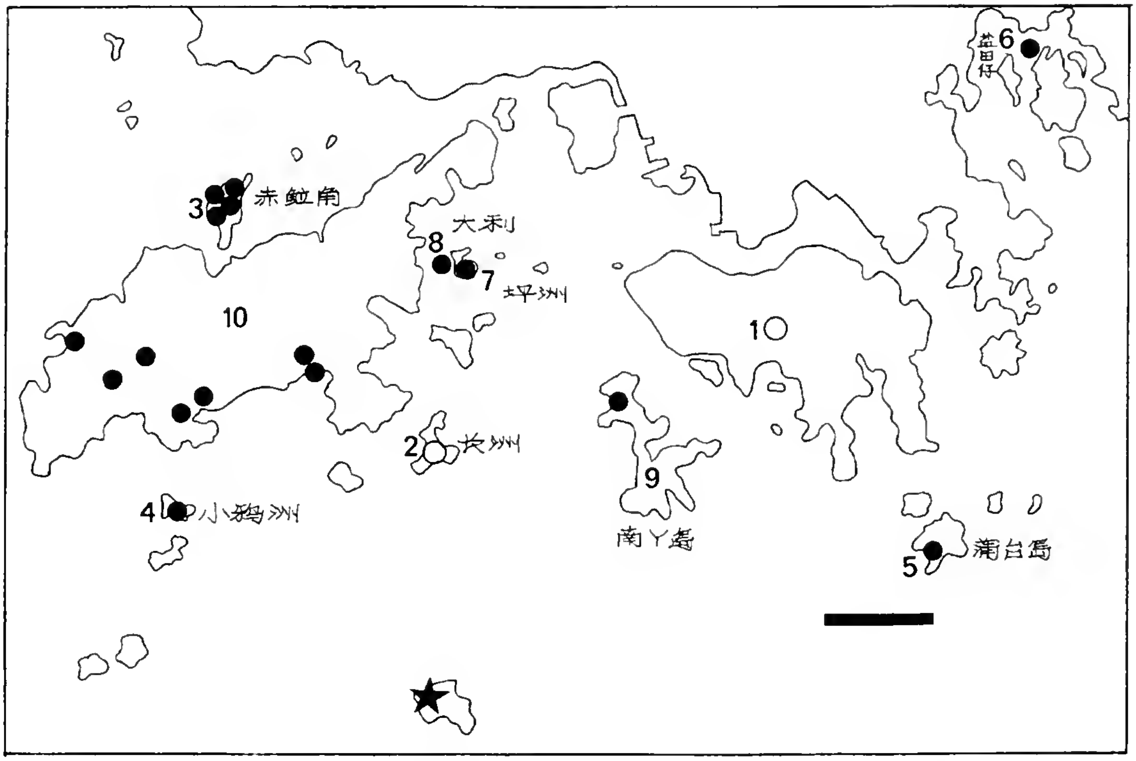

Figure 2. Island localities for *Kaloula p. pulchra* vouchered by MCZ specimens (solid dots) or from Karsen et al., 1986 (open circles). 1, Hong Kong; 2, Cheung Chau; 3, Chek Lap Kok (now blasted away); 4, Siu-A-Chau, Soko Islands; 5, Po Toi; 6, Yim Tin Tsai; 7, Peng Chau; 8 Tai Lei; 9, Lamma; and 10, Lantau (Tai Yue Shan). Star is Wai Ling Ding. Bar, bottom right, is 5 km.

Introduction

More than 40 vegetated islands lie south and west of the British Territory of Hong Kong, on the inundated continental shelf of the South China Sea, within Guangdong Province. Collectively, the group is called Wanshan; two of the larger islands, in the extreme southwest, were well known historically as the Ladrones: DaWanshan and XiaoWanshan today (Empson 1992). To the north lies the Zhizhou cluster, and to the east and southeast lie the Dangan and Jiapeng groups, respectively. Centrally located is the Sanmen complex, the largest of which is Wai Ling Ding, ca 3.3 km^2 and 310 m above sealevel, some 25 km southwest of Hong Kong (Fig. 1).

Access to these islands has heretofore been very limited (Pan et al., 1985), while the 100 or more islands within Hong Kong Territory have received considerable attention (Karsen et al., 1986; Zhao and Adler 1993). In an attempt to develop commerce, Chinese authorities now permit regular tourist access to at least Wai Ling Ding from Hong Kong. We made the trip on 20 July 1994.

Results

We were able to collect for only two hours during overcast weather with intermittent showers. Heavy rain developed at midday and soon terminated our efforts. Only five species were vouchered. All specimens are in the Museum of Comparative Zoology (MCZ).

1. *Kaloula p. pulchra* (Anura: Microhylidae), MCZ 116225. Found under debris on a hillside, ca 60 m above sealevel. A second individual was not collected. This abundant species is widespread on coastal islands including Hong Kong and Cheung Chau (Karsen et al., 1986), Chek Lap Kok (MCZ 115497-502; population now extirpated by destruction of the island), Siu-A-Chau in the Soko Islands (Lazell 1988a; MCZ 109400), Po Toi (MCZ 116089), Yim Tin Tsai (MCZ 117716-8), Peng Chau (MCZ 109403), Lamma (MCZ 109402), many localities on Lantau (e.g. MCZ 116081-8, Shui Hau), and even tiny Tai Lei off Peng Chau, area 2.9 ha (MCZ 110964-5). See Fig. 2.

2. *Rhacophorus leucomystax* ("*Polypedates megacephalus*") (Anura: Ranidae or "Rhacophoridae"),

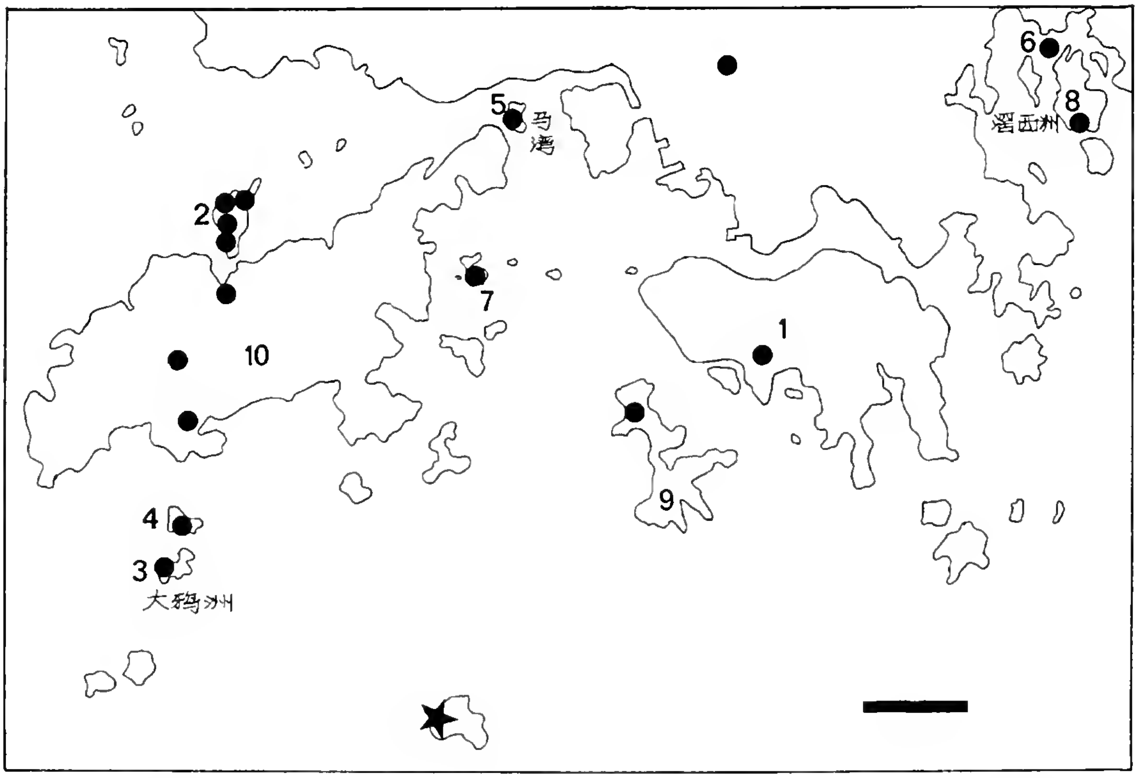

Figure 3. Localities for *Rhacophorus leucomystax* or "*Polypedates megacephalus*" vouchered by MCZ specimens (solid dots). 1, Hong Kong; 2, Chek Lap Kok (now blasted away); 3, Tai-A-Chau, and 4, Siu-A-Chau, Soko Islands; 5, Ma Wan; 6 Yim Tin Tsai; 7, Peng Chau; 8, Kau Sai Chau; 9, Lamma; and 10, Lantau (Tai Yue Shan). Star is Wai Ling Ding. Bar, bottom right, is 5 km.

MCZ 116226. Tadpoles were also collected for the Department of Zoology, University of Hong Kong. The voucher is a metamorph. All specimens were found in rain water pools on the hillside above the village at about 70 m elevation.

The nomenclature for this frog is unsettled. Zhao and Adler (1993: 74) notwithstanding, the sole consistent character given by Liem (1970) separating "*Polypedates*" from *Rhacophorus* is the diplasiocoelous vertebra of the former. One of us (JL) finds this character prone to individual variation in adult frogs and questions whether any genus founded on such a single character could be monophyletic. Zhao and Adler (1993: 156) accepted the notion of Matsui et al. (1986) that Chinese specimens should be called *megacephalus* (type locality Hong Kong: Hallowell, 1861) "based on comparisons of Taiwanese and Bornean specimens." Taiwan and Borneo are both continental shelf islands. Borneo is more than twice as far from Wai Ling Ding (and Hong Kong) as is Taiwan, but we see no rationale for assigning populations on that basis, and opine that this species, abundant at Hong Kong (Karsen et al., 1986: 31), should be judged on evaluation of topotypic material. Nor do we believe the minor differences noted by Matsui et al. (1986) necessarily imply species-level distinction. Karyotypes often vary within species (e.g. Schmid et al., 1994). A demonstration of sympatry would be convincing.

In addition to the New Territories mainland and Hong Kong Island, noted by Karsen et al. (1986), this species has been vouchered on Chek Lap Kok (MCZ 115709-36; population now extirpated by destruction of the island), Siu-A-Chau (Lazell 1988a; MCZ 109426-30) and Tai-A-Chau (Lazell 1988a; MCZ 110969-71) in the Soko Islands, Peng Chau (MCZ 109425), Ma Wan (MCZ 115737-40), Lamma (MCZ 109437), Yim Tin Tsai (MCZ 109437) and Kau Sai Chau (MCZ 116227) in the Port Shelter Islands, and several localities on Lantau (e.g. Shui Hau, MCZ 115742-4). See Fig. 3.

3. *Hemidactylus bowringi* (Squamata: Gekkonidae), MCZ 179462-3. Both were collected under debris in the village area at the northwest of the Island. Several others were seen. This is probably the most ubiquitous and widespread member of the Hong Kong

Table 1. MCZ specimens of *Scincella modesta* from Hong Kong and Guangdong, tropical China.

MCZ number	Locality	Elevation, m
39207	Hong Kong: The Peak	550
172779	Lantau: Tei Tong Tsai	360
172780	Lantau: Tei Tong Tsai	360
172781	Lantau: Keung Shan	100
176240	Lantau: Ngong Ping	420
176241	Lantau: Ngong Ping	420
176242	Lantau: Ngong Ping	490
176243	Lantau: Tai Tung Shan	320
176244	Lantau: Keung Shan	100
176245	Hong Kong: Pokfulam	190
176246	Mainland New Territories: Pat Sin Leng	200
176746	Guangdong: Wanshan: Wai Ling Ding	60

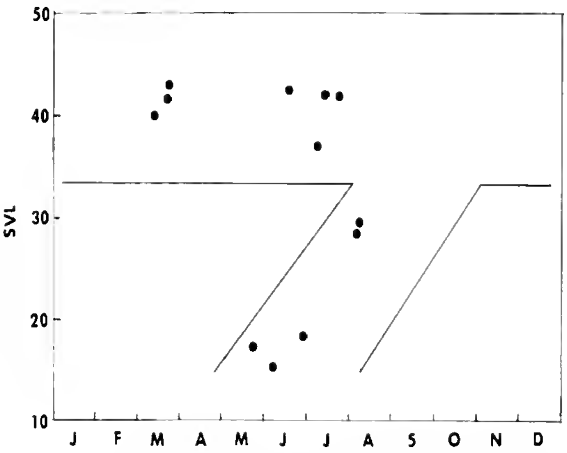

Figure 4. Ontograph of MCZ specimens of *Scincella modesta* from Guangdong and Hong Kong. Lines indicate the size/time zone in which we expect specimens to occur in this tropical, monsoonal region.

herpetofauna (Karsen et al., 1986; Lazell 1988a) and is to be expected on all continental shelf islands with more than herb stage vegetation in the South China Sea.

4. *Eumeces quadrilineatus* (Squamata: Scincidae), MCZ 179461. This, the only individual seen, was found under debris inside an abandoned hut at the village periphery at about 60 m. This spectacular species is widespread but not especially common in the region. Karsen et al. (1986) record it from Hong Kong, Lantau, and Cheung Chau islands; Lazell (1988a) added Tai-A-Chau in the Soko group (MCZ 173399-100). An ontogenetic and biogeographic study of this species is underway (JL).

5. *Scincella modesta* (Squamata: Scincidae), MCZ 176746. This individual was found under debris inside an abandoned hut above the village at ca 60 m. *S. modesta* on Wai Ling Ding is our most notable find. Nowhere common in this region, the species has heretofore been recorded only on Hong Kong, Lantau, and Cheung Chau islands off the mainland, and is usually encountered at moderate to high elevation (Karsen et al., 1986; Table 1). Karsen (pers. comm.) informs us that the Cheung Chau record is not based on a specimen, but sight only. He suspects it may have been *Scincella reevesi*.

Zhao and Adler (1993) recognized two subspecies of *S. modesta* but did not admit to either occurring in South China, Hong Kong, or on any islands. The identity of these tropical skinks, widely disjunct from their relatives to the north, was not considered by Zhao and Adler and remains open to question. Ontogenetic data are provided in Fig. 4.

Discussion

In addition to our five species, Pan et al. (1985) record three species of frogs: *Rana guentheri*, *R. limnocharis*, and *R. rugulosa*. Li and Pan (1995) added *Kaloula pulchra*.

We saw only the extreme northwest portion of Wai Ling Ding. The village where we landed had all the appearances and aromas of a typical, impoverished, fishing community burdened by an influx of workers attempting to construct a facade attractive to tourists. This community was called simply "Ling Ding Tsuen" (Nowhere Alone Town). The area we saw was extremely ecologically degraded with vast areas of barren rock interspersed with cutgrass (*Panicum* sp.). There were clumps and strips of scrub vegetation largely consisting of native species such as *Melastoma* sp., *Dicranopteris* sp., and *Rhodomyrtus tomentosa*. The trees, however, were exotic species: *Acacia confusa*, *Casaurina* sp., and unidentified eucalypts.

In view of the number of endemic species known from Hong Kong islands, including some found at low elevation such as *Philautus romeri*, *Megophrys brachykolos*, and *Dibamus bogadeki*, the Wanshan Islands will repay a thorough investigation.

Acknowledgments

We are indebted to ornithologist Dr. Martin Williams, of Cheung Chau, Hong Kong, for arranging our trip, and to Nick Goodyer, Brian Moseley, and Eddie Wu Chon Wai for assistance in the field. Our trip was sponsored in part by The Conservation Agency and the Explorers Club.

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Captive propagation of the Mandarin Rat Snake (*Elaphe mandarina*) at Moscow Zoo

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Abstract. -Some results of a long-term breeding project aimed at captive propagation of the Mandarin Rat Snake (*Elaphe mandarina*) are presented. Data on breeding periods, clutch size, number of young and their sizes are given.

Key words: Reptilia, Serpentes, *Elaphe mandarina*, captive reproduction.

Introduction

The Mandarin Rat Snake (*Elaphe mandarina*) is distributed in south-eastern Asia from upper Burma (Myanmar) through southern China to northern Vietnam, inhabiting mountain forests and rocky slopes covered with bushes. It probably is one of the most sought after species of the genus, for a large part due to it's unusual and quite colorful coloration. However, these snakes are rather difficult to maintain, as most of those becoming available are wild-caught and usually arrive very stressed and in a poor shape after prolonged transportation and transfers. Also, one of the main reasons for a low percent of success when trying to adapt a newly received wild-caught Mandarin Rat Snake is a nearly obligatory and quite heavy parasite infestation, including both subcutaneous and internal helminths. From more than a dozen of wild-caught Mandarin Rat Snakes, that have been in our possession in course of about 10 years, only three survived and adapted to captivity, mainly because of prompt and extensive medical treatment of the above mentioned problems. Lately, as a routine, we treat all newly arrived snakes with Metronidasol (Flagyl) 250 mg/kg, repeated after 10 days; 2,5% Albendasol (Valbasen) 0,2-0,4 ml/kg, repeated twice every 7 days if symptoms persist; Prasiquantel (Baytril) 5mg/kg every 24 hours for 3-5 days, administered either per os or subcutaneous, depending on clinical signs. Another traditional mistake made when dealing with this species is over-heating which also can (and usually does) cause health problems. Thus, probably the largest chances for success are with either captive-born or very young wild-caught animals, provided the general care is correct.

Husbandry and Reproduction

In 1989, a pair of new-born Mandarin Rat Snakes was received from probably the first breeder of this species, Mr. Munzenmaier. The animals were 290+65 mm and 330+68 mm long (body length + tail length, male and female, respectively) and weighed 13.3 and 13.9 g. They were housed together in a glass enclosure, measuring 40 x 25 x 25 cm (L x W x H) with typical assortment of water basin, several shelters, moisture chamber (which they frequented eagerly), etc. An incandescent heating bulb was present in the terrarium, however, for the most part it was switched off, as the preferred temperatures for these snakes apparently were 22-26°C during daytime and 16-18°C at night (both according to previous owner's and to our own observations). Humidity was maintained at a rather high level, by daily sprinkling with warm water. Rations included pink mice and, eventually, adult mice and small rats (even as adult, the male prefers pink mice to any other food), offered at first twice a week and then, as the snakes grew, weekly. Chicken and frogs were offered as well, but without any success. The snakes grew fast and eventually were housed separately, in glass enclosures 60 x 40 x 40 cm.

By October, 1992, the snakes measured 734+175 and 742+154 mm and weighed 231.8 and 327.7 g (male and female, respectively) and were considered mature. After a preparatory period of 30 days they were put to hibernation at 11-14°C for approximately 3 months. After hibernation, in February-March, the snakes were housed separately and were offered food more often than prior to hibernation, i.e. twice a week. No vitamins were added and no UV radiation was present.

On 1 April, 1993, the female was introduced to the male's enclosure, with male showing immediate interest and beginning to purchase the female at once. Approximately two hours later, first copulation was observed, lasting for 28 minutes, during which period the male was holding the female by the "neck" with

Table 1. Egg measurements of clutch from 1993.

#	L max, mm	L min, mm	W*, g
1	51	24	
2	57	27	
3	50	23	(= 84.06)
4	50	24	
5	53	26	

*all eggs were glued together and no individual weights were taken.

Table 2. Measurements of the young.

Year	#	Lc, mm	Lcd, mm	W, g
1993	1	250	51	13.07
	2	220	45	8.66
	3	248	56	13.81
	4	235	54	12.60
1994	1	221	48	11.08
	2	215	46	11.58
	3	210	48	9.70
	4	192	46	5.89
	5	210	45	10.83
	6	208	45	9.92
1995	1	196	43	10.65
	2	235	52	13.30
	3	218	44	10.00
	4	220	44	12.34
	5	212	41	9.90
	6	192	38	9.54

his teeth. Several hours after they parted, the snakes were separated again. This routine continued for three weeks, with at least 5 copulation occurring (sometimes the snakes were left together for the night and no observations were made on their behavior).

By mid-May, 1993 the female looked obviously gravid and 5 eggs could be palpated. Starting from about that time, she refused food and in the morning of 5 June laid 5 large eggs (see Table 1). The eggs were placed in an incubator, at 25-28°C and very high humidity, with sphagnum moss for a substrate. Incubation period consisted continued for 48 days and the first egg hatched on 22 July, with the young emerging on the same day. Of 5 eggs 4 hatched, with the last young emerging on 24 July. Measurements of the young are presented at Table 2. For the first time they shed on 8-11th day and started to feed on pink mice soon after. There were no real problems with their feeding as all young were very aggressive and bit their preys at the slightest provocation, after which usually strangled and swallowed them. The same as their parents, young Mandarin Rat Snakes grew fast and by December they were about 1.5 times their hatching size.

Starting from 1993 , the same pair of snakes produced three clutches from which more than 15 young hatched. The general incubating routine was more or less the same and most eggs hatched successfully, with typical sex ratio being 2:1 (males:females).

Conclusions

Basing upon our 6-year experience with Mandarin Rat Snakes, we consider this species not as difficult to maintain and to breed in captivity as the general public perception believes it to be, of course, provided the animals are either captive bred or, if they are wild-caught, are treated for parasites immediately upon arrival. Antibiotic prophylaxis is also very advisable. Temperature requirements are of vital importance as, if overheated, these snakes tend to become ill and die rather fast. It also should be noted that Mandarin Rat Snakes are easily stressed and for successful husbandry they should be provided with enough shelters and better are kept separately.

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Population Dynamics and Growth in a Natural Population of *Limnonectes limnocharis* (Anura: Ranidae)

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Abstract. -The study is based on measurement of specimen, collected from nature over a period of 12 months, during 1987-88. Based on the size, the juveniles, mature males and gravid females were divided into various size groups. Except the juveniles, the female size groups were comparable with the males. In addition, the females are comparatively larger than the males of the same age group. The availability of various size groups during different months of a year, is attributed to the continuous growth of the species in natural population

Key words: Anura, *Limnonectes limnocharis*, population, growth.

Introduction

The first available information on growth study of anurans was by Wright (1914), who analyzed growth pattern of *Rana pipiens* and *Rana catesbeiana*. Since then, several other studies (Wright, 1920; Flower, 1925; 1936; Force, 1933; Hamilton, 1934; 1955; Raney and Ingram, 1941; Cowan, 1941; Raney and Lachner, 1947; Wilson, 1950; Ting, 1951; Ryan, 1953; Fitch, 1956a; 1956b; Jameson, 1956; Martof, 1956; Cohen and Howard, 1958; Durham and Bennett, 1963; Schroeder and Baskett, 1968) reported the growth pattern of anurans either in captivity or in natural environment by analyzing individuals. Turner (1960) reviewed all the above literature on anuran growth and since then additional data has become available for *Bufo hemiophrys* (Breckenridge and Tester, 1961), *Rana sylvatica* (Bellis, 1961), *Rana arvalis* (van Gelder, 1973; van Gelder and Oomen, 1970), *Rana erythraea* (Brown and Alcala, 1970), *Rana septentrionalis* (Hedeen, 1972), *Bufo boreas* (Lillywhite et al., 1973) and *Bufo woodhousei fowleri* (Clarke, 1974). All the above studies (except Brown and Alcala, 1970) deal with anurans from temperate zones. The present study is the second one for any Indian anurans. The first study was conducted by Sahoo (1991) on *Bufo melanostictus*.

Materials and Methods

A total of 962 specimens (388 males, 267 females and 307 juveniles were collected over a period of 12 months, from a perennial pond near village Chakeisani, Bhubaneswar, India. Specimens ranging from 17.0-38.0 mm snout-vent length (SVL), were sexed and the rest were treated as juveniles.

Results

Out of 962 specimens sampled, the lowest (43) and the highest (110) captures were during March and September respectively. The ratio of male to female for each month

indicated more males than females, except during the month of February, when the number of males were slightly less than that of the females. Cumulative ratio was also indicative of more males. The population dynamics of juveniles indicated maximum (53) during the month of June (Table 1). Further, juvenile population decreased drastically from December through January and no juveniles were collected during February and March. The low population density of juveniles during December and January and non-availability during February and March is associated with non-breeding season, because, basically the species breeds during monsoon period (June-August) when the number of juveniles in the natural population is more than non-breeding months.

To analyze the growth pattern in natural population, size range of juvenile (J), males (M) and females (F) were recorded (Table-2) and divided into various size groups (Table-3). Specimens measuring a maximum of 16.0 mm were not sexed and were considered as juveniles. The lowest SVL (8.0 mm) of juveniles from April through September is attributed to metamorphosis time of the species during these months, because the metamorphosing froglets were found to be with a SVL of about 8.0 mm. Based on SVL, the juveniles were divided into two size groups (8.0-11.0 mm and 12.0-16.0 mm). Both the size groups were found from May to October and the former was also available during April. This is indicative of early breeding of the species, because metamorphosed froglets were found during this month. From November until January, the larger size group juveniles were found and this indicated growth in size.

A total of 388 males were collected over a period of 12 months (Table 1) and the SVL ranged from 17.0-36.0 mm. All the males were grouped into three size groups (17.0-22.0 mm; 23.0-30.0 mm and 31.0-36.0 mm) and the first two size groups were available during all the months (except three specimens of the third group which were collected during May). The above data indicated that both the juvenile, maturing and mature males of various sizes were found in nature.

The data on female population is comparable with males, except the lower number (267) of the former, which is typical for the species. Like males, the females were also grouped into three similar size groups and all the size groups were available throughout the year. However, the number of two smaller size groups were less than the largest size group of females. The above population trend and size range is also indicative of continuous growth of the species in natural environment.

Discussion

Several previous studies (refer to introduction) reported the growth pattern of temperate climate species of anurans and some of these studies (Wright, 1914; Breckenridge and Tester, 1961; Bellis, 1961; Hedeen, 1972; Lillywhite et al., 1973; Clarke, 1974) provide data on specific species. Turner's (1960) review of available data on anuran growth pattern suggested that most of the studies have either been conducted in captivity or in natural populations, by analyzing marked individuals.

In general, growth rates of anurans have been determined in three ways, depending on measurement of 1. preserved materials, 2. captive individuals and 3. individuals either marked or samples taken from the same natural population at different times during the same growing season (Turner, 1960). The present analysis of growth pattern of *L. limnocharis* fits to the third category, because specimens of *L. limnocharis* were collected from their natural population over a period of 12 months. Further, the sampling method adopted was random. A total of 962 specimens (307 juveniles, 388 males and 267 females) were sampled and the data indicated maximum number of juveniles collected during the month of June (Table 1). This could obviously be due to metamorphic event of the species during June. Dash and Mahanta (1993), while studying the community structure of ten anurans in natural populations, reported that *L. limnocharis* is the dominant anuran in paddy fields. Hence, the availability of more juveniles than males and females during May-September could be compared with population dynamics data of the species reported by Dash and Mahanta (1993).

Acknowledgments

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Appendix I

Tables 1-3

Table 1. Cumulative data on population size of specimens of *L. limnocharis* collected for 12 months.

Year/Month	Juveniles (J)	Males (M)	Females (F)	Ratio (J:M:F)
1987				
May	44	31	15	2.933:2.067:1
June	53	29	11	4.818:2.636:1
July	42	31	26	1.615:1.192:1
August	49	29	29	1.690:1:1
September	44	42	24	1.833:1.75:1

(Continued)

Year/Month	Juveniles (J)	Males (M)	Females (F)	Ratio (J:M:F)
October	25	39	18	1.389:2.167:1
November	22	35	29	0.759:1.207:1
December	9	30	18	0.500:1.667:1
1988				
January	3	32	31	0.097:1.032:1
February	0	31	33	0:0.939:1
March	0	26	17	0:1.529:1
Total	307	388	267	1.150:1.453:1

Table 2. Cumulative data on size range, mean and Standard Deviation of specimens of *L. limnocharis* collected for 12 months.

Year/Month	Sex	SVL Range (mm)	Mean ± SD (mm)
1987			
April	J	8.0 - 10.0	8.625 + 0.719
	M	20.0 - 29.0	25.455 ± 2.559
	F	31.0 - 38.0	34.750 ± 2.543
May.	J	8.0 - 16.0	10.568 ± 2.526
	M	18.0 - 36.0	25.645 ± 4.742
	F	21.0 - 36.0	31.933 ± 5.284
June	J	8.0 - 16.0	11.528 ± 2.2fl7
	M	18.0 - 28.0	23.621 ± 3.201
	F	27.0 - 38.0	31.182 ± 3.842
July	J	8.0 - 16.0	11.619 ± 2.214
	M	18.0 - 30.0	22.839 ± 3.928
	F	18.0 - 35.0	26.423 ± 5.934
August	J	10.0 - 16.0	12.612 ± 1.850
	M	18.0 - 29.0	24.793 ± 2.920
	F	18.0 - 34.0	27.828 ± 4.167
September	J	8.0 - 16.0	11.773 ± 2.530
	M	17.0 - 30.0	23.262 ± 3.818
	F	17.0 - 38.0	31.333 ± 7.516

(Continued)

Year/Month	Sex	SVL Range (mm)	Mean ± SD (mm)
October	J	10.0 - 16.0	12.96 ± 1.670
	M	17.0 - 28.0	23.71fl ± 3.266
	F	29.0 - 38.0	32.333 ± 3.068
November	J	14.0 - 16.0	14.909 ± 0.750
	M	17.0 - 27.0	22.543 ± 2.941
	F	18.0 - 36.0	29.44R ± 5.736
December	J	15.0 - 16.0	15.889 ± 0.333
	M	17.0 - 24.0	19.667 ± 1.795
	F	18.0 - 36.0	26.167 ± 6.635
1988			
January	J	16.0	16.000 ± 0.0
	M	18.0 - 30.0	23.125 ± 4.098
	F	18.0 - 38.0	27.032 ± 7.276
February	M	19.0 - 29.0	22.903 ± 4.215
	F	19.0 - 36.0	24.667 ± 6.623
March	M	20.0 - 28.0	22.923 ± 2.481
	F	20.0 - 35.0	26.000 ± 5.612

Table 3. Cumulative data of different size (SVL in mm) groups of *L. limnocharis* collected for 12 months.

Year/ Month	Juveniles		Males			Females			Total
	8.0-11.0	12.0-16.0	17.0-22.0	23.0-30.0	31.0-36.0	17.0-22.0	23.0-30.0	31.0-38.0	
1987									
April	16	-	5	28	-	-	-	16	65
May	29	15	9	19	3	2	1	12	90
June	29	2411	18	-	-	5	6	93	
July	22	20	13	18	-	8	12	6	99
August	16	33	8	21	-	3	21	5	107
September	22	22	20	22	-	5	1	18	110
October	5	20	10	29	-	-	8	10	82
November	-	22	17	18	-	5	7	17	86

(Continued)

Year/ Month	Juveniles		Males			Females			Total
	8.0-11.0	12.0-16.0	17.0-22.0	23.0-30.0	31.0-36.0	17.0-22.0	23.0-30.0	31.0-38.0	
December	-	9	28	2	-	8	4	6	57
1988									
January	-	3	15	17	-	15	1	15	66
February	-	-	19	12	-	22	-	11	64
March	-	-	13	13	-	6	7	4	43
Total	139	168	168	217	3	74	67	126	962

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The Karyotypes of Megophryinae (Pelobatidae) with a Discussion on their Classification and Phylogenetic Relationships

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Abstract. -The karyotypes of nine Megophryinae species from China were studied. *Megophrys omeimontis* Liu has 2n=26 with 5 large, 1 moderate and 7 small pairs, 8M+3SM+2ST, NF=52, 1 secondary constriction in 6p. *Megophrys giganticus* Liu has 2n=26 with 5 large and 8 small pairs, 5M+5SM+2ST+1T, NF=48. *Megophrys minor* Stejneger has two different forms. One is 2n=26 with 6 large and 7 small pairs, 8M+2SM+2ST, NF=52; the other is 2n=30 with 6 large and 9 small pairs. The large group is identical to that of the 2n=26 form, 8M+2SM+3ST+2t, NF=56. *Megophrys kuatunensis* Pope has 2n=24 with 6 large and 6 small pairs, 5M+2M(SM)+2SM+3ST. *Megophrys lateralis* (Anderson) from Tengchong, Yunnan has 2n=26 with 6 large and 7 small pairs, 8M+3SM+2ST, NF=52. *Megophrys lateralis* (Anderson) from Hekou, Yunnan has 2n=26 with 6 large and 7 small pairs, 5M+1M(SM)+4SM+2ST+1T. *Megophrys parva* Boulenger has 2n=26 with 6 large and 7 small pairs, 4M+5SM+1SM(ST)+3T, one secondary constriction 1Q; few metaphases with 2n=26+1 and 4 pair of T chromosomes. *Megophrys palpebralespinosa* Bourret has 2n+26 with 5 large and 8 small pairs, 5M+4SM+1SM(ST)+2ST+1ST(T). *Megophrys daweimontis* sp. nov. Has 2n=26, 5 large and 8 small pairs, 6M+3SM+1SM(ST)+1ST+1ST(T), one secondary constriction in 6Q. *Ophryophryne microstoma* Boulenger has 2n=26 with 6 large and 7 small pairs, 7M+1M(SM)+2SM+1ST+T. The karyotype of *O. pachyprocta* Kou resembles that of *O. microstoma.*

Karyotypes of the Megophryinae can be divided into 5+8 and 6+7 types. The karyotype of *M. omeimontis* appears to be an intermediate between 5+8 and 6+7. Combining the cytological, morphological and ecological characters, the classification of Megophryinae can be reviewed. The genus *Atympanophrys* is probable only needed to verify its main generic character. *Brachytarsophrys and Ophryophryne* are valid genera. *Megophrys* can be divided into four groups: I. *M. giganticus*, II. *M. montana* and *M. nasuta*, III. *M. palpebralespinosa* and *M. daweimontis* sp. nov., IV. Other species generally with small-sized bodies and 6+7 karyotypes. *M. giganticus* should probable belong to the genus *Atympanophrys;* a new genus should be erected for groups III and IV, whereas *Megophrys* should refer only to group II. A new species, *M. daweimontis*, is described below.

Key words: Megophryinae, *Brachytarsophrys*, *Megophrys*, *Ophryophryne*, karyotype, classification, phylogenetic relationships, *Megophrys daweimontis* sp. nov.

Materials and Methods

Megophrys lateralis were collected from Tengchong, Yunnan in 1991 and Hekou, Yunnan in 1993; *M. omeimontis* and *M. minor* from Jingdong, Yunnan in June, 1990 and May, 1991; *M. giganticus* from Jingdong in May, 1991; *M. palpebralespinosa* and *M. daweimontis* sp. nov. From Kekou, Yunnan in July 1993; *M. parva* and *Ophryophryne pachyprocta* from Mengla, Yunnan in May 1993; *M. kuatunensis* from Chongan and Dehua, Fujian; *: O. microstoma* from Hekou, Yunnan in June 1992 and July, 1993. All the specimens were brought alive to the laboratory for karyotyping.

Specimens were injected intraperitoneally with colchicine at a dosage of 20 ug/g body-weight. After 24 to 36 hours the femur and tibia bones were removed and the ends cut off. The marrow cells were then washed out with 1% tri-sodium citrate solution, ground in hypotonic 0.64% KCl solution and fixed in 3:1 solution of methanol;acetic acid for two periods of 20 minutes each. Slides were prepared by the air-drying method and stained with 10% Giemsa PBS for about 20 minutes.

Chromosomes were divided into 4 groups according to the ratio of long arm/short arm in length: M= metacentric, the ratio is 1-1.7; SM= submetacentric, 1.7-3.0; ST= subtelocentric, 3.0-7.0; T= telocentric, more than 7.0. Chromosomes designated M, SM and ST possess 2 arms and those designated T possess only 1 arm. The fundamental number (NF) represents the total arm numbers for all chromosomes in one karyotype.

Results

The karyotype of *M. lateralis* from Tengchong, northwest Yunnan has 2n=26; 6 large and 7 small pairs; Nos. 3, 11 and 12 are SM, Nos. 8 and 13 are ST, the rest are M and NF=52. There are no satellite or secondary constrictions (Fig. 3c). This karyotype mostly agrees with that recorded by Wu (1987) for *M. lateralis*.

The karyotype of *M. lateralis* (Anderson) from Hekou, Yunnan is 2n=26; 6 large and 7 small pairs; Nos. 1, 5, 6, 10 and 11 are M, Nos. 2, 3, 7, and 12 are SM, Nos. 8 and 9 are ST, No. 13 is T, No. 4 can be M or SM and NF=52. Sometimes one secondary constriction is close to the centromere of the short arm of No. 2 (Fig. 3). This karyotype is different from that of specimens from Tengchong, Yunnan, especially in Nos. 2, 7, 9, and 13, and the location of the secondary constriction (it is in 5p in the results of Wu, 1987). We think that a morphological comparison should be made between the two populations as part of any evaluation of their specific status.

The karyotype of *M. omeimontis* from Jingdong, Yunnan has 2n=26; 5 large, 1 moderate, and 7 small pairs; Nos. 3, 7 and 12 are SM, Nos. 8 and 13 are ST, the rest are M and NF=52. One secondary constriction was near the base of the short arm of No. 6; there is no satellite (Fig. 3d). This karyotype agrees with that reported by Zheng and Wu (1989) for *M. omeimontis* based upon a population from Mt. Omei in Sichuan, but their results indicate that the secondary constriction was in the long arm of No. 6.

The karyotype of *M. giganticus* is 2n=26; 5 large and 8 small pairs are obvious; Nos. 2, 3, 4, 7 and 12 are SM, Nos. 9 and 13 are ST, No. 8 is T, the rest are M and NF=48. No satellite or secondary constrictions were found (Fig. 3e). This karyotype is not the same as that recorded by Li et al., (1993) for *M. giganticus*. Recognition of 5 large and 8 small pairs is the same as the karyotypes of *Brachytarsophrys*.

The karyotype of *M. minor* is variable in specimens from the same locality in Jingdong. One karyotype is 2n=26; 6 large and 7 small pairs; Nos. 7 and 13 are SM, Nos 8 and 12 are ST, the rest are M and NF=52. No satellite or secondary constrictions were found (Fig. 3a). The second karyotype is 2n=30; 6 large and 9 small pairs. The large chromosomes are identical to those of the 2n=26 form, but the small ones are different. Among them Nos. 7 and 10 are SM, Nos. 8, 12 and 13 are ST, Nos. 14 and 15 are T, the rest are M and NF=56 (Fig. 3b).

The karyotype of *M. kuatunensis* Pope is 2n=24; 6 large and 6 small pairs; Nos. 1, 2, 6, 10 and 11 are M, Nos. 5 and 8 are SM, Nos. 7, 9 and 12 are ST, Nos. 3 and 4 can be M or SM and NF=48. No satellites or secondary constrictions were found. It is the only karyotype where 2n=24 in the Megophryinae. Further study is needed to evaluate the taxonomy of this species (Fig. 3j).

We found the karyotype of *M. parva* Boulenger to be 2n=26; 6 large and 7 small pairs; Nos. 1, 2, 3, 4 and 5 are SM, Nos. 6, 7, 8 and 10 are M, Nos. 11, 12 and 13 are T, No. 9 varies between SM and ST and NF=46. One secondary constriction is near the centromere of the long arm of No. 1 (Fig. 3h). A few metaphases with 2n=26+1 and 4 pair of T chromosomes were found. This karyotype is different than that recorded by Li et al. (1993) from the same localities, especially in the arm length for large chromosomes, and the location of the secondary constriction (5q in the Li et al. result).

The karyotype of *M. palpebralespinosa* Bourret is 2n=26; 5 large and 8 small pairs; Nos. 1, 2, 4, 5 and 12 are M, Nos. 3, 6, 8 and 10 are SM, Nos. 7 and 13 are ST, No. 9 varies between ST and T, No. 11 can be SM or ST and NF=52 or 50. No satellites and secondary constrictions were found (Fig. 3g).

The karyotype of *M. daweimontis* sp. Nov. Is 2n=26; 5 large and 8 small pairs; Nos. 1, 2, 4, 5, 9 and 13 are M, Nos. 3, 6 and 8 are SM, No. 12 is ST, No. 7 varies between ST and T, and No. 10 can be SM or ST and NF -52 or 50. One secondary constriction is close to the centromere of the long arm of No. 6.; This karyotype is similar to that of *M. palpebralespinosa* (Fig. 3f).

The Karyotype of *Ophryophryne microstoma* Boulenger is 2n=26; 6 large and 7 small pairs; Nos. 1, 2, 4, 5, 6, 8 and 10 are M, Nos. 3 and 7 are SM, No. 9 is ST, Nos. 12 and 13 are T, No. 11 can be M or SM and NF=48. No satellites and secondary constrictions were found (Fig. 3k). This karyotype is similar to the 6+7 type of some *Megophrys* species.

The karyotype of *Ophryophryne pachyprocta* Kou resembles most closely that of *O. microstoma;* 2n=26; 6 large and 7 small pairs. The metaphase preparation for *O. pachyprocta* is not good enough to provide a plate here.

Discussion

Although *Megophrys omeimontis* is widely distributed in southwestern China, its type locality is Mt. Omei, Sichuan. In Table 1, its karyotypes come from two populations (Mt. Omei and Mt. Wuliang) and they are very similar: all are with 5 large, one moderate and 7 small pairs. One secondary constriction occurs in the moderate sized No. 6. Two differences exist. Zheng and Wu (1989) considered No. 6 large, but it should be called moderate according to the relative length which they measured. The secondary constriction is in a short arm. Probably the two populations from Mt. Omei and Mt. Wuliang belong to one species. Fei et al. (1990) recognized the population from Mt. Wuliang as a separate species, *M. jingdongensis*.

The karyotype of *Megophrys giganticus* is of the 5+8 type, the same as those of the *Brachytarsophrys* species and *Atympanophrys shapingensis*. Further research is needed on the systematic positions of *M. giganticus* and *A. shapingensis*.

Megophrys kuatunensis is the only Megophryinae species discovered which has 2n=24. This karyotype is the 6+7 type since it has 6 large pairs of chromosomes. This species only occurs on Mt. Chongan and Mt. Daiyun, Dehua, Fujian Province, China, at the eastern edge of the distribution of the Megophryinae.

Three karyotypes occur in *M. lateralis* (see Table 1). Form I and II, based on the specimens from Tengchong, northwest Yunnan, are generally identical, but both of them are different from Form III in chromosome No. 2 and chromosome No. 13, and the location of the secondary constriction which is in the terminal short arm of chromosome No. 5 in form I, but in the base of the short arm of No. 2 in form III. Form III is based on the specimens from Hekou, southeast Yunnan, far away from Tengchong. The taxonomic status of the Hekou population needs additional attention after comparing their morphology to other populations.

Table 1. Karyotypes of some Megophryinae species.

Species	2n	NF	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
O. microstoma	26	48	M	M	SM	M	M	M	SM	M	ST	M	M/ SM	T	T		
O. pachyprocta	26	?	6 pairs						7 pairs								
M. parva (I)	26	46	SM	SM	SM	SM	SM	M	M	M	ST/ SM	M	T	T	T		
M. parva (II)	26	46	M	M	SM	M	M	M	SM	M	M	M	T	T	T		
M. lateralis (I)	26	52	M	M	M	M	M	M	M	ST	M	M	SM	SM	ST		
M. lateralis (II)*	26	52	M	M	SM	M	M	M	M	ST	M	M	M	M	ST		
M. lateralis (III)	26	50	M	SM	SM	M	M	M	SM	ST	ST	M	M	SM	T		
M. minor (I)	26	52	M	M	M	M	M	M	SM	ST	M	M	M	ST	SM		
M. minor (II)	30	56	M	M	M	M	M	M	SM	ST	M	SM	M	ST	ST	T	T
*M. boettgeri**	26	50	M	M	SM	M	M	M	SM	M	SM	M	SM	M	T		
M. kuatunensis	24	48	M	M	M/ SM	SM	M	M	ST	SM	ST	M	M	ST			
M. omeimontis (I)*	26	52	M	M	SM	M	M	M	SM	ST	M	M	M	SM	ST		
M. omeimontis (II)*	26	48	M	M	SM	M	M	M	SM	M	T	M	M	SM	T		
M. palpebralespinosa	26	52/ 50	M	M	SM	M	M	SM	ST	SM	ST/ T	SM	SM /ST	M	ST		
M. daweimontis sp. nov.	26	52/ 50	M	M	SM	M	M	SM	ST/ T	SM	M	SM /ST	M	ST	M		
*M. shapingensis**	26	52	M	M	SM	M	M	M	SM	SM	SM	M	M	SM	ST		
M. giganticus (I)*	26	48	M	SM	SM	SM	M	M	SM	T	ST	M	M	SM	ST		

(Continued)

Species	2n	NF	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
M. giganticus (II)*	26	50	M	SM	SM	SM	SM	ST	M	M	M	M	M	M	M		
M. nasuta (I)*	26	50	M	SM	M	SM	M	M	SM	ST	SM	M	M	SM	SM		
M. nasuta (II)*	26	50	M	SM	SM	M	M	SM	M	ST	M	M	SM	M	SM		
*M. monticola**	26	?			5 pairs						8 pairs						
B. sp. nov. (I)*	28	48	M	SM	M	M	M	M	M	SM	T	T	M	M	T	T	
B. sp nov. (II)*	26	44	M	SM	M	M	M	M	M	M	T	M	T	T	T		
*B. feae**	26	50	M	SM	M	M	M	SM	M	M	SM	T	M	M	SM		
B. carinensis	?	?			5 pairs (?)						(?)						
Groups					Large Group						Smalll Group						

* M. lateralis (II) and M. shapingensis are from Wu (1987); M. boettgeri from Gao et al. 1990; B. sp. nov. (II) from Tan et al. (1987, as B. carinensis); M. omeimontis (II) from Zheng and Wu (1989); M. giganticus (II) and M. parva (II) from Li et al. (1993); M. nasuta (I) and M. monticola (synonym of M. montana) from Morescalchi et al. (1977); M. nasuta (II) from Schmid et al. (1987). M. lateralis (II) based on specimens from Tengchong, Yunnan; M. lateralis (III) based on specimens from Hekou, Yunnan; M. giganticus (I), B. sp. nov (I) and B. feae are from Rao and Yang (in press).

Two different forms of karyotypes of *Megophrys parva* are also shown in Table I; forms I and II are based on the specimens from Mengla, Yunnan. This species is more primitive in that it has 3 pairs of T chromosomes in both forms. It may be primitive because it is widely distributed in upper Burma and southwest Yunnan.

Although *Megophrys palpebralespinosa* occurs in Hekou, Yunnan, it is very close to *M. boettgeri* of Fujian in skin and color characters. They are very different in karyotype; the former has a 5+8 type karyotype while the later has a 6+7 type. *M. palpebralespinosa* has tubercles on the outer edge of the upper eyelids, folds on the back and a reddish inner palm tubercles, while *M. boettgeri* does not. They are geographically widely separated. This suggests that they are not closely related.

Megophrys daweimontis sp. nov. is like *M. palpebralespinosa* in having a 5+8 karyotype, tubercled upper eyelids and reddish inner palm tubercles, and both occur on Mt. Dawei.

It is interesting that *Megophrys palpebralespinosa* and *M. daweimontis* sp. nov. Have 5+8 type karyotypes. Generally the 5+8 type karyotype occur in species which are large-sized and possess a hidden tympanum, such as *M. nasuta*, *M. monticola* (synonym of *M. montana*), *M. giganticus*, *M. shapingensis* and *Brachytarsophrys* species. Species with small-sized bodies and a distinct tympanum generally have 6+7 karyotypes common in the Megophryinae. *M. palpebralespinosa* and *M. daweimontis* sp. nov. are relative small; body length is about 35 mm. In males and 40 mm. In females. Additional study of their taxonomic position is needed.

Karyotypes of *Ophryophryne microstoma* and *O. pachyprocta* are of the 6+7 type, the same as those of *Megophrys* species which are generally small-sized. These observations agree with Dubois (1980) who considered *Ophryophryne* a subgenus of *Megophrys*. However, on the basis of other characters, habitats and habits, which are different from other Megophryinae species, we recognize this genus as valid and separate. According to Kou (1985), *O. pachyprocta* has a bump above the anus. We think this bump is probably the protruding coccyx and *O. microstoma* also has a protruding coccyx. On the basis of this character, we think that the two species should be recognized as a single species.

The main differences among the species are shown in Table 1. But another should be noted: *Megophrys boettgeri* has a secondary constriction in 6q and *M. shapingensis* also has one near the centromere of 1q.

Megophrys minor from Jingdong, Yunnan has various karyotypes, but we can't find anatomical differences between the different specimens with different karyotypes. Karyotype variation is common in Pelobatidae, such as *Leptolaylax pelodytoides* (Li et al., 1991). Because there are various karyotypes in the same species, it is difficult to identify a species according to its karyotype, especially for some widely distributed species, such as *M. lateralis*, *M. omeimontis* and *M. minor*. In contrast, some Pelobatidae have very stable karyotypes with simple chromosome arrangements and secondary constrictions, such as *Oreolaxax*, *Scutiger* and *Vibrissaphora*. The karyotypes of some genera are variable, such as *Leptolaylax* and some *Megophrys* species. Thus, karyotypes can be used to resolve some taxonomic problems in some genera, but not in others. In general, karyotypic variation in Megophryinae occur among small chromosomes, while the large chromosomes are relatively invariable. The karyotypes of Megophryinae species, which are similar in morphology and habitats, are relatively similar. So karyotypic characters can be used for taxonomic purposes to separate genera and for evolutionary analyses.

Up to now, karyotypes of 16 species (about 2/3 of total) of Megophryinae have been obtained (Table 1). They can be generally divided into two types on the basis of the numbers of large and small chromosomes: 6+7 and 5+8. *Brachytarsophrys feae*, *B.* sp. nov., *Megophrys shapingensis* (previously *Atympanophrys shapingensis*), *M. giganticus*, *M. nasuta*, *M. monticola* (synonym of *M. montana*), *M. daweimontis* sp. nov., and *M. palpebralespinosa* have the 6+7 pattern, whereas *M. parva*, *M. lateralis*, *M. minor*, *M. boettgeri*, *Ophryophryne microstoma* and *O. pachyprocta* have the 6+7 pattern. Although *M. kuatunensis* has 6 large and 6 small pairs it belongs to the 6+7 type. *M. omeimontis* has 5 large, 1 moderate and 7 small pairs. Thus it seems this pattern is intermediate between 5+8 and 6+7 types. In morphology *M. omeimontis* is similar to species which share the 5+8 pattern.

Morescalchi (1973, 1977) thought that the 5+8 pattern was derived from the 6+7 pattern through the lose of a fragment from one of its large chromosomes (usually No. 6).

The No. 6 chromosome of *M. omeimontis* is peculiar (see Fig. 3d). It seems that this chromosome is easily broken at the site of secondary constriction in the short arm and becomes 5+8 if the separated part is lost. This hypothesis supports the conclusion of Morescalchi with respect to the evolution of karyotypes in Pelobatidae. The karyotype of *M. omeimontis* should be considered derived from the 6+7 type. We suggest that one of the large chromosomes transferred a fragment to a small chromosome and the large one became small. The small one (T or ST chromosome) became the No. 6. The transferred fragment is the satellite on the short arm of No. 6 and it retains the former body type in morphology because the fragment is not lost. If the chromosomal fragment was lost, then the karyotype would have resembled the 5+8 pattern.

All the large sized species have 5+8 type karyotypes. While the species which are generally small sized have two karyotypic patterns. *Megophrys palpebralespinosa* and *M. daweimontis* sp. Nov. Have a 5+8 pattern, and the other *Megophrys* and *Ophryophryne* species have a 6+7 pattern.

It is interesting that *M. giganticus*, *Atympanophrys shapingensis*, *Brachytarsophrys* species, *M. nasuta* and *M. monticola* have not only the same type (5+8) of karyotype, but also similar morphological characters and habitats; i. e. very large bodies; very large, wide and flat heads; a hidden tympanum, round digital tips; and usually sit under stones at the edges of streams during the breeding season (Bourret, 1942; Inger, 1954; 1966; Liu and Hu, 1961; Tian et al., 1986; Yang et al., 1991).

The Classification of Megophryinae

The megophryinae is currently divided into 4 genera: *Atympanophrys*, *Brachytarsophrys*, *Megophrys*, *and Ophryophryne*. Some recent researchers think that the genus *Atympanophrys* is not valid because its main distinguishing character (no tympanum) is wrong and this genus should be a synonym of *Megophrys* (Fei et al, 1990). *A. shapingensis* has a unique karyotype as well as other morphological characters. This genus has a 5+8 karyotype, relatively large sized body, relatively flat and wide head, a hidden tympanum and round digital tips. It occurs always under stones at the sides of streams.

Brachytarsophrys includes three species (Rao and Yang, in press): *B. feae* (previously *M. feae*), *B. carinensis* and a new species from China. *B. feae* and the new species have 5+8 karyotypes. It is probable that *B. carinensis* also have this kind of karyotype. All the species in this genus have very large sized bodies, widened and flattened heads, a hidden tympanum, shortened legs and horny-bearing eyelids. They occur under stones at the sides of streams. In our opinion, this genus is valid.

Ophryophryne has three species: *O. microstoma*, *O. pachyprocta* and *O. poilani*. The former two have 6+7 karyotypes. All the species in this genus have small bodies, marrow mouths, small high heads, a distinct tympanum, and tubercled eyelids. They are usually found on grass and leaves beside very small streams (this is unique among the Megophryinae). This genus is valid, and it is related to the species of *Megophrys* which have 6+7 karyotypes.

Megophrys is a large genus, with about 22 species. Their body forms are varied. The karyotype patterns differ. *M. giganticus* is very large, it has 5+8 karyotype, an obviously wide and flat head, a hidden tympanum, and round digital tips. The habitats and habits for this species are similar to those of *Brachytarsophrys* and *A. shapingensis*. *M. montana* (including former *M. monticola)*, and *M. nasuta* all have 5+8 karyotypes, broad heads, relatively short legs, an indistinct or hidden tympanum similar to *Brachytarsophrys*. However, they have elongate free dermal flaps on the snout and long soft horn-like appendages on the eyelids. Their habitats and habits are similar to *Brachytarsophrys*. The genus *Megophrys* was first described on the basis of the type, *M. montana*.

Megophrys palpebralespinosa and *M. daweimontis* sp. nov. have 5+8 karyotypes, a small sized body tubercled eyelids, reddish inner palm tubercles, and widened and sucker-like digital tips. They are usually found on grass at the sides of small streams. The rest of *Megophrys*, including *M. lateralis*, *M. minor*, *M. kuatunensis*, *M. parva* and *M. boettgeri* have 6+7 karyotypes, are generally moderate or small in body size, with regular body forms and head, a distinct tympanum, no tubercles on the eyelids, and widened and sucker-like digital tips. They are found on stones or roots at the sides of streams or rivers. Although *M. omeimontis* seems to be intermediate between the 5+8 and 6+7 karyotype, it is similar to *M. lateralis M. parva* in morphology, habitats and habits.

Thus, the species of *Megophrys* may be divided into four groups according to their karyotypes, morphology, habitats and habits: 1). *M. montana* and *M. nasuta;* 2). *M. giganticus;* 3. *M. palpebralespinosa* and *P. daweimontis* sp. nov.; 4). *M. lateralis*, *M. omeimontis*, *M. parva*, *M. minor*, *M. kuatunensis*, *M. boettgeri* and probably including *M. nankianensis*, *M. kempii*, *M. baluensis*, *M. aceras*, *M. brachykolos* and *M. robusta*.

Because of these differences in karyotype and morphology, we recognize a new genus for the *M. lateralis* and the *M. omeimontis* group. *Megophrys* should be restricted to the *M. montana* and *M. nasuta* group. The *M. lateralis* group is generally small in size, the heads are not wide, tympanum is present, legs long, digital tips flat and sucker-like, temporal fold thin and bent, and a 6+7 karyotype. Frogs of this group are usually found sitting on rocks next to rivers. The *M. montana* group is somewhat similar to *Brachytarsophrys* in cytology, morphology and habitats: 5+8 karyotype, very large body, wide and flat head, a hidden tympanum, straight and thick temporal fold, transverse shoulder groove, and short legs; but it is different in lacking tubercles on the upper eye-lid.

As for *M. giganticus*, it is narrowly distributed in Jingdong and Yondge, Yunnan. It is similar in morphology to *A. shapingensis* with digital tips round, hidden tympanum, wide and flat hear, straight and thick temporal folds, and 5+8 karyotype. *M. giganticus* is different than *Brachytarsophrys* and the *M. montana* group in having much longer legs, lacking any elongated tubercle on the upper eye-lid and no transverse groove on the shoulder. We suggest that *M. giganticus* should be placed in the genus *Atympanophrys* along with *A. shapingensis*.

Megophrys palpebralespinosa and *M. daweimontis* sp. nov. are more similar to the *M. lateralis* group even though they have 5+8 karyotypes. But they have tubercles on the upper eye-lid and reddish inner palm tubercles, which is different from the *M. lateralis* group. These species may be derived from an ancestor with 6+7 karyotype.

Based on the above information, Megophryinae is reviewed below:

1. The genus *Brachytarsophrys* is valid and it contains three species: *B. carinensis*, *B. feae* and *B.* sp. nov. (Rao and Yang, 1996). The type species if *B. feae*.

2. The genus *Ophryophryne* is valid and it contains three species: *O. microstoma*, *O. pachyprocta* and *O. poilani*. The type species is *O. microstoma*.

3. The genus *Megophrys* should be confined to the *M. montana* group. It includes two species: *M. montana* and *M. nasuta*. The type species if *M. montana*.

4. *Atympanophrys* should be re-named and its diagnosis should be revised. The genus should include *M. giganticus*.

5. A new genus *Panophrys* should be recognized for the *Megophrys lateralis* and *M. omeimontis* group. Its type species is *P. omeimontis*. This new genus can be distinguished on the basis of small size, tympanum present, head not very wide and flat, long legs, upper eye-lids tubercles absent (except for *P. palpebralespinosa* and *P. daweimontis)*, temporal fold thin and bent, digital tips flat and sucker-like. They are usually found on rocks.

As for the relationships of this subfamily, two branches are recognized (Fig. 1): one for *Brachytarsophrys*, *Megophrys*, and *Atympanophrys* and another for *Panophrys* and *Ophryophryne*. The two

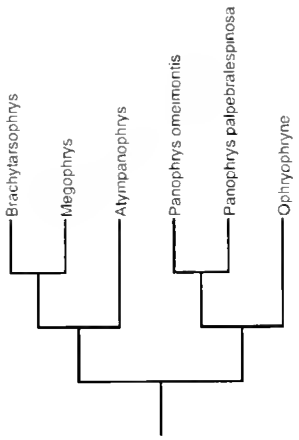

Figure 1. Evolutionary tree of Megophryinae.

Figure 2. *Megophrys daweimontis* sp. nov. female X 1.

branches diverged early in megophryine evolutionary history. Both branches share almost the same distribution.

Description of a New Species

The specimens collected from Mt. Dawei, Pingbian County, southeast Yunnan are similar to specimens of *M. brachykolos*, *M. parva* and *M. longipes.*, but they have horn-like tubercles on the eyelids and the head is not flattened. In this character they can be distinguished from *M. parva*. The Mt. Dawei specimens have relatively long legs where the heals can overlap when the flexed legs are held at right angles to the body axis. The specimens have markings on the backs for heads and trunks, which are different from those of *M. brachykolos*. These markings are similar to those similar to those of *M. longipes*. According to Taylor (1962), *M. longipes* has rudimentary webs between the toes, no metatarsal tubercles, upper eyelids with small horn-like tubercles, and a body length of 47 mm in males and 65 mm in females; whereas the specimens from Mr., Dawei lack metatarsal tubercles, have smaller tubercles on the eyelids, lack webs between the toes, and are shorter (37 mm in males and 45 mm in females). Therefore we recognize the specimens from Mt. Dawei as a separate species.

Megophrys daweimontis sp. nov. (Fig. 2)

Holotype: KIZ 93088, adult male, collected from Mt. Dawei, Pingbian County, southeast Yunnan, China., altitude 1900 m., July, 1993.

Paratypes: 17 adult males (KIZ 93069-KIZ 93085) and 3 adult females (KIZ 93086, KIZ 93087, KIZ 93089) collected at the same place and time as the holotype.

Diagnosis: A small tubercle on outer edge of upper eyelid; vomerine teeth present; snout projecting beyond jaw; tibiotarsal articulation reaching tip of snout; vocal sac in male; toes without rudiment of web; an inner palm tubercle and very small outer palm tubercle, a reddish inner metatarsal tubercle; body length from shout to vent 34-37 mm in males and 40-46 mm in females.

Description: Tongue pyriform; vomerine teeth present; head slightly wider than long, depressed; snout very short; interorbital space concave; tympanum distinct, round. Arms long and slender, the first finger extending beyond second; palm tubercles reddish, the inner tubercle is very large and the outer very small. Legs long, the distal end of femur reaching shoulder; tibiotarsal articulation reaching tip of snout; toes slender, swollen at tips, completely without webbing. Superarticular tubercles lacking; a reddish outer metatarsal tubercle.

Skin smooth above, with small warts on flanks and sides of body; two pairs of delicate oblique folds on the scapular region extending posteriorly to waist, a pair of folds on the back-side; fold extending from eye above tympanum to shoulder; upper eyelid with very small tubercle on outer edge; lower surfaces smooth.

Olive-brown above, a triangular marking between eyes, followed with V-shaped marking above shoulder, or X-shaped marking on the back of trunk; black marking beneath the vent and behind heel; transverse lines above thigh; inner lower surface of legs reddish.

Measurements of holotype are: 33.5 mm snout-vent; 12.5 mm head length; 12.5 mm head width; 52.5 mm hind leg; 18 mm tibia.

Distribution: Known only from type locality.

Variation: Body length 33-37 mm in males and 40-46 mm in females.

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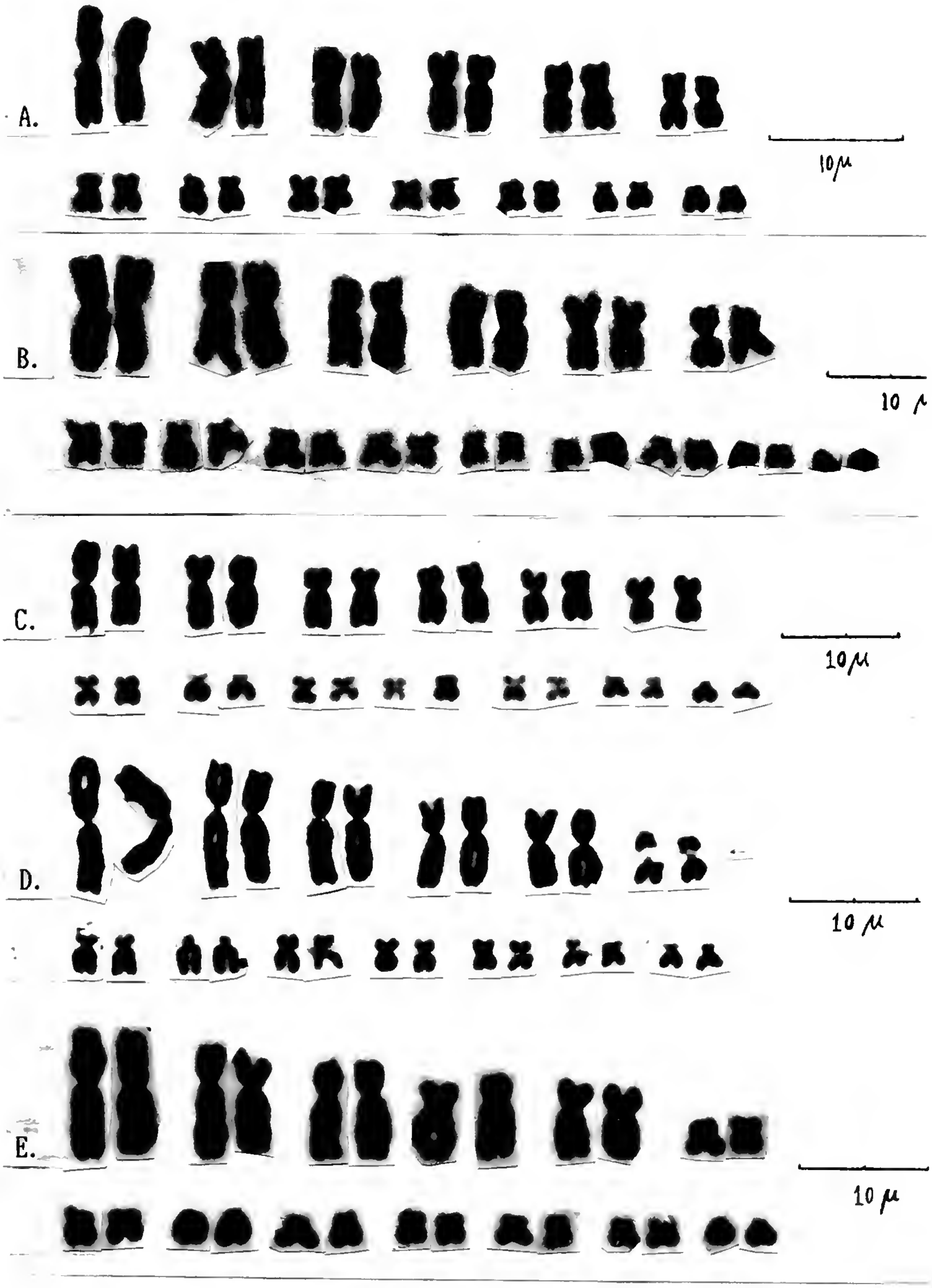
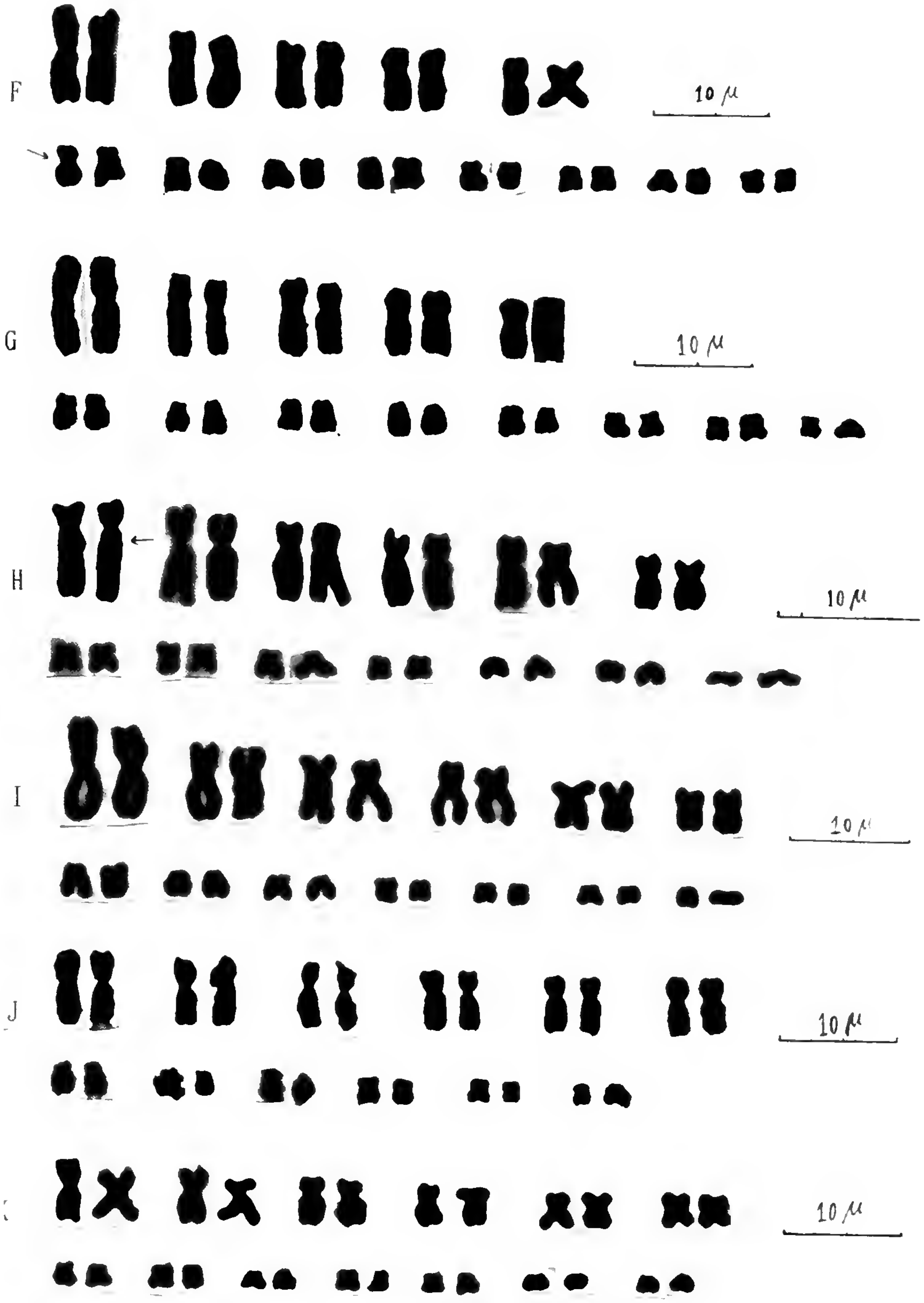
Appendix I

Figure 3. The karyotypes of Megophryinae species: A-B. *Megophrys minor;* C. *M. lateralis* (Tengchong); D. *M. omeimontis;* E. *M. giganticus;* F. *M. daweimontis* sp. nov.; G. *M. palpebralespinosa;* H. *M. parva;* I. *M. lateralis* (Hekou); J. *M. kuatunensis;* K. *Ophryophryne microstoma.*

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The Variation in Karyotypes of *Brachytarsophrys* from China with a Discussion of the Classification of the Genus

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Abstract. -Different karyotypic forms of *Brachytarsophrys* occur in populations from Jingdong and Dayao, Yunnan. These forms, along with morphological evidence, suggest that *Brachytarsophrys* should be divided into two different species. The Jingdong population is identified as *B. feae* (previously *Megophrys feae*). The Dayao population is a new species, resembling in morphology, *B. carinensis* which occurs in south Burma and Thailand. The Dayao population is geographically far removed from *B. carinensis*. A valid sister species, *B. feae*, is found between the distribution of the Dayao population and *B. carinensis*. The new species is found in a different climatic zone and in different habitats than *B. carinensis*. *B. intermedius* in south Vietnam probably is not a valid species because it is more similar to *B. carinensis* in morphology and shares the same climatic zone and habitats.

Key words: Brachytarsophrys, B. platyparietus sp. nov., *B. feae*, karyotype, biogeography, classification

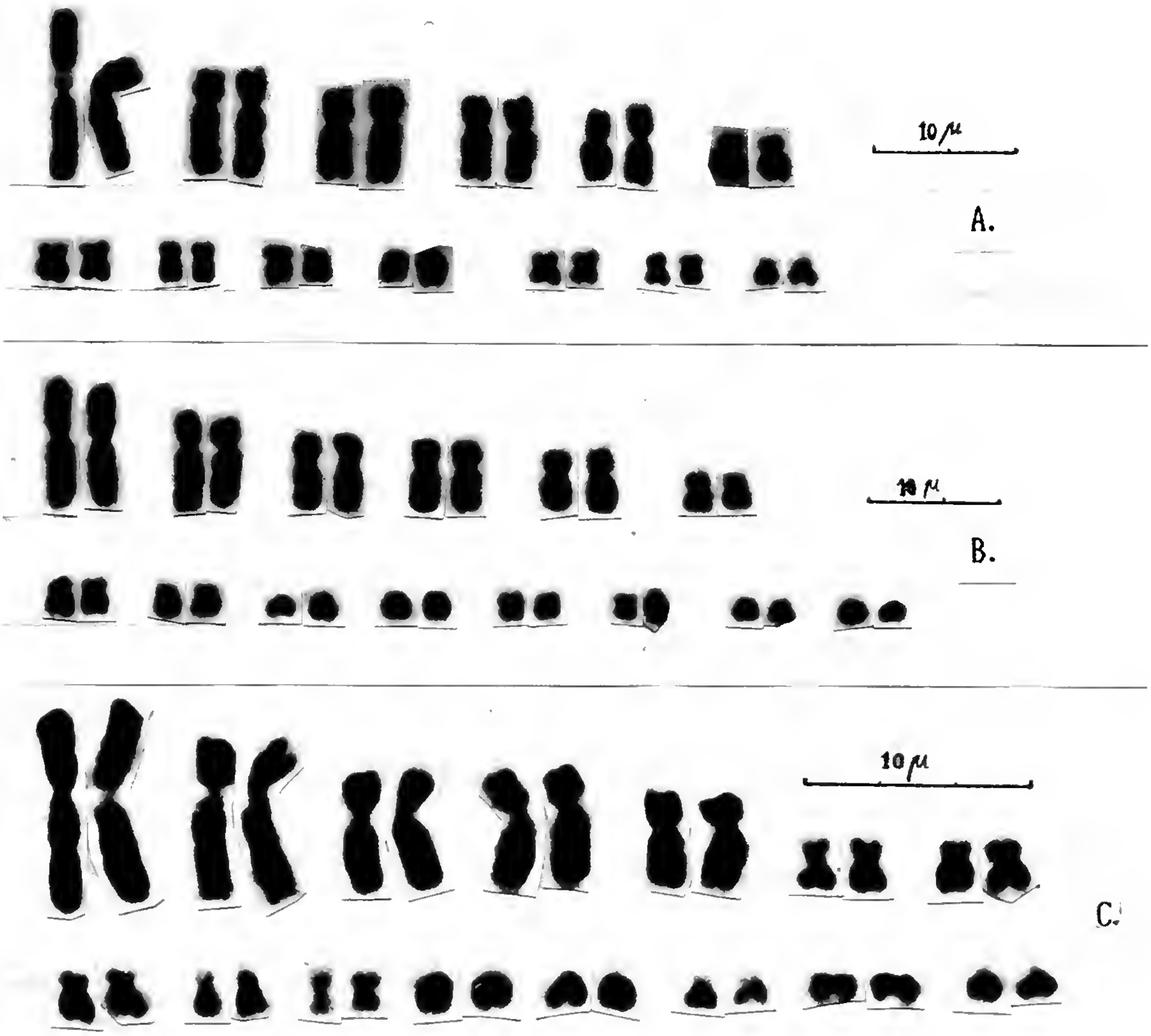

Figure 1. The karyotypes of *Brachytarsophrys* of China. A; Jingdong population; B-C: Dayo population.

Introduction

Brachytarsophrys in China were considered to be only *B. carinensis* until Ye and Fei (1992) described a second species, *B. feae*. Our studies of cytology and morphology agree with Ye and Fei that *Brachytarsophrys* in China belong to two different species. The Jingdong population we studied belongs to *B. feae*. We do not agree with them with respect to the Dayao population, which they identified as *B. carinensis*.

Materials and Methods

Specimens used in cytological research were collected respectively from Jingdong, Yunnan in June, 1990 and May, 1991, and Dayao, Yunnan in May, 1990. All specimens were taken to the laboratory before processing. Karyotypes were prepared using the method of colchicine-hypotonic-air drying: specimens were injected intraperitoneally with colchicine at a dosage of 20 μg/g body weight for about 24-36 hours, then the femur and tibia were cut off at their two ends. The marrow cells were washed out with 1% tri-sodium citrate solution, ground, then placed in a hypotonic solution of 0.64% KCl and fixed in 3:1 solution of methanol:acetic acid for two periods of 20 minutes each. Slides were air-dried and stained with 10% Giemsa PBS for about 15 minutes. Specimens from middle, southern, southwestern, northwestern and northern Yunnan were examined and some from Jingdong, Menglian, Tengchong, and Xishuanbanna were dissected.

Cytological Results

The karyotypic form of the specimens from Jingdong is 2n=26, 5 large and 8 small pairs. Nos. 1, 3, 4, 5, 7, 8, 11, are M (metacentric); Nos. 2, 6, 9, and 13 are SM (submetacentric); only No. 10 is T (telocentric). The NF (fundamental number) is 50. One secondary constriction is found in the near base of the short arm of No. 1; no satellite was found. The karyotypic form of the specimens from Dayao is mostly 2n=28, 5 large and 9 small pairs, Nos. 1, 3, 4, 5, 6, 7, 11, and 12 are M; Nos. 2 and 8 are SM and Nos. 9, 10, 13, and 14 are T chromosomes, NF=48. No satellite or secondary constrictions were found. We also found a third karyotypic form with 2n=30 in Dayao specimens, with 5 large and 10 small pairs, Nos. 2, 7, and 8 are SM, Nos 9 and 13 are ST and Nos. 11, 12, 14, and 15 are T; the rest are SM chromosomes, NF=48. No secondary constrictions and satellites were found. A few specimens had 2n-26, as reported by Tan et al. (1987) for specimens from Miyi and Huili, Sichuan (omitted from this article, Table 1).

Table 1. Comparison of karyotypes of *Brachytarsophrys* from different localities in China.

			Large Group					**Small Group**									
Locality	2n	NF	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Jingdong	26	50	M*	SM	M	M	M	SM	M	M	SM	T	M	M	SM		
Dayao	28	48	M	SM	M	M	M	M	M	SM	T	T	M	M	T	T	
Dayao	30	48	M	SM	M	M	M	M	SM	SM	ST	M	T	T	ST	T	T
Sichuan	26	44	M	SM	M	M	M	M	M	M	T	M	T	T	T		
					(SM)	(SM)									(ST)		

Discussion of Karyotypes

Table 1 shows that the large chromosomes are similar in the three populations examined, but the small chromosomes vary. The karyotype of the specimens from Dayao is closer to that from Sichuan than that from Jingdong. The karyotype of the population from Jingdong has 2n=26, NF 50, an obvious secondary constriction in 1p, only 1 telocentric pair (No. 10) of chromosomes, 3 pairs of SM chromosomes (Nos. 6, 9, 13). Small chromosomes are more numerous in this population than in the other two populations. The karyotype of the Dayao population is 2n=28, NF=48, no secondary constriction was found, only 1 SM chromosome (No. 8), and 4 small T chromosomes (No. 9, 10, 13, 14). This is more than the Jingdong, Sichuan population karyotypes which were mainly 2n=26, NF=44, 1 secondary constriction in each of two T chromosomes (No. 9, 11), no SM chromosomes, and 4 T chromosomes (No. 9, 11, 12, 13) (Tan, et al., 1987). Because of these differences in karyotype, the populations of Jingdong and Dayao should be recognized as two different species.

Morphological Results

The specimens from northeastern Yunnan (Lijiang, Yangbi, Bianchuan, Dayao, Yuxi, Kunming, Shuangbai, Shiping and Xinping), from Sichuan (Miyi, Huili), and from Guizhou (Leishan, Anlong) (Wu et al., 1986) are probably the same as those from Guangxi (Longsheng, Jinxui), from Hunan (Yizhang), and from Jiangxi (Jingganshan). The toes are obviously webbed and the web may reach or exceed 1/3 of the toes. The tops of the skulls in specimens from middle and northern Yunnan are very flat. Specimens from southwestern Yunnan (Jingdong, Meglian, Xishuanbanna, Tengchong, Yongde and Longchuan, near the type locality of *Megophrys feae)* are nearly free of webbing or with a mere rudiment of a web. The tops of their skulls are obviously depressed. These differences suggest that these forms be recognized as two different species.

Bourret (1942) and Taylor (1962) described *B. carinensis* (previously *Megophrys carinensis)* as follows: eyelid with two to four pointed tubercles near edge, vomerine teeth normally present, heel reaches to shoulder or jaw-angle, skin with bony deposits above head and anterior part of body, a vocal sac, paired elongate glandular folds of back, male 123 mm and female 150 mm, and toes about 1/3 webbed. It is distributed in Thailand (Chang Mai, Lampang provinces and Mergui) and south Burma (type locality is Karen Hills in southwestern Burma).

B. feae (M. feae) is characterized by eyelids with small tubercles, one much more elongate than the others, no longitudinal glandular folds on dorsum, a vocal sac, tibiotarsal articulation which reaches near jaw-angle, bony deposits on head, length 106 mm, head depressed, and toes free or with a mere rudiment of web. It is distributed in north Burma and the type locality is Kakhien Hills, Burma which is near Longchuan and Tengchong, Yunnan, China.

The population of southwestern Yunnan is here assigned to *B. feae* and is not *B. carinensis*. The populations of northeastern Yunnan and Sichuan are similar to *B. carinensis*, but lack paired glandular folds.

Discussion

The populations from north and middle Yunnan, including the Dayao population, are similar to *B. carinensis* in possessing eyelids and toe-webs, but they obviously lack paired elongate granular folds on the back that are present in *B. carinensis* (Bourret, 1942; Taylor, 1962). Also these Yunnan populations are geographically widely separated from *B. carinensis* and are found in different habitats and climate zones. *B. carinensis* occurs in tropical habitats whereas populations of northeastern Yunnan occur in temperate zones, and are separated from *B. carinensis* by a valid sister species. *B. feae*.

Physiological characteristics limit amphibian ability to disperse. Distributions should be continuous and presently discontinuous distributions should be vestiges of a once continuous range. The distribution of a species should be continuous, and even when populations are separated by a valid sister species or different climatic zones, such populations should be widely separated. We think that the population of northeastern Yunnan, Sichuan and nearby localities should be a new species and not recognized as *B. carinensis*.

B. intermedius in south Vietnam (Lang Bian) has paired elongate folds; it is similar to *B. carinensis*, and inhabits the same climatic zone (tropical). It is probably a population of *B. carinensis*.

Karyotypic and morphological evidence and geographical distribution (Liu and Hu, 1961; Yang et al., 1991; Wu et al., 1986; Tian and Jiang, 1986), suggest that the population from Jingdong (including those of southwestern Yunnan) is *B. feae*. The populations from Dayao (including northeastern Yunnan, Sichuan, Guizhou, Guangxi, Hunan and Jiangxi) is a new species and not a population of *B. carinensis*. *B. carinensis* is distributed in southwestern Burma (type locality) and north Thailand. *Megophrys intermedius*

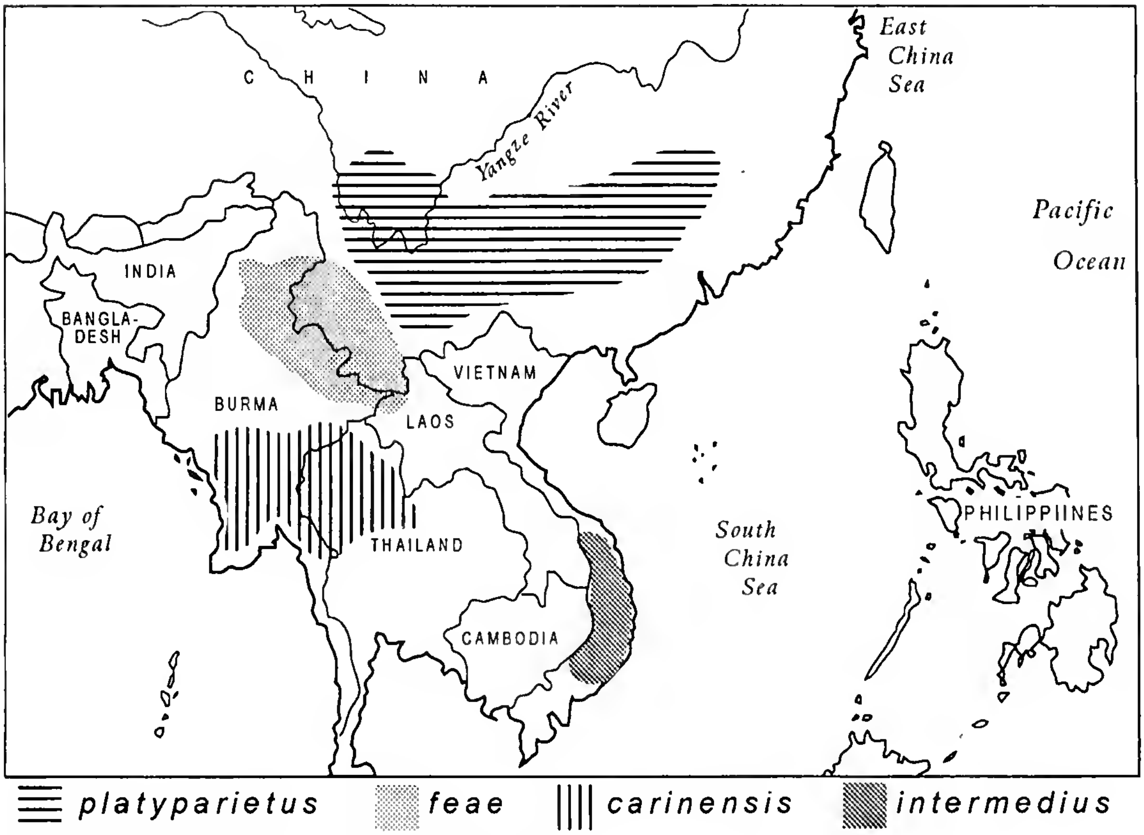

Figure 2. The distribution of the genus *Brachytarsophrys.*

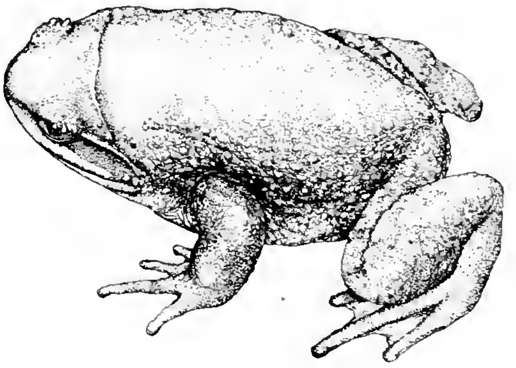

Figure 3. *Brachytarsophrys platyparietus* sp. nov. Holotype (KIZ 90275), adult male X 1.

Smith (1921) in south Vietnam (Annam) is a population of *B. carinensis.* We recognize three species in the genus *Brachytarsophrys: B. carinensis* in southwestern Burma, Thailand and south Vietnam; *B. feae* in north Burma and southwestern Yunnan; and a new species in northeastern Yunnan, southern Sichuan, Guizhou, Guangxi, Hunan and Jiangxi (Fig. 2).

Taxonomic Account

Brachytarsophrys platyparietus sp. nov. (Fig. 3)

Holotype: KIZ 90275, adult male, collected from Duo-Di-He, San-Tai, Da-Yao, Yunnan, China, altitude 2100 meters.

Paratypes: 1 adult male (KIZ 90274) and adult female (KIZ 90276), from the same locality as the holotype.

Diagnosis: Body very large, male may reach 116 mm from snout to vent, female 131 mm; eyelids with three circular tubercles in a line, the middle longest, and not very sharp; tympanum hidden; arched diagonal fold from eyelid to above arm insertion; toes widely fringed and obviously webbed (at least extending to 1/3 toes); the top of skull obviously very flat; no longitudinal granular folds on the body side; no subarticular tubercles. The karyotype with 2n=28, few are 26 or 30; 5 pairs of large chromosomes, always with 4 pairs of small telocentric chromosomes, no secondary constriction in the No. 1 chromosome.

Description of Holotype: Head large, flat and wide, length nine-tenths of width; snout obtuse, very short, its length in front of the level of eyes 12 mm; distance between nostrils 11 mm; canthus rostralis not very sharp; loreal region only slightly diagonal; eyelid elevated, projecting, bearing three elongate and circular tubercles in a line, among which the middle one is longer than the other two, and with much smaller tubercles (3-4) behind them; tongue broad, nearly round, mostly free behind, free on sides, one notch in front; chaoanae partly concealed by maxillary shelves; vomerine teeth present; arm rather long in proportion to leg; first finger shorter than second; third longest; no web between fingers and no fringe; legs relatively short, tibiotarsal articulation reaching to back of skull; toes about one-third (or more) webbed and widely fringed; a large flat inner metatarsal tubercle, as long as first toe; no tarsal fold; digits without widened tips; heels separated by about 20 mm when legs are folded; no subarticular tubercles.

Skin above generally smooth, but laterally with numerous flat tubercles; a strong fold from edge of eyelid to above arm insertion on each side, the folds are arched; back without pair of curving ridges from head to shoulders, and without any dorso-lateral ridges on dorsal side and above groin; no paired conical symmetrical tubercles in front of shoulders; no sharp ridges and tubercles on sides; tibia without any ridges. Body length 113 mm, head length 47 mm, width of head 57 mm.

Variation: One female (KIZ 90276) with body length 131 mm, head length 52.5 mm, head width 61 mm.

Distribution: Yunnan (Yangbi, Lijiang, Bianchuan, Dayao, Kunming, Yuxi); Sichuan (Miyi, Huili, Duko, Muli, Jiulong); Guizhou (Anlong, Leishan); Guangxi (Longshen, Jinxiu); Hunan (Yichang); and Jiangxi (Jingganshan).

Comparisons: *B. feae* is only very narrowly fringed and not webbed in the toes. The top of the skull is obviously depressed and the eyelid tubercle is very long and sharp. The karyotype is 2n=26 with five large pairs, only one pair of small telocentric chromosomes, and a secondary constriction in the short arm of the No. 1 chromosome. *B. carinensis* has webbed toes, obvious granular folds on the back and above the groin. The eyelids have three sharp pointed flattened tubercles. *B. intermedius* from south Vietnam is very similar to *B. carinensis*. It also has longitudinal granular folds on the back. We suggest that it should be considered a synonym of *B. carinensis*.

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Behavior of *Varanus griseus* during Encounters with Conspecifics

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Abstract. - In 1990-1993 in the western region of the deserts of Kyzylkum (Uzbekistan), constant observations of a group of desert monitors in natural conditions were conducted. Described are manifestations of various emotional states of monitors, and common types of monitor interaction. Given are detailed descriptions of the course of contacts between the animals, illustrated by photographs. Fights were rarely noted and only between unfamiliar lizards. It is proposed that ritual combat arises from displays of dominance and not from a ritualization of the fight. The behavior of monitors during contacts is highly varied and not stereotypical. Data from observations attests to the existence of a complex, mammal-like social structure in the population. Considered are probable mechanisms of intraspecific communication of monitor lizards.

Key words: social behavior, social relations, Reptilia, Sauria, *Varanus griseus*

Introduction

In the article at hand we have made an attempt to reveal the communicational function of common behavioral acts of desert monitor. We have made also an attempt to describe some types of interactions between monitors and the role of these interactions in social organization of population. We will not touch upon behavior connected with courtship and mating in the present article.

In 1989, when a program for the study of endangered species of reptiles was developed by us, the principal emphasis was put upon their ecology. When we stumbled onto the fact, that the behavior of the monitor lizard is much more complex than was imagined, we no longer had the opportunity to alter the program of study. Hence, the gathering of ethological material had to be conducted at the same time as the primary tasks. Although we are aware of the incompleteness of our data and the necessarily schematic and fragmentary nature of our description, we do not consider its publication to be in vain. This issue has not only theoretical but practical significance since desert monitor populations arouse serious apprehension in many regions of Middle Asia (Darevsky, Orlov 1988, Khodzhaev 1989)

There exists a vast literature dedicated to the elementary behavioral acts of lizards (see the survey of Carpenter, Ferguson 1977). The behavior of some species of monitor lizards has also been described in some detail (Auffenberg 1981a; 1981b; 1983; 1988; Carter; 1990; Davis et al. 1986; Deraniyagala 1958; Gaulke 1989; Horn et al. 1994; Mertens; 1946). But in the most of herpetological papers the social motives and purposes of behavioral acts are not examined. Behavior of animals during intraspecific contacts is usually considered as a succession of behavioral acts, but not as a social interaction directed at the maintenance of long-term interrelations within a socium. The analysis of behavior is reduced to statistical analysis of the sequence of the behavioral acts of contactants. Generally, the task of the analysis is limited to discovery of the most probable response of a lizard to the acts of another lizard. In analysis one seldom allows for the circumstances, under which the interaction took place. The history of interrelations of contactants, as a rule, is not taken into account at all. Actually, the social interaction is considered as a closed system with internal self-regulation, independent of the structure of the socium.

Viability of the population (the ability for balanced reproduction in particular) is to a considerable extent determined by its social structure. The social structure of many species is rather impressed by environmental conditions and the reptiles are not an exception (Panov, Zykova, 1985; Polynova, Panyushkin 1982; Polynova, 1990; Stamps; 1977). A social response of population to environmental changes is often species-specific (Polynova, 1990) and is not necessarily adaptive (Plyusnin, 1990). Peculiarities of response of socium to the external influences are determined for the most part by two closely interdependent, species-specific systems of animal activity: a) a production of the signals which carry information about the animal and its circumstances; b) a perception, processing and analysis of these signals in conjunction with others external and internal irritants. The principles of organization of these processes may be termed as a "language" and a "mentality" of a species. This issue is closely linked to the problem of management of populations and demands careful study.

The Region of Studies

The studies were conducted in the western area of the sand deserts of Kyzylkum, Uzbekistan. The coordinates of our permanent camp were 40° 40' N and 62° 08' E. The landscape in this region is typical of the Kyzylkum -- sandy ridges, bushy undergrowths (mainly *Haloxylon persicum*, and *Calligonum sp.*), and sparse grass (*Carex physodes* predominates) (Fig. 1). In the region of studies there is a rather high abundance of rodents, for the most part *Rhombomys opimus* and *Spermophylopsis leptodactylus*. Both inhabited and abandoned colonies of *Rh. opimus* -- with their complex system of underground passages and location not farther than 150-200 meters from one another -- serve the monitors as refuges and hunting grounds.

Materials and Methods

Observations were conducted from 1990 to 1993 for periods of four to seven months annually. In all, observations were made for a duration of more than 20 months. In the beginning of April, the period in which monitor lizards come out of hibernation, they were caught, measured, weighed, marked, and released at the site of their capture -- usually in the course of a few hours after being caught. A special mark permitted us to identify the animals by their tracks (Tsellarius and Cherlin, 1991). Henceforth, for the greater part of the season of monitor lizard activity we conducted continuous observations of the animals -- following their tracks and observing them visually from camouflaged holes situated in the places where the appearance of monitors was most probable. In order to determine age, we amputated the last phalanx from one of the fingers of a number of the monitor lizards. The specimen was processed by E M. Smirina (Moscow) to whom we owe our sincere gratitude. The region of operations was regularly inspected and all points at which a tracks of the marked animals was apparent were plotted on a chart. As a result, we have at our disposal data on age, the location of home ranges, and the nature of the interrelations between the majority of the mature individuals settled in the region of operations.

Indirect exchange of information predominates in the population (Tsellarius and Men'shikov, 1994). The monitor lizards comparatively rarely enter into direct contacts. A possibility of observations of contacts is all the more rare. Therefore, in order to gather sufficient data, we provoked contacts. To this end, the monitor lizard was specially caught, usually in the morning hours. In the evening of that same day we attempted to establish from tracks the site where another monitor would spend the night. At dusk we released the monitor captured earlier into a nearby burrow. In the morning, as the monitors emerged from their overnight shelters, encounter was inevitable. It was only possible to perform these operations from time to time so as not to disturb the lizards and disrupt the normal course of their lives. In some instances discussed in this article, data from tracking was also used when it was possible to precisely and fully reconstruct the course of events from the tracks. During observations from hiding, detailed stenographic notes were taken which were deciphered immediately after observations were concluded. Some of the encounters were photographed (from 5 to 16 frames per encounter). Unfortunately, a lack of means prevented us from employing photographic documentation to the extent that was necessary. In all, we observed 37 instances of contact between males, 8 instances of contact between females, and 21 instances of contact between the sexes.

Results

The Spatial Structure of the Population and Annual Dynamics of Activity

Data pertaining to the spatial structure of the population is currently being readied for publication in a separate article. Here, however, it is only necessary to address a few words to this issue. The number of monitor lizards in the region of studies consisted on the average of four adult individuals per square kilometer. The monitors were, however, distributed over the space unevenly: areas of high concentration alternating with thinly populated areas. Areas in which populations were more densely concentrated (settlements) measure nearly 100-150 hectares. The distance between the centers of neighboring settlements ranges from 3-5 kilometers. Each settlement is formed from a group of adult settled individuals consisting of five to six males of various ages and three to four females. In each of two settlements which were under constant surveillance, only one female took part in reproduction. The rest of the females were not impregnated over the entire period of observations although they were in fact courted by the males. The home ranges of all of the animals in a settlement almost fully overlap each other. In the sparsely settled areas between settlements, home ranges may, to a varying degree, either overlap or be located at certain distance from one another. The home ranges of settled animals range from 30 to 200 hectares in size. From time to time, each of the males makes brief, distant excursions beyond the borders of his home range, during which time he may visit the territory of a neighboring settlement. It should be kept in mind that this is a simplified scheme. The real picture is complicated by the presence of stray and nomadic individuals among the settled ones, altering the make-up of the settlements and so forth. The area of a settlement amounts to a kind of "public property" for settled inhabitants of this settlement. It is not specially guarded. We did not observe any territorial behavior either between settlements or within them. The degree of unrest and aggressiveness during encounters with acquaintances was, however, incontrovertibly lower than during encounters with strangers (Tsellarius and Men'shikov 1994) and made the incorporation of newcomers into the settlement difficult. The majority of the animals mentioned in this article were members of one of two adjacent settlements which were under constant surveillance.

In the region of research the hibernation lasts approximately from the beginning of October to the beginning of April. During 1.5-2.0 months after emergence from hibernation, monitors widely travel within their home ranges and intensively forage. In this period the social activity of monitors is high enough: they readily enter into contacts with conspecifics and show great interest in their tracks, but males do not make any attempts to court the females in this period (Tsellarius and Men'shikov 1994). Mating period continues for a short time, it starts from the first days of June and comes to end till the twentieth of June. Females, which have taken part in mating, dig the nest burrows in the end of June or beginning of July, and diligently protect the clutch during 1-3 months after deposition (Tsellarius and Men'shikov 1995). Social activity of other animals rapidly decreases during 1-2 weeks after the end of mating period. Mobility and activity of the foraging of monitors (females with clutches excluded) also decrease. In the end of July the range, daily inspected by a monitor, is a third or quarter of daily range in May. In addition, in the second part of the summer lizards may, from time to time, spend several days in burrows without emerging to the surface.

The Most Ordinary Behavioral Acts of Desert Monitor

"Confident gait". The animal moves calmly, carrying his body high over the earth (Fig. 2). The monitor lizard holds his head and tail horizontally and sometimes the tip of the tail draws upon the earth while he is in motion. When the monitor examines any object with its tongue (e.g. tracks of other animals, burrow entrances and so forth), the lizard slightly lowers his head.

In ordinary conditions these behavior and body posture were observed during the most part of period of monitor's activity when for example the hunting monitor travels over familiar area. "Confident gait" may be generally characterized as a pose of routine activity. In this time the animal is in a state of psychological comfort. A conflict of motivations is absent or it is possible to realize through the behavioral pattern several motivations simultaneously (e.g. the search for food and a sexual partner in the course of search behavior). The physical state of the animal and its external circumstances do not pose obstacles to the fulfillment of the corresponding type of activity (Ovsyanikov and Badridze, 1989).

The "confident gait" was often observed in course of encounters between monitors (see section "Examples of behavior of monitors...", exs 1, 7; fig 14a). This gait probably testifies to the self-confidence and calm of the animal. His contactant evidently interprets it as a threat of attack or the possibility of such threat. In all directly observed instances the approach by "confident gait" provoked an unambiguous response. The approached animal manifests anxiety (see exs 7, 9 and Fig. 14, 16) or displays a peaceableness/submission (ex 1). The latter instances are rare.

Attack. When a monitor attacks a large prey he either immediately rushes on it, abruptly starting a sprint, or sneaks up to it before rushing from a distance of 3-5 m away. The sneaking up monitor walks with a rapid step, creeping along the ground, often uses shrubs and relief of the land as a cover. The act of lowering himself to the ground is also characteristic of the monitor that is avoiding danger (Fig. 3b). When sneaking up and when rushing the monitor holds his head and tail horizontally. During an ordinary hunt all observed actions were directly connected with prey-catching. Any special displays were absent. In general, posture of body of a monitor in assault is the same as in "confident gait".

Attacks on conspecifics were observed only in two situations: a) when a female protects her nest burrow (Tsellarius and Men'shikov 1995); b) when an animal with a lower social status rudely breaks the "rules of etiquette", suddenly appearing, for example, at a distance closer than individual distance (ex 4 and Fig. 12). In such circumstances the emotional state of the attacking monitor may be characterized as anger or rage. Any signals which are expressed through specialized postures and movements during an attack were not recorded. In 1992 we observed how a large monitor, considerably larger than the proprietress of the burrow, returned repeatedly over the course of a few days to the nesting burrow of the female that we had named Biteress and attempted to dig up the burrow in her absence (Tsellarius and Men'shikov 1995). The female, having found the arrival at work, drew close to him with quick dashes from shrub to shrub, slightly lowering herself to the ground, and lunged at him from a distance of 2-5 meters away. Biteress`s behavior was, down to the most minute details, similar to the behavior of a monitor stealing up to his prey. In all observed instances attacked animal immediately resorted to flight.

The "threatening gait". The lizard moves in the direction of an adversary at a slow pace. His tail may not touch the ground but may, on certain occasions, leave distinct imprints on both sides of his trail (giving the impression that the lizard is whipping his tail enroute). When walking the monitor "drags his feet", leaving distinct tracks in the sand from the dragging of his fingers and claws. We can say nothing more definite about this pose because it has been noted only in encounters whose course has been reestablished from tracks. The track of "threatening gait", however, is very distinct from all other tracks. The female leaves such a trail when she moves away from her nesting burrow in the direction of an approaching conspecific. Such trails have also been noted a few times on the part of the female who directed it at a male that is pursuing her. The "threatening gait" was recorded in encounters between males when individual distance was abruptly broken (ex 4, Fig. 12). In such a situation the threat was always displayed by animal with higher "social standing"[1]. In every instance, the animal to which the threat was addressed sharply changed the direction of his movement and in the majority of cases moved away from the site of events, sometimes taking flight. The lizards did not engage in direct contact.

"Threatening gait" and attack were recorded in very similar circumstances, sometimes "threatening gait" was followed by an attack. The state of the animal in "threatening gait" may be interpreted as anger rather closely linked to size, the duration of residence in a given settlement, and age.

"Sitting dog" posture. Monitor "sits down", lifting forepart of torso and head and looking around (Fig. 6). Very often animal assumes this pose when at great distance away is some disturbing object (observer, for example). "Sitting dog" posture probably is a classic orientation response. This reaction is formed with presence of weak fear (Hinde, 1970).

A monitor often raises his head during contact with subordinate individual when the latter assumes submission posture (exs.1, 3, 5 and Fig. 9). Therefore it may be possible that the "sitting dog" posture (Fig. 6) or very similar pose also has a trace of dominance in it. "Sitting dog" posture was observed in course of conflict between males, when both contactants manifested an unwillingness to yield (ex 9).

"Stooping"". The lizard slightly lowers his head, simultaneously inflating his throat and pressing his tail to the sand (Fig. 15a). This takes place during the encounter of an animal with an unknown object in a familiar area (e.g. a backpack, a shirt hung on a bush), in the event of a careless movement of the observer in hiding when the monitor lizard is not able to precisely identify the character and source of the movement, or during a direct encounter with another monitor that is unknown or whose intentions the animal is not in a position to determine, i.e. during an encounter with an irritant that attests not to an obvious danger but to the possibility of its beginning. In this circumstance the state of the animal may be characterized as a weak degree of fear, unease, lack of self-confidence. This state can even be unmistakably recognized in a lizard's tracks because his tail in these instances leaves a distinct, straight furrow in the sand (Tsellarius and Men'shikov 1994).

Zatir. If the unease is combined with strong excitation, the monitor presses his cloaca and the hind part of his abdomen to the sand and crawls, leaving behind a stripe of flattened sand (Fig. 5). This stripe serves as a signal mark which combines in itself visual and olfactory cues (Tsellarius and Men'shikov 1994). Formerly considering the marking behavior of monitors in a special article (Tsellarius and Men'shikov 1994) we termed this act as "dragging" and mark itself as the "drag". The term is an unfortunate one as it is being used for designation of another type of activity (Carpenter and Ferguson 1977). We propose to use the transliteration of the russian term "zatir".

"Showing of the back". A monitor flattens the torso dorsoventrally and incline laterally in the direction of opponent, showing the back, as it were (Fig. 11, 13d).

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[1] When speaking of the social status of an individual, we had in mind the "frequency of dominance". In other words, the more the monitors of a given settlement occupy a subordinate position in relation to a given individual, the higher his status. As one would expect, the social status of males turned out to be rather closely linked to size, the duration of residence in a given settlement, and age.

At this time the tail is lowered, but not pressed, to the ground and the throat may be slightly inflated. The monitor always orients himself laterally towards a threat. On certain occasions one may note a tendency of "arching of the back".

We observed "showing of the back" when the monitor encountered retaliatory aggression (active self-defense) on the part of prey and during the hesitant behavior of a human who neither attempted to capture the monitor nor made any sharp movements and yet did not leave the lizard alone. During intraspecific contacts the "showing of the back" was more often observed in situations when, on one hand, it may be suggested that the behavior of the conspecific excites apprehension of the monitor, on the other hand the motivation for present activity is rather strong and monitor refuses to take to flight. The emotional state in such situation may be characterized as alarm.

If another lizard both does not have self-confidence and does not disrupt the contact, the showing back monitor may fall into active self-defence (ex 8). If the opponent does not manifest any symptoms of fear and confidently goes on with approach, the monitor commonly takes to flight. We have never observed that attack or appeasement followed the "showing of the back". However, during contacts with human the "showing of the back" may fall into the "arching of the back". The latter may be followed by attack.

"Arching of the back". In this posture (Fig. 7a) a display of readiness for active self-defense (i.e. the monitor orients himself laterally towards his adversary, the tail is raised for a blow, and the head is turned in the direction of the danger) and elements of passive intimidation (i.e. the animal tries to appear larger than he actually is: the back is arched, the thorax is expanded, the body is raised upon erect front legs, and the throat is inflated) are combined.

Such posture is assumed by a monitor when the danger is serious and paths to retreat are cut off. "Arching of the back" is very common as a response to a threat on the part of human. In such contacts it sometimes follows the "showing of the back". We have never seen this posture in encounters between conspecifics.

If the human does not manifest hostile intentions, the animal slowly retreats (Fig. 7b). In the opposite case the monitor deals a blow with his tail and, after this, either takes flight (if a chance is given) or starts to make a lunge in the direction of the aggressor. When lunging the monitor turns to his adversary breaking the lateral orientation and strongly decreasing the displays of passive intimidation. In the rare cases an infuriated monitor may fall into attack. The state of the animal during "arching the back" is probably very similar to it in "showing the back" but the degree of fear is more high. A fear changes into anger and rage as a degree of threat increases.

"Gape". If the danger is very serious and unexpected, the monitor will display extreme readiness for self-defense: he opens his mouth wide (Fig. 8a) and lunges in the direction of his adversary. Evidently this display attests to an extreme degree of fear. When a monitor, which is sleeping near entrance of burrow, is being suddenly caught, he often convulsively moves his legs wide apart, and feverishly turns his head with opened mouth in all directions. At this time a "strength" of heartbeat is noticeably increased. The general picture shows strong resemblance to displays of intense fear in man and other mammals (Darwin, 1872; Deryabin, 1974).

The "gape" may be followed by an attack. The animal becomes enraged, the urge for flight is curbed, the monitor chases his adversary and, if he is successful in catching hold of the latter, can be very difficult to deter (Fig. 8b). "Gape" was observed only in encounters of monitors with human.

"Lurking". If during an encounter with danger the monitor thinks that he has gone unnoticed, he will conceal himself by lying down and pressing himself tightly to the ground (Fig. 3a). Furthermore, depending on the circumstances, the lizard will either remain prone or exit stealthily (Fig. 3b).

It is difficult to define the emotional state of a monitor in this situation. Some degree of fear takes place for certain. However, "lurking" is not an involuntary display of fear unlike such reactions as "arching of the back" or "gape". It should be kept in mind that absolutely identical posture is typical of the state of contentment (e.g. basking, resting of replete monitor in the shadow of bush and so forth). This thing should be taken into account when the behavior of a monitor in intraspecific contacts is being interpreted. It may be important for interpretation that in an encounter with danger the monitor's eyes remained open (in every instance of this that we were able to make out) and in state of contentment the lizard very often closes his eyes.

The "lurking" is customary in the social interactions of various species of lizards (Carpenter and Ferguson, 1977) and has traditionally been interpreted as a display of submission. Such behavior is a usual characteristic of the desert monitor also. The female often assumes this posture during the approach of an adult male (ex 1). In this case the "lurking" may truly be a display of submission, but we have never observed such a posture on the part of the subordinate in encounters of males. On the other hand, however, we have observed how it is assumed by the obviously larger and stronger animal in response to a female's or a smaller male's display of readiness for active self-defense (exs 2, 7 and Fig. 10, 14). We have never observed that "lurking" follows display of fear, unease or alarm during intraspecific contacts. The primary significance of this posture is probably not a display of subordinance as such but a display of a peaceableness. In general, recumbent postures are most characteristic of contacts of a "friendly" type (see below).

Flight. In encounters of a desert monitor with human or another large animal the monitor seldom falls into flight at the first moment. Usually a flight follows "showing of the back", "arching of the back" or "lurking". If a danger arises at a distance more than critical one (the latter is from 4 to 8 m) the animal will lurk as a rule. In opposite cases the animal usually manifests a readiness for active self-defence. In the case when human does not show aggressive intents, the lizard will slowly retreat either stealthily (Fig. 3b) or keeping the posture of readiness for self-defence (Fig. 7b) and falls into flight (if falls) only outside of opponent's sight. The flight is not accompanied by any special displays (Fig. 4).

During encounters between monitors in the majority of cases, a flight is probably an action of ritual nature. Very often flight taken place without any previous symptoms of fear (exs 5, 6 and Fig. 13). No matter how the interaction would turn, in every observed incidence of "sniffing", fighting, and ritual combat, flight on the part of one of the contactants inevitably terminated the contact regardless of the stage to which contact may have progressed. In the event of flight, the "conquered" generally retreated to a distance of 2-3 meters away, more rarely 10-15 meters, resuming his usual pace afterward, with the "victor" generally not displaying intention to pursue (exs 3, 5, 6, 8, 9). Exceptions to this rule are those cases in which one of the contactants immediately sets about an attack (ex 4 and Fig. 12). In this case as well, however, the attacker's rage and the retreatee's fear are certain only in the first moment of encounter. From that point on both flight and pursuit begin to increasingly take on the character of display (Fig. 12 and ex 4). It is symptomatic of this behavior that in not one of the observed incidences did the attacker catch up to his adversary.

Behavior Characteristic of Certain Types of Interrelations

Manifestations of dominance. We were able to closely observe the interrelations of some monitors for a length of 3-4 years. During these years we observed a stable asymmetry of behavior in all encounters between certain individuals. One monitor of two always (or in overwhelming majority of cases) displays relatively more anxiety in contacts with another and another's tracks. We regarded the first animal as a subordinant. Another lizard displays a self-confidence and was regarded as a dominant.

In the case of monitors, the behavioral syndrome of dominance is divided into two groups of "symptoms". On one hand there are distinctive features of behavior which are connected with the social status of an animal and which are manifest in many types of activity. These features are displayed from the first moment of interaction during direct contact between lizards. On other hand there is the "behavior of the victor" which is displayed only in agonistic contacts and only when the "correlation of forces" has been revealed.

The idea was formed that behavior of monitor during contact with conspecific is more strongly impressed by the social status of the animal (i.e. general experience and history of interrelations with conspecifics at all) than by concrete dominance and subordinance. The lizard with low status even during an encounter with his subordinant sometimes displays the most anxiety than high-ranking animal in contact with his dominant. On the whole, the behavior of a high-ranking animal is distinguished by self-confidence: the monitor rarely displays signs of unease or, rarer still, alarm. This is especially apparent in tracking studies (Tsellarius and Men'shikov 1994). Absolutely dominant in one of the settlements, the fourteen year old male named Vasya, boasting a snout-vent length of nearly 600 mm and a weight of 3.5 kg, did not display substantial alarm even upon encountering a human. In Vasya's case we did not observe postures of active self-defence (Fig. 7a) at all. As a rule, the monitor turned sideways towards the human encountering him, lowered his head, and slightly inflated his throat. The "showing of the back" was faintly expressed if expressed at all. In such a position the monitor first drew back a few steps and then moved away only at a slightly quickened pace, periodically sitting and looking back (Fig. 6).

It is highly probable that, during encounters between animals, behavior attesting to states of comfort are devoid of any expression of a conflict of motivations (exs 1, 7 and Fig. 14) and is in itself a display of high rank. We have observed such behavior primarily in males which have high social standing. Females may assume a submissive posture (ex 1) during such an approach by a male but low-ranking males display a great degree of alarm and often resort to flight. The specific "threatening gait" and lifting of the head are also apparently linked to high social status.

Observers of monitor behavior have described an absolutely unambiguous "victor's pose" that is assumed when the victorious monitor mounts the defeated one (Auffenberg, 1981a; Deraniyagala, 1958; Gaulke, 1989; Horn et al., 1994). A posture of this sort (e.g. topping, riding, straddling) is characteristic of many species of lacertilias and is displayed in the course of both agonistic and sexual interaction (Auffenberg, 1981a; 1983; Carpenter and Ferguson, 1977; Horn et al., 1994; Noble and Bradley, 1933). In the case of the desert monitor, we observed such posturing only during mating attempts but it is impossible to rule out its use as a "victor's pose" as well.

Within a certain context, it is possible that, when one of the contactants assumes the posture of submission, the act of licking the "defeated" plays the role of a "victor's pose" (ex 1). In opinion of Auffenberg (1981a), tongue licking in the case of *Varanus bengalensis* has a signaling function.

Displays of amicability. Informal contacts, founded upon personal attachments, are common to many species of animals and may play a substantial role in the formation of the social structure (Panov, 1983b). A similar sort of connection probably exists in the case of *Varanus komodensis* (Auffenberg, 1981b), *V. bengalensis* (Auffenberg, 1983), *V. rosenbergi* (Green and King 1993) and some other species. In the case of monitors, the basis for this connection probably lies in the habit of neighborhood as a familiar lizard evokes much less unease than a strange one (Tsellarius and Men'shikov, 1994). It may be possible that the personality traits of an animal are of significance as well. Mertens (1946) long ago noted the clearly expressed individual differences in character among monitors. According to our observations, in the case of the desert monitor, individual differences in the degree of excitability, aggressiveness, and the ability to alter behavioral patterns in changed circumstances may be very pronounced.

We only observed friendly contacts between settled monitors whose home ranges were broadly overlapping for a long period of time. The aggressive reaction of animals during such contact may be suppressed to such an extent that the female guarding her nesting burrow will allow another individual to visit it. For example, Mafiozi repeatedly visited the area of Docentess's nesting burrow and even spent the night with her in a single burrow (Tsellarius and Men'shikov 1995). It must be added that sexual contacts between these animals were not observed either that year or later.

Characteristic of friendly contacts are the absence or only very faint display of signs of unease on either individual's part and the mutual display of "submission" (exs 6, 10 and Fig. 17). During such contact the lizards never hold their bodies high over the ground, much as in normal movement or during the "threatening gait". The monitors lie down and either draw together with short, a few steps at a time, crossings or crawl across in each other's direction. Expressions of a peaceful nature do not, however, impede the proposition of ritual combat (exs 5, 6 and Fig. 13).

Common Ceremonies and Their Probable Function

We designate as a ceremony those interdependent actions which occur during contact between two or more individuals and are directed at the maintenance or establishment of certain social relations, and also the rules by which these actions are guided. The social status of the contactants, the dynamics of their motivational and emotional states, and the displays connected with them determine the course of the ceremony and its result for each of the participants but are not linked to the essence (goal) of the ceremony itself.

Mutual "sniffing". Mutual "sniffing" is an almost obligatory act in the encounter of two animals over a definite period of time. Exceptions may include those contacts connected with the protection of a nesting burrow and cases of sudden, involuntary violations of individual distance. In these situations one of the contactants may immediately resort to threat or attack, omitting the "sniffing" procedure. Only in early spring, immediately following the emergence from hibernation, and in the period when all regular activity ceases before hibernation, was the "sniffing" procedure rarely observed in encounters between animals. Monitors encountering one another often (albeit not always) did not engage in contact at all.

During "sniffing" the monitors usually first lick the snout of their conspecific, then his side, the sacrum region, and the base of the tail. Sometimes "sniffing" proceeds without displays of alarm or unease on the part of the contactants for the duration of the ceremony (exs 6, 10 and Fig. 17). More frequently, however, unease or alarm occurs. It is extremely common for animals to display alarm after mutual "sniffing" of the snout and to try to avoid being licked in the sacrum region. In these instances, the monitors "waltz": they circle, as if attempting to catch up with each other's tail (Fig. 13d, 15b). One or both of the animals always "shows the back". If the contactants begin to display alarm at the very start of contact, then they may immediately orient themselves not to the facial but to the sacrum region, which inevitably leads to "waltzing".

The motivation for "sniffing" is, apparently, quite strong. Animals frequently draw together and do not interrupt their contact until each contactant has licked the other, even when the other evokes in each a strong unease (ex 8).

The primary goal of "sniffing" is probably the receipt of certain information about a conspecific. Familiar animals are probably capable of recognizing each other by some external features. In every instance of contact between unacquainted individuals, however, sex and reproductive state were determined only by olfactory means (Tsellarius and Men'shikov 1994). Therefore, it may be possible that the urge to lick one's conspecific has as its basis the urge to receive information about the physiological status of the encountered individual.

Apart from this, however, mutual "sniffing" appears thereby to be a required ceremony in the course of which the social status and the personal interrelations of the contactants are determined (or confirmed). The analogous significance of the ceremony of "sniffing" has been well known for socialized species of carnivorous mammals, canids in particular (Schenkel, 1947; Lorenz 1969).

Fight. We designate as a fight that type of agonistic interaction in which: a) monitors enter into direct contact, b) measures are taken that can lead to the mutilation or death of the contactants, c) on both sides displays of anxiety and readiness for self-defence take place in the course of the interaction. Following Auffenberg (1981a) and other researchers, we treat blows of the tail as measures which can cause mutilation, although, strictly speaking, in the case of monitors they are a ritualized measure, a lesser one, in contrast to bites which are likely to inflict injury on an opponent.

In all, we observed three instances which may be qualify as fights, although with some stretching the point a bit. In each of the three instances unknown or unfamiliar males from various settlements entered into contact. Displays of alarm and unease were clearly expressed by both sides (ex 8, Fig. 15). Following the "sniffing", accompanied by the "showing of the back" and "waltzing", one of the animals, always the one which originally manifested alarm to the greater degree, dealt a blow with his tail which invariably put his adversary to flight. The larger male did not necessarily emerge victorious from the fight. Nor was the victor necessarily a resident of the settlement on whose territory the encounter took place.

The frequency of fights probably depends on a number of circumstances but first of all on the social structure of the population in a given area and at a given time. In other words, it depends on the predominance of a certain type of interrelation. The social structure is not an unchanging, species-specific feature. Although the interrelations between monitors in the region of studies from 1991 to 1993 may be characterized as highly peaceful, in the previous period these relations were, evidentally, of a rather different nature. The majority of monitors caught for marking in 1990, males and females alike, had fresh, deep scars or wounds located primarily in the sacrum region or on the shoulders, rarely on the side. These scars and wounds are reminiscent of the teeth tracks which are left when a monitor takes something in his "mortal grip". In 1991 wounds and fresh scars were a rarity, and from 1992-1993 were noted two times in all.

Ritual combat. Ritual combat is that type of agonistic interaction in which animals enter into direct contact but measures which could lead to the mutilation of an opponent are excluded. Until now, ritual combat in the case of the desert monitor has gone undocumented, although it has been described for many other species of this genus (Green and King 1993; Greer, 1989; Horn et al., 1994).

In every instance, ritual combat is preceded by the ceremony of "sniffing" (exs 5, 6 and Fig. 13). Combat may be broken off at the initiative of one of the participants at any moment and in the majority of cases this took place at the very first stage of combat, the "crossing of necks" (ex 6). We only observed one instance of all-out ritual combat (Fig. 13). Every instance of ritual combat or the attempt to propose it was noted only during contacts between animals from the same settlement.

Ritual combat was recorded only in the case of males. It may be possible, however, that such combat also takes place among females. At the end of June 1993, we observed the tracks of an encounter between two females from the same settlement, Frosya, five years old, and The Fourth, four years old. The trampled patch of sand that remained at the sight of their encounter was somewhat similar to those that are left after ritual combat between males. Frosya followed The Fourth's tracks for nearly 45 m to this patch. The females were obviously within each other's field of vision and both, probably, "showed their back" from time to time. From the trampled patch the females headed in different directions. Notably, The Fourth ran for nearly 17 m and Frosya moved at an easy pace. In the case of certain varanids, ritual combat has been noted between males, between females, and in contacts between the sexes (Auffenberg,1981a; Gaulke, 1989).

The significance of ritual combat for varanids is unclear (Greer, 1989; Horn et al., 1994) and attempts to link this type of interaction with the struggle for a specific resource (e.g. food, territory, females) have not been successful. In those cases where a few males are competing on account of a female, skirmishes have been observed but ritual combat did not take place (Carter, 1990). Encounters near sources of food may lead to a form of ritual combat but more often proceed otherwise (Auffenberg, 1981b; Gaulke, 1989). Territoriality for the majority of varanids, including the desert monitor, has not been established (Green and King, 1993; Greer, 1989; Tsellarius et al., 1991; Tsellarius, 1994). In the case of the desert monitor it is precisely these skirmishes which, stretching the point a bit, may be regarded as territorial (i.e. the encounter of a settled male with an unknown animal, a female's guarding of her nesting burrow) proceeding more in the form of a fight than ritualized interaction.

If we examine ritual combat in the case of varanids on the whole, then the impression is made that the essence of combat consists in the mutual attempt to knock over the opponent and assume the "victor's pose". The animal throws his front paw (or the front and the hind) over the back of his adversary and tries to stand up over him. This is quite apparent in both our photographs (Fig. 13) and in detailed descriptions of combat among different species of varanids (Auffenberg, 1981a; Davis et al., 1986; Deraniyagala, 1958; Gaulke, 1989; Horn et al., 1994). This grappling, the attempts of each opponent to attain the "victor's pose" while simultaneously trying to frustrate the other, is the essence of the combat. The struggle in a standing position on the hind legs evidentally developed as an attempt to occupy a more favorable position for toppling an adversary. It is significant that a struggle attained to the end has been finished by "victor's pose" (Deraniyagala, 1958; Horn et al., 1994).

If this is true, then ritual combat is most closely linked not with the fight for a specific object but with purely social interaction. Combat is a development of ritual behavior connected primarily with the display of dominance and is not a ritualization of the fight.

In the case of the desert monitor and some other varanids, all-out ritual combat is extremely rare in natural conditions. The reason for this probably lies in the fact that a certain combination of circumstances must be present for ritual combat to occur: uncertainty should exist in the interrelations between animals, their social status should be about equal, and dominance in relation to one another unestablished. In so doing, in the case of an obvious inequality in strength (i.e. in the majority of cases) the question of dominance is resolved by the process of "sniffing" and direct struggle to establish seniority is unnecessary.

In the conditions of a stable settlement, social rearrangements, taking into account the long life expectancy of monitors, are relatively rare: the animals know one another personally and the rank of each is known to all the rest. The need not only for combat but even for the sharp display of dominance rarely arises. In the event that the social structure is destabilized to the point that a large number of lizards appear that are not sufficiently well known to one another, the social rank of an animal is more likely to be established in a series of fights and the conditions for ritual combat rarely take shape.

Examples of Behavior of Monitors During Encounters with Conspecifics.

1. *The encounter of a settled male with a female from a neighboring settlement.* May 26, 1993. The Contactants: the male Mafiozi, six years old, SVL 475 mm, weight 1.3 kg; the female The Fourth[2], four years old, SVL 425 mm, weight 1.2 kg. Over the course of two years Mafiozi had encountered The Fourth's tracks but until this moment probably had had no direct contact with her, in this year in any case. The Fourth had been released the previous evening into a burrow located seven meters from Mafiozi's shelter that night and in the morning came to the surface later than he did. On the morning Mafiozi, lying near his burrow, spied the walking female, rose, and, without hesitation or displays of unease, headed for her. The female immediately lay down and Mafiozi, having reached her, licked her head and sacrum region. After this he moved off a few steps to the side, raised his head (Fig. 9) and lay down, turning away from The Fourth. Mafiozi twice more approached the female, with an interval of a few minutes between, and again licked her. Only after this did he move away. When the

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[2] All females mentioned in this section of article did not take part in reproduction for all period of investigations.

male had left. The Fourth, not rising, lifted her head but lowered it again as soon as Mafiozi turned towards her. After every lick of his tongue, Mafiozi lifted his head high and held it this way for some time.

2. *The encounter of an adult, nomadic male with a young, settled female.* May 14, 1991. The course of events was reestablished from tracks. The Contactants: the male Grigory, seven to eight years old, SVL 505 mm, weight 1.9 kg; the female Frosya, three years old, SVL 425 mm, weight 1.6 kg. Grigory hibernates in this region and in the summer appears here episodically, one or two times a month. Frosya has lived in this area permanently for at least two years. The monitors came into contact while circling a shrub from different sides (Fig. 10). Judging by the tracks, Frosya immediately turned sideways to the male and, probably, "showed her back". Grigory lay down at once. Having taken a few short steps in his direction, Frosya also lay down. After some time Frosya rose and, walking around the male, left in the same direction she had come before the encounter. Grigory followed her tracks for nearly 50 meters, leaving powerful "zatirs", and then also moved in the direction he had kept to before the encounter.

3. *The encounter of an adult, but never impregnated, settled female with a settled male.* May 22, 1993. The Contactants: the male Es the Ninth, eight years old, SVL 480 mm, weight 2 kg; the female Frosya, five years old, SVL 450 mm, weight 1.2 kg. The animals have belonged to the same settlement for no less than four years and are well acquainted with one another. In 1992, Es the Ninth persistently, but unsuccessfully, courted Frosya. Frosya encountered Es the Ninth on the morning when he was laying, half of his body sticking out of his burrow, and slowly headed for him, lowering her head and slightly inflating her throat. Es the Ninth, obviously disturbed, made a movement in her direction, stooping slightly. Frosya "showed her back" and began to move off sideways, not letting the male draw right up to her (Fig. 11). Then she ran a few meters away and the monitors froze. After a few seconds of immobility, the female slowly moved away, frequently looking back. Es the Ninth remained in place until she was hidden from view, watching her from behind in the "sitting dog" posture. Then he attentively licked her track, left a zatir, and also moved away.

4. *A skirmish of two settled males that resulted from the violation of individual distance.* June 26, 1991. The course of events was reestablished from tracks. The Contactants: Feodor, nearly 10 years old, SVL 550 mm, weight 3.0 kg; Mafiozi, 4 years old, SVL 430 mm, 1.5 kg. Feodor has the highest status among the males in the given settlement. The animals are members of the same settlement and knew one another well for not less than a year before the encounter. None of the conflicts between them before the one described below, or for a year and a half following it, have been noted. On the morning, Mafiozi, walking around a bush, literally stepped on Feodor, who was basking in the sun after emerging from his night shelter (Fig. 12). The latter jumped on him, apparently without warning, and Mafiozi jumped aside and took to flight. Evidentally, for the first 15-20 m the monitors ran as fast as they could. For the next 15 m the length of their step decreased. Feodor then shifted to a walk and followed Mafiozi for about 5 m by the "threatening gait". As soon as the young male also shifted to a walk, however, Feodor made a burst of speed, compelling Mafiozi to again take flight. The chase continued in this fashion for more than 200 m. Finally, having startled Mafiozi again in routine order, Feodor shifted to an easy pace and, sharply changing direction, went to one of the nearest colonies of *Rhombomys opimus* where he began to hunt. Events proceed in like manner when a female is chasing a monitor who has encroached upon her nesting burrow.

5. *Ritual combat between two settled males.* June 1, 1993. The Contactants: Mafiozi and Edik, both 6 years old, measure SVL 475 mm, and weigh 1.3 kg. The animals know each other well and have been members of the same settlement for at least four years. At the end of 1992, the leader of the settlement, the old male nicknamed Feodor, disappeared. Among the remaining males Mafiozi is one of the largest and most energetic. He is active over the entire space of the settlement and regularly goes far beyond its borders. Edik's primary region of activity lays on the northeastern edge of this settlement and he visits its central area only episodically. The encounter took place on the morning. The monitors spent the night in the same colony of *Rhombomys opimus* and emerged from their burrows almost simultaneously. It is highly probable that the animals had made contact in the burrow. The lizards lay for a few minutes near the exit from the burrows and then Mafiozi moved toward Edik who, in his turn, took a few steps in his direction. Meeting, the monitors lay down and, lying down, licked one another first on the snout and then on the side and sacrum (Fig. 13a). Next, they crossed their necks, each attempting to deflect the neck of his opponent to the side while simultaneously trying to seize with his paw the supporting foreleg of rival (Fig. 13b). Until this moment neither of the monitors had displayed any alarm or substantial unease. Then,

Mafiozi succeeded in budging his opponent (Fig. 13c) and the monitors began to "waltz" (Fig. 13d) at which time Edik (left) "showed his back", displaying obvious alarm. At some moment the monitors were side to side and their heads were directed in the same way. Mafiozi immediately threw his front paw over Edik's shoulders. The latter did the exact same thing at once. The lizards made attempts to overturn each other, slipping their heads under their opponent's neck. One time that Mafiozi succeeded in doing this, the monitors rolled over on their backs and ended up in their previous position. The lizards gradually shifted to the "face to face" position (Fig. 13e) and, continuing the struggle, began to rise on their hindlegs. Having assumed a vertical position and closed their front paws on each other's backs (Fig. 13f), the males continued their vigorous attempts to topple their opponent. The males fell down together a few times, breaking their grip in the process (Fig. 13g), but immediately jumped up and seized one another anew. The entire skirmish was conducted very energetically and the positions of the opponents changed rapidly. Edik suddenly ran to the side for 3-4 m and the monitors watched one another motionlessly for nearly 30 seconds. Edik then slowly moved away, describing a zigzag and frequently looking back. Mafiozi, remaining in place, watched him from behind, raising his head. The entire struggle, from the moment the adversaries crossed necks, lasted no longer than two minutes. The entire encounter, from the moment the monitors emerged from their burrows, lasted 14 minutes.

6. *Encounter and ritual combat between two settled males.* June 2, 1993. The Contactants: Rhombik, 5 years old, SVL 445 mm, weight 1.2 kg. Mafiozi is older and larger (see ex 5 for his description). The monitors belong to the same settlement and have known each other well since at least 1991. On the evening of June 1, 1993, without our interference, the monitors spent the night in the same colony of *Rhombomys opimus* which that day, in the morning, a young female from a neighboring settlement, The Fourth, had repeatedly visited. Emerging from their burrows the next morning, the monitors lay for a long time near each other, basking in the sun and yawning in turn. Their behavior was not unlike the usual behavior of monitor that have emerged from his night shelters. After approximately 30 minutes the animals crawled together and the procedure of mutual "sniffing" lasted for nearly 10 minutes. It was not accompanied by any apparent displays of unease. Mafiozi then crossed necks with Rhombik and attempted to press him to the ground. Rhombik very calmly freed himself, ran a few meters off, switched to an easy pace, and left. Mafiozi licked his tracks and went off in a different direction.

7. *The encounter between a settled male and a nomad.* May 24, 1993. The Contactants: Alitet, 5 years old, SVL 470 mm, weight 1.4 kg; Shot Glass, 10-11 years old, SVL 560 mm, weight 1.8 kg. Alitet is a settled resident of the settlement on whose territory the encounter took place. Shot Glas has spent the winter within the borders of this settlement for at least three years but about a month after coming out of hibernation goes far east and appears here only episodically, for two to three days, until the end of the season of activity. As far as we know, these monitors had not had direct contact this year, although they regularly came across one another's tracks. The encounter took place on the morning. The monitors saw each other practically simultaneously, at a distance of nearly 15 meters, and froze motionless for some time. Then, Shot Glass decisively headed toward Alitet (Fig. 14a) who, having allowed him to approach within 1.5-2.0 m, inflated his throat and "showed his back". Shot Glass immediately lay down (Fig. 14b) and Alitet, stepping slowly, walked around the recumbent monitor from the side and, looking back from time to time, went away. About a minute later, Shot Glass rose and, pressing his tail to the ground, licked Alitet's tracks (Fig. 14c), left a zatir, and followed the trail of his conspecific. Having followed the tracks for nearly 34 m, he "sniffed" Alitet's excrement and peacefully went away, sharply changed direction.

8. *An encounter between two unfamiliar males which ended in a fight.* May 31, 1993. The Contactants: The Tip, 6-7 years old, SVL 460 mm, weight 1.4 kg; Dusty, 12 years old, 590 mm, weight 2.2 kg. The Tip is a settled resident of the settlement on whose territory the encounter took place. For at least three years, Dusty has spent the winter near the borders of this settlement but immediately after coming out of hibernation has traveled to places located several kilometers to the southeast. In 1993 he remained in the region of hibernation for the summer for the first time. The encounter took place early in the day. Having noticed The Tip at a distance of about eight meters, Dusty lay for a few seconds and then headed for The Tip who immediately turned sideways to him. The Tip displayed greater and greater alarm as Dusty approached and the "showing of the back" became more and more apparent (15a). Dusty's lowered head, inflated throat, and tail pressed to the ground appear threatening but actually attest to his unease and lack of self-confidence. After the mutual "sniffing" of the snout, Dusty attempted to "sniff" The Tip's sacrum but the latter

drew back, "showing his back" (15b). As a result, the monitors described a few circles in place. Suddenly, The Tip dealt a blow of his tail and Dusty quickly scurried aside. Having moved about six meters away, he stopped and the monitors watched each other for some time. Then Dusty slowly moved away, barely looking back. After one or two minutes The Tip also left, not even having been interested by his opponent's tracks.

9. *An encounter between two unfamiliar males.* June 18, 1993. The Contactants: The Tip, 6-7 years old; C-59, approximately the same age as The Tip but a bit larger, his SVL is 480 mm and he weighs 1.5 kg. C-59's home range is situated in a zone little settled by monitors between two settlements located far from one another. Hence, he periodically makes excursions far beyond the borders of his range. The previous evening C-59 was released into a burrow not far from The Tip's night shelter in almost the center of the latter's settlement. C-59 was caught nearly a day before this. Over the previous three and a half years he had appeared in the given region not more than two or three times. Emerging from his night shelter in the early morning, C-59 walked for some time about the colony of *Rhombomys opimus* and, finding the burrow where The Tip had spent the night, hid in it. About 10 minutes later the monitor again appeared on the surface from a different opening, having traveled nearly three meters underground. Emerging from the burrow, C-59 looked around, licked the sand, yawned, and, having moved a few meters away, lay under a bush, head raised. The Tip emerged from his own burrow a few minutes later and headed confidently for C-59 who remained in the very same posture but kept an eye on The Tip, turning his head to follow the latter's movements. The Tip made a circle, having drawn close to C-59 who at that moment rose halfway, inflated his throat, and "showed his back" (Fig. 16a). Later, The Tip made yet another circle and again returned to C-59. Both monitors assumed the "sitting dog" posture (Fig. 16b) and remained motionless for some time, located at a distance of about two meters from one another. Then The Tip again began to make a circle, at the same time inspecting the burrows of *Rh. opimus* as if not noticing the newcomer. When he came near to C-59 the latter jumped up and turned in his direction, having lowered his head, inflated his throat, and flattened his trunk dorsoventrally. The Tip did the same and the monitors simultaneously lunged at one another. Each having struck the sacrum of his opponent with his nose, and each "showing his back" (Fig. 16c), they made a full revolution after which The Tip jumped aside, ran 9-10 meters off, shifted to a walk and after 25-30 m entered a burrow of *Rh. opimus.* C-59 immediately assumed a normal position and, once The Tip was hidden from view, walked about the site of the encounter, inspecting burrows, and then peacefully went away.

10. *A friendly encounter between an old male and a young male.* May 12, 1993. The Contactants: Chuck Norris, not less than 10 years old, SVL 520 mm, weight 1.8 kg; Egghead, 4 years old, 425 mm, weight 1.2 kg. The home ranges of both monitors broadly overlap but lay beyond the boundaries of the region where regular observations were conducted and their status and the history of their interrelations is unknown. Having caught sight of each other, both monitors lay down and for a long time crawled around each other, "sniffing" their partner's snout, side, and base of the tail, displaying virtually no signs of unease. From time to time the animals would break off their activity and for 10-15 minutes lie near to each other, occasionally closing their eyes (Fig. 17). After this the "sniffing" was resumed. At the end of the encounter the young male began to make "zatirs" (signal marks), crawling across Chuck's back and neck in doing so, after which he left. The old male immediately entered a burrow. Contact lasted for 47 minutes in all.

Discussion

On a certain stage of investigation of social structure of population the researcher will inevitably clash with necessity of a studying of mechanisms of the social reciprocal influences, that is the problem of intraspecific communication.

In classic ethology the concept of animal communication is based on the three postulates: a) it is proposed that behavioral acts, that carry socially important information, must be rather exotic, in order that a perceiving animal will be able to correctly single a communicative signal out of series of non communicative, routine behavioral acts; b) a communicative act must be very stereotyped, in order that a monosemantic interpretation will be provided; c) a set of responses to certain act must be strictly limited to provide its adequacy and coordination of interactions. Thus, a communicative system is being considered as the system of discrete, ritualized behavioral acts with fixed significance (Hinde,1970; MacFarland, 1985). A process of communication is being regarded as the stereotyped succession of acts, which is founded on either innate or learned automatism of responding.

These three principles are formulated by Tinbergen and his followers in course of investigations of behavior of invertebrate animals, pisces and aves. It should be noted that behavior connected with reproduction (courtship, mating, parental care) was mainly examined. This behavior is directed at the reaching of limited set of strictly specific aims. An investigations of "everyday" social behavior (especially in mammals) led to accumulation of facts which poorly harmonize with basic principles (for survey see Panov, 1983a). Evidently, it should be admitted that development of communication on the base of other principles or on the base of several principles simultaneously is possible.

A contradistinction of exotic behavioral acts of the desert monitor and non-exotic ones is very relative and quite useless both for ascertaining of communicative significance of these acts and for analysis of their forming and origin. In the point of view of a researcher, who observes the monitors during all periods of their activity, the "confident gait" is an element of common, routine behavior, and the "showing of the back" is a bright, exotic posture. But in monitor's point of view the "showing of the back" or "stooping" are far more usual acts than "confident gait", since monitor observed his conspecifics during contacts only. Only the monitor's "point of view" is important for formation and evolution of his communicative system. A coincidence of researcher's and monitor's "points" about exoticness of the posture should be possible only in the case if a monitor would be aware of his behavior and identify his own behavior with that of a conspecific. As far as we can judge by behavior of monitors during contacts, all features of behavior ,exotic and non-exotic, are equally important for communication.

A large majority of behavioral acts of desert monitors may be expressed in varying degrees: they may be very distinctive or hardly noticeable. Many different acts may smoothly turn one into another. Some signaling elements of behavior, inflating of the throat for example, take part in many displays, which have distinctly different significance. It was noticed in many species (Auffenberg,1981a; Panov and Zykova, 1986; Hikida, 1989) and, evidently, it is not an exception, but a rule.

The data from our observations conforms poorly to the widespread perception of lizards as animals that display relatively primitive behavior based upon simple stereotypical reactions. A behavior of the monitor during encounter with conspecific is definitely not an automatic response to the behavior of partner. Behavior is conditioned by many circumstances, among them the most important ones are such interdependent factors as a) initial emotional state of contactants; b) a history of interrelations of given animals; c) a social status of animal, i.e. personal experience of previous intercourse with conspecifics.

When a problem of decoding of any system of signals arises, it should be useful to formulate a supposition of what a kind of information is transmitted by this system. It should be quite correct to use an analysis of nonverbal communication of our own species for solution of this problem. A majority of nonverbal behavioral signals of Man carry information about the emotional and/or motivational state of an individual. Direct information about the intents of an individual or his external circumstances is not contained in the majority of behavioral acts. Nonverbal behavioral signals carry information about circumstances and/or the intentions of given individual so far as a particular external circumstance frequently provokes a particular emotional state and this emotional state is, in a particular situation, a base of a particular action. A human's response to behavioral signal may be very diverse and depends upon the situation, his emotional state and his personal experience. It is evident that communicative systems of other mammals is organized in a similar way (Schenkel, 1947; Ladygyna-Kots, 1958; Lorenz, 1969). We have not any reasons to expect some things of a fundamentally different nature in other higher vertebrates.

It is strictly imagined that the majority of behavioral acts of the desert monitor clearly reflect the emotional state of an animal and are in this regard perfectly unambiguous. But displays of even diametrically opposed states may contain identical behavioral elements. In addition, the intensity of every emotional state may be various and, accordingly, the intensity of display may be various too. Emotional states are not discrete and, between them, there exist an entire gamut of transitions. It concerns the manifestation of these states also.

It seems to us that, without an understanding of the dynamics of the motivational and emotional states of animals engaged in social interaction, a correct interpretation of the course of these interactions and their result is often complicated or altogether impossible.

A human perceives the behavior of a conspecific as a stream of integrated mental pictures. Separate elementary behavioral acts, as a rule, are not perceived individually. This stream of nonverbal signals first of all influence the emotional state of the perceiver, and do not act upon behavior immediately. Adjustment of behavior is being realized by indirect way through a change of subjective feeling of situation and emotional estimation of it. It is quite probable that the mechanism of the animal's perception of conspecific's behavior is the same. If this suggestion is right, we arrive at a picture of nonverbal communication as a "process of tuning each of communicants into the behavior of its partner" (Panov, 1983a). A mechanism of this tuning is influence of animals the emotional and motivational state of each other through the exchange of information about the alteration of these states. Communication of this sort asks for analogy to our own highly developed systems of nonverbal communication, such as music, dance, etc.

During many decades amidst ethologists it was considering as an indisputable tenet that animal's subjective feelings (including emotions) are unable to be subject of scientific analysis. Actually it meant that existence of subjective feelings in animals is denied since a veto upon the use of this idea for explanation of mechanisms of behavior was imposed. But till now no one succeeded in creating a general theory of behavior within the bounds of behavioral approach.

Psychologists and neurophysiologists, having looked at the matter the other way round, propose a concept of evolution of the psyche of vertebrate animals and influence of psyche on their behavior. This concept well conforms to facts (Anokhin, 1968; Delgado, 1969; Shepherd, 1987; Vartanyan and Petrov, 1989). Using a concept of emotion, one generally managed to obtain the harmonic, economical explanation of observed behavior. Suppositions were warily declared that not only emotions, but also the higher kinds of psychological processes, those are termed a "mind" in respect to Man, are characteristic of animals (Gallup, 1985; MacFarland, 1985; Sevastyanov, 1989). The existence of emotions is not called to question in respect to mammals with a developed brain. The analogy of basic and some secondary emotions of Man and other mammals is not refused also. But in respect to reptiles, a use of the concept of emotion is unusual for the majority of zoologists. However, if we denied the existence of a sharp border between the psyche of Man and that of other mammals, we find ourselves before the necessity to seriously warrant a placing of such boundary-line in any other case.

Emotions are an internal regulator of psychological activity and behavior, and are a universal measure of values that have a great adaptive importance. Under the shortage of prognostic information or absence of possibility of processing of it the emotional estimate of situation allows one to quickly find one's bearings and to make one's choice (Anokhin ,1968; Simonov, 1970). Probably emotions are a very ancient mechanism of estimating the influence of internal and external irritants, which developed long before arising of new cortex. Morphological and neurophysiological ground for forming of emotions probably arose as long ago as the anamnia arose (MacLean, 1949; Dethier and Stellar 1967). A presence of afferent tone is the indispensable component of conditioning reaction, without it a forming of feedback mechanism is impossible (Wiener, 1958).

Essential resemblance of the behavior of lizards and mammals (MacLean, 1978; Regal, 1978; Tsellarius and Men'shikov 1994), unstereotyped course of interactions, universality and non-discrete nature of the majority of lizard's signals (Auffenberg, 1981a; 1981b; 1983; Carpenter and Ferguson 1977; Gaulk, 1989; Panov and Zykova, 1986), rather high ability for education (Brattstrom, 1978; Krushinsky, 1977) make quite permissible the supposition that reptiles have rather developed forms of psychological activity.

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Appendix I

Figures 1-17

Figure 1. Landscape of the region of operations. (photo by Yu. G. Men`shikov)

Figure 2. The carriage of a peacefully moving monitor. (photo by A.Yu.Tsellarius)

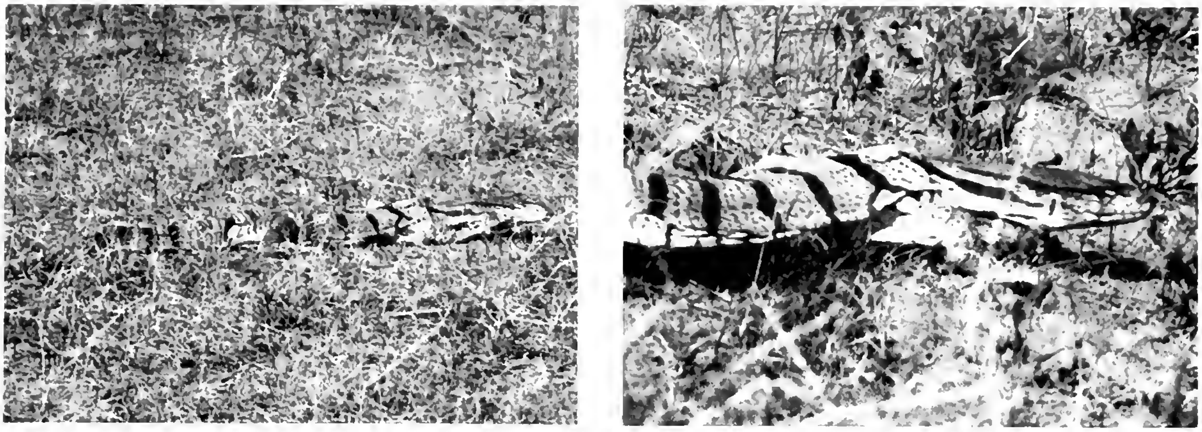

Figure 3. Concealing himself, the monitor presses his body tightly to the ground (3a, above left) and remains motionless. The animal's eyes remained open in every instance of this that we were able to make out. Convinced that he has not been noticed, the monitor moves away from the site of the encounter after a short time, creeping along the ground such that his elbows and knees frequently rise higher than the level of his back (3b, above right). The animal moving away from the observer in this fashion uses shrubs and elements of relief so skillfully as cover

Figure 4. The carriage of the monitor in flight. The animal is fleeing the observer. (photo by Yu. G. Men`shikov)

Figure 5. The male drags his body along the ground, flattening the substratum in his wake (signaling marks, below transliterated from the Russian as "zatirs") in the area which a female from his settlement (The Fourth) and males from a neighboring settlement (Rhombik and Mafiozi) had visited not long before. This took place on June 5, 1993 in a region where the borders of neighboring settlements touch and animals from both settlements visit. (photo by A.Yu.Tsellarius)

Figure 6. The "sitting dog" posture. When the monitor is moving away from a site where he had encountered danger, the more frequent display of the reference reaction "What's going on?" is quite apparent. The lizard periodically -- sometimes every few steps -- sharply "falls" on his rear, raises his head and the frontal section of his body on erect forelegs, and looks around. (photo by A.Yu.Tsellarius)

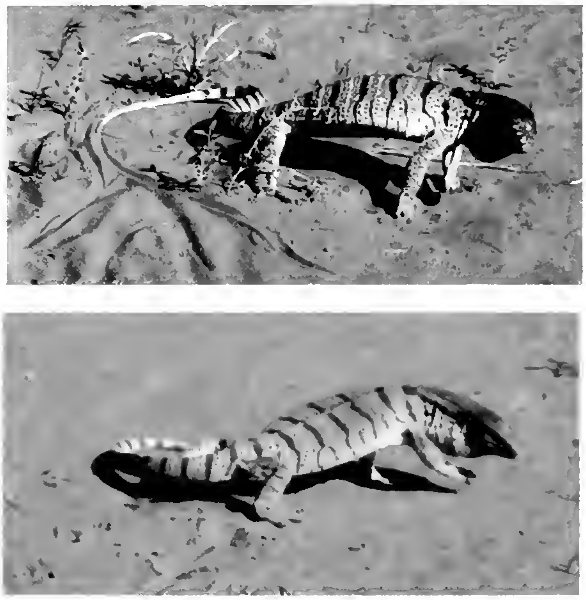

Figure 7. The display of readiness for active self-defense characteristic of the monitor lizard facing a threat from a human or another large animal (7a, at left, top). If an opponent does not start an active operations the monitor, continuing the display of readiness for defence, slowly retreats (7b, at left, bottom). (photo by A.Yu.Tsellarius)

Figure 8. Finding himself in an unavoidable position, the monitor opens his mouth widely in the direction of the danger (8a, above left). An attack very frequently follows this and the monitor seizes his enemy in a "mortal grip" (8b, above right). (photo by A.Yu.Tsellarius)

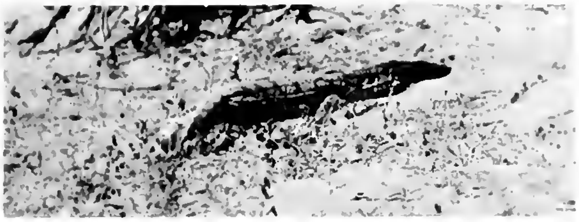

Figure 9. The male lifts a head moving away from the female which assumes the posture of submission (for detail see description of encounter in section "Examples of behavior...", ex 1). (photo by A.Yu.Tsellarius)

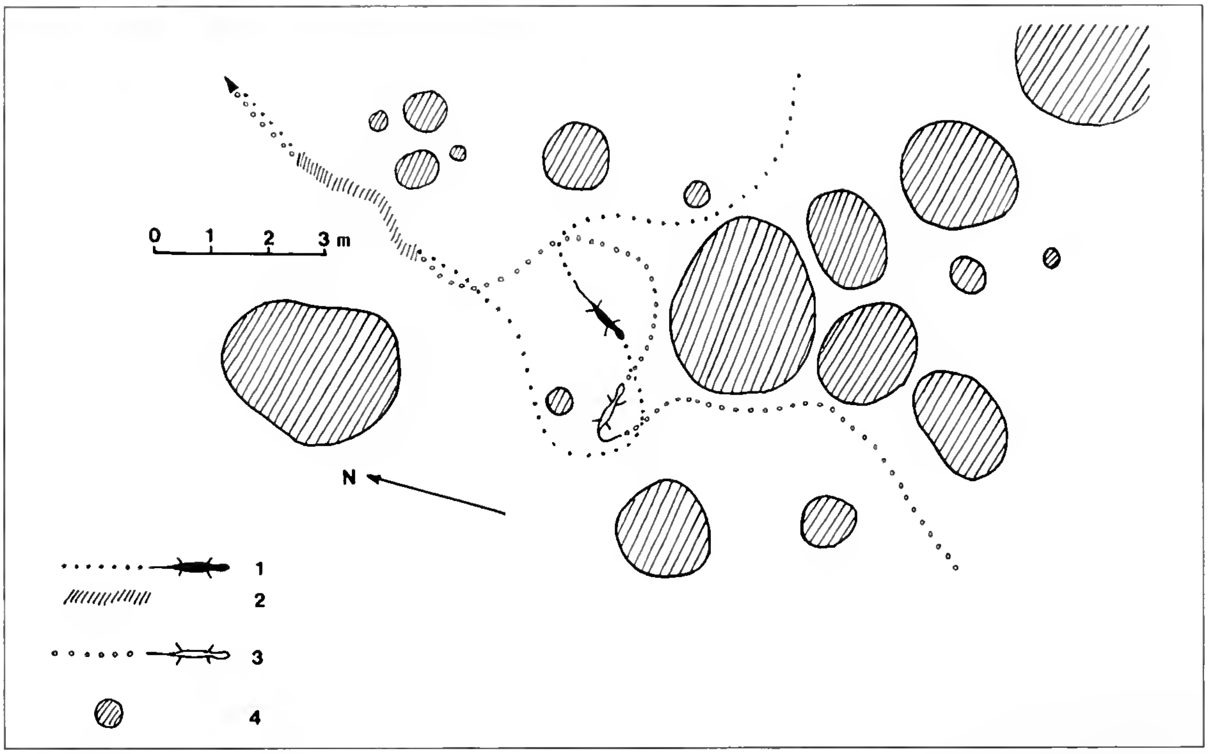

Figure 10. Diagram of trails of encounter between male and female (for detail see ex 2). 1 - male's trail and place of lying; 2 - zatir of mail; 3 - female's trail and place of lying, 4 - shrub.

Figure 11. Female "shows the back" to familiar male which goes out of burrow (see ex 3). (photo by A.Yu.Tsellarius)

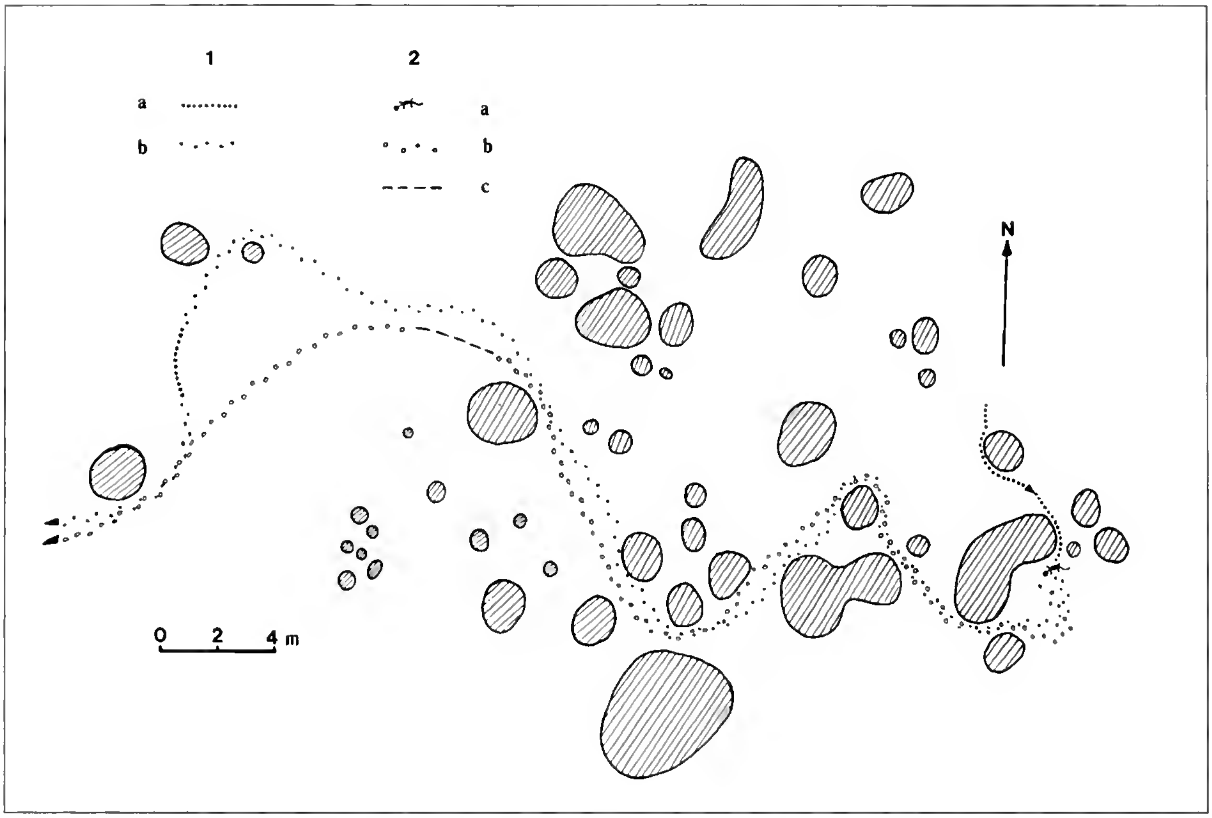

Figure 12. Diagram of trails of encounter between two males (see ex 4). 1 - trail of young male (a - the step, b - the run); 2 - trail of old male (a - place of basking, b - the run, c - "threatening gait").

Figure 13a

Figure 13b

Figure 13c

Figure 13d

Figure 13e

Figure 13f

Figure 13g

Figure 13 (a-g). Ritual combat between males (for detail see ex 5). a - mutual "sniffing'; b, c - wrestling by necks; d - "waltz" with "showing of the backs"; e - transition to standing position on the hind legs; f - wrestling in vertical position; g - loss of equilibrium. (photo by A.Yu.Tsellarius)

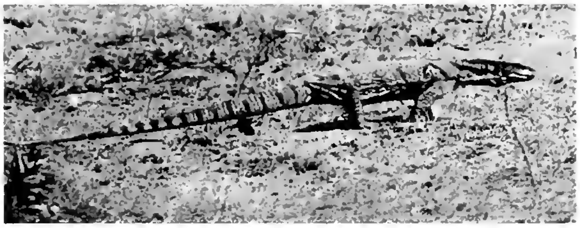

Figure 14a

Figure 14b

Figure 14c

Figure 14. The encounter of a settled male with a nomad (see ex 7). a - the nomad heads for the settler by "confident gait"; b - the nomad assumed a posture of appeasement; c - the nomad "sniffs" the track of the settler. (photo by A.Yu.Tsellarius)

Figure 15a

Figure 15b

Figure 15. The encounter of a settled male with a new settler (see ex 8). a - stooping new settler approaches to the "host"; b - new settler (above right) attempts to "sniff" the sacrum of "host". (photo by A.Yu.Tsellarius)

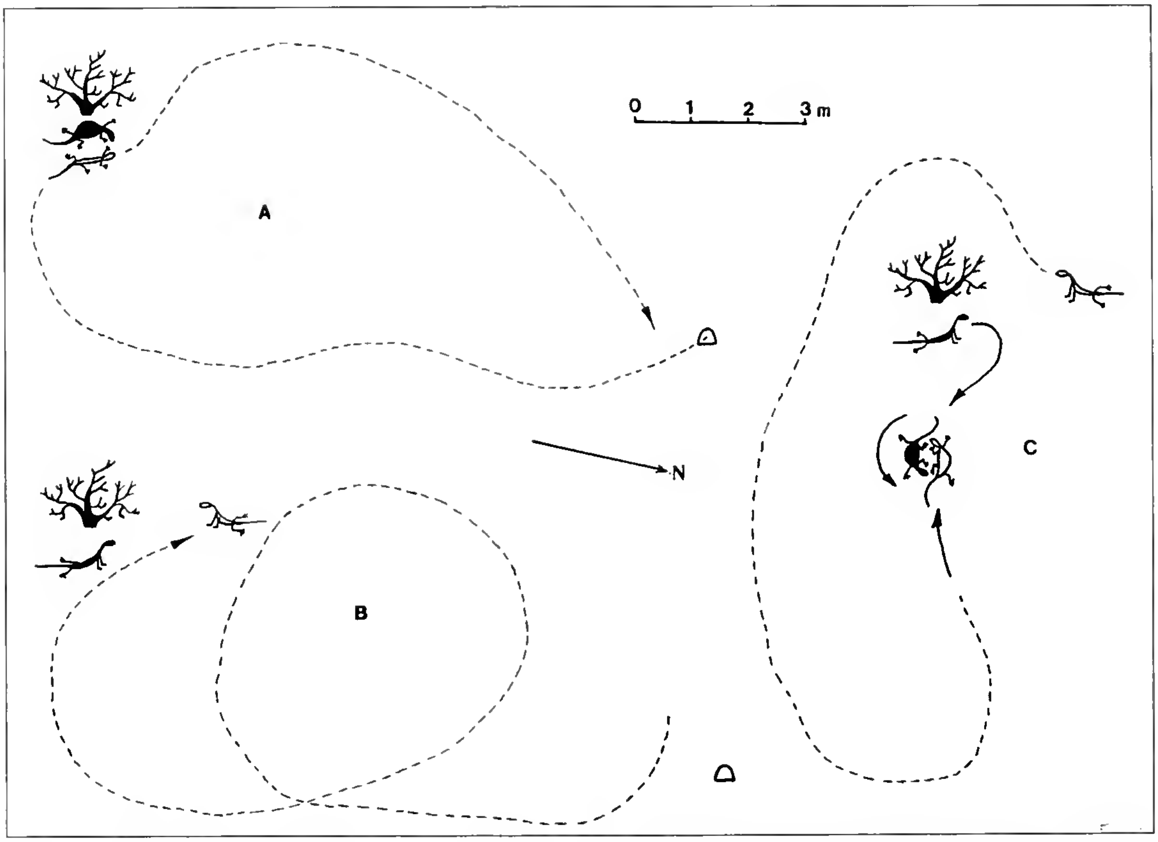

Figure 16. Diagram of encounter between two unfamiliar males (see ex 9). A, B, C - the succession of events. The resident is designated by light figure, the stranger by black.

Figure 17. Mutual amicable "sniffing" of an old male (left) and a young male (for detail see ex 10). (photo by A.Yu.Tsellarius)

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On the Distribution of *Coluber ravergieri* and *Coluber nummifer* in Turkmenistan and the Possible Evolutionary Reasons for their Polymorphism

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Abstract.- In Turkmenistan, *Coluber ravergieri* is found in mesic environments. This species was encountered in mountainous habitats, where there are springs, streams, and small rivers. Along large, permanent rivers that flow into the desert this species penetrates the desert zone. *C. nummifer* is more xerophilous and can tolerate temporary drying-up of riparian habitat, but in Turkmenistan, *C. nummifer* is not found in waterless regions as are typical desert snakes. It has been suggested that the polymorphism found in these two species may be due to mimicry with poisonous snakes. We believe that environmental background matching is the primary function of the coloration in these species and mimicry may only be considered a secondary explanation.

Key words: Reptilia, Squamata, Colubridae, *Coluber ravergieri*, *C. nummifer*, Turkmenistan, polymorphism.

Introduction

Two closely related species of snakes, *Coluber ravergieri* Menetries, 1832 and *Coluber nummifer* Reuss, 1834, were studied in Turkmenistan in Central Asia. The distribution of these snakes after their division (Schätti and Agasian, 1985) in general is known, but however the questions of polymorphisms within the species is of interest. The presence of partial and complete melanism in some individuals of the *ravergieri-nummifer* complex in the Central Asian region raises a special interest. The finding of a specimen similar to the so-called Glazunov's mountain racer (*Coluber ravergieri* morpha *glazunovi*) in the Eastern Kopetdag Mountains and the additional information on the distribution of both species in Turkmenistan serve as a basis for the this paper.

Methods and Materials

Approximately 30 specimens were collected from 1989-1993 throughout Turkmenistan. Scale characters were analyzed on 18 specimens; some of them are kept in the collection of the Institute of Zoology of the Turkmenian Academy of Sciences (IZT), and in the collection of the Caucasian State Biosphere Reserve (CSR), other animals were returned to nature. The characters examined included the number of scales around the middle of the body (Sq.), the number of ventral (Ventr.) and subcaudal (S.cd.) scales as well as gender, coloration and scalation of the head and body. Analysis also included habitat characteristics especially the availability of water and arboreal or shrub vegetation.

Results

Coluber ravergieri was found throughout the Kopetdag region from the Chandyr River Valley in the Kyurendag Mountains in the southwest to the Chaacha River in the east (Fig. 1) and in Badkhyz in the far east of Turkmenistan in the Kizilayak district on the Amu Darya River. Throughout the species range in Turkmenistan, we noted black-headed forms and specimens with the typical contrasting coloration as well as snakes that were only gray in color (Fig. 2-3). It is of special interest that a melanistic specimen was found in the Eastern Kopetdag (IZT, number free, Manysh settlement, Eastern Kopetdag, 04-06-1984, Coll.Ch.Atayev). This large female had a body length (L.) of 730 mm, a tail length (L.cd.) of 225 mm and 21 rows of scales around the middle of the body (Sq.), 199 belly scales (Ventr.), 87+1 ventral tail scales (S.cd.), and 9 upper labial scales (Lab.) on each side of the head. The coloration of the body on the upper side is dark-brown-black (Fig. 4). In side light, there's seen a darker contrasting coloration, typical for *C. ravergieri*. In the front one third of the body, there are 8 transverse light yellow stripes. Separate light-colored scales are present on the dorsal side of the anterior half of the body. The snake is a deep black color from below. On the laryngeal part of the belly there are yellow spots and separate light spots are on ventral scales to scale #47 inclusive (figs. 5-7). Situated very

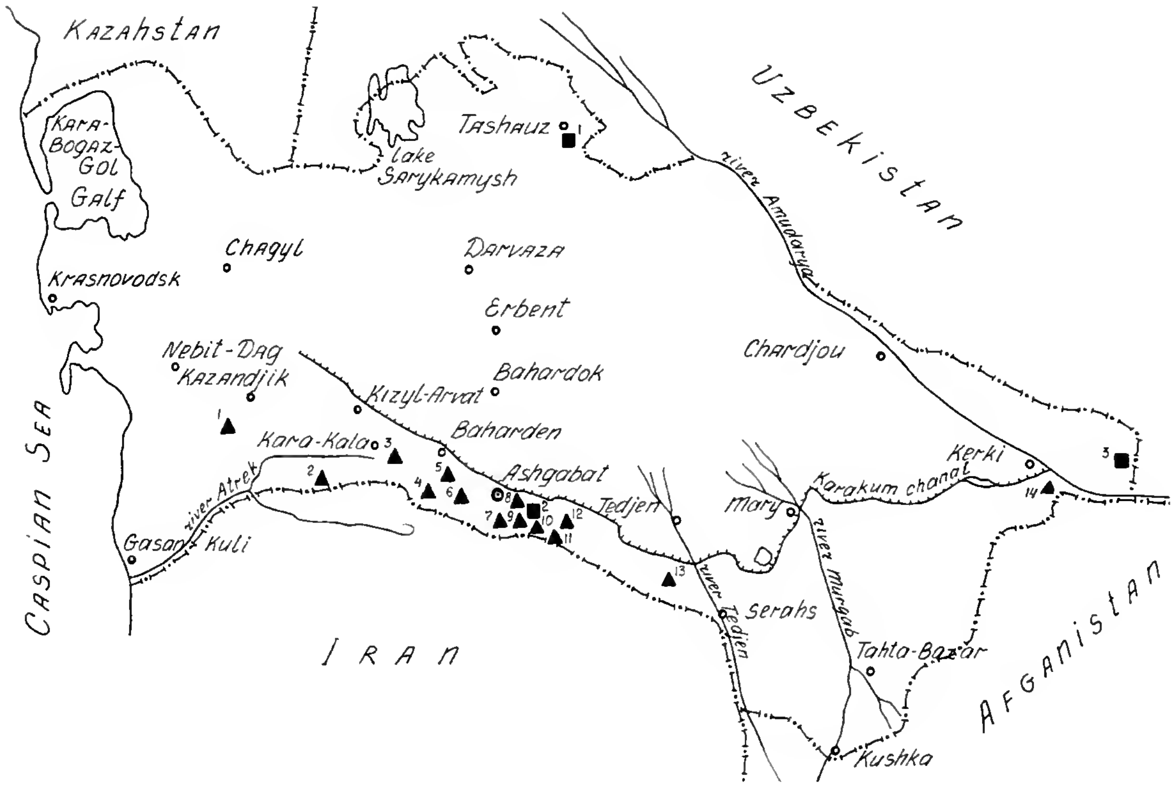

Figure 1. The distribution of *Coluber ravergieri* and *Coluber nummifer* in Turkmenistan: 1. *C. ravergieri*; 2. *C. nummifer*. Coluber ravergieri: 1. Danata Village, Kyurendag Ridge (IZT, Coll. Atayev); 2. Ack Village,Chandyr River, Southwestern Kopetdag Mountains (IZT, 10.10.1990; Coll. Atayev); 3. Sayvan Village, Western Kopetdag (IZT, 10.10.1990; Coll. Atayev and CBR, No. 450-452.05.1992; Coll. Tuniyev); 4. Tretiy Birleshik Village, vicinity of Geoktepe settlement (IZT, 03.10.1966; Coll. Atayev); 6. Phiryuza Canyon, Central Kopetdag (IZT, Coll. Atayev); 7. Keltechinar River (IZT, Coll. Atayev); Gamy Village (IZT, 1977; Coll. Atayev); 8. Anau Village (IZT, 27.09.1970; Coll. Atayev); 9. Yablonevka Village (Khomustenko, 1985); 10. Manysh Village, Eastern Kopetdag (IZT, 04.06.1984; Coll. Atayev); 11. Kharchinnan River, Eastern Kopetdag; 12. Laensuv River, Khiveabad Village; 13. Chaacha River (CBR, No. 447-448, 04.1992. Coll. Tuniyev); 14. Khatab Village, Kizilayak region (IZT, 03.05.1977. Coll. Atayev).

Coluber nummifer: 1. Tashauz, Tahtynsky region (IZT, 1970, Coll. Annayev); 2. Keltechinar River (IZT, Coll. Atayev); 3. Kugitang Mountains, Svintzovy Rudnik (IZT, 1981, Coll. Zakharova).

near to Eastern Kopetdag. The presence of melanistic forms of *C. ravergieri* in the Eastern Kopetdag and the western part of Pamiro Alaj underlines the faunistic originality of this sector of Kopetdag mountains.

The polymorphism of the species *C. ravergieri-nummifer* complex is of evolutionary interest and has become a classical example of Batesian mimicry in the literature. The similarity to Viperids was described for different parts of distribution. Lantz (1916) noted the likeness of young *Zamenis ravergieri* coloration with that of adders. In spite of this, Lantz underlines that the behavioral mimicry in young *C. ravergieri* is persistent and when in danger instead of fleeing they coil up in a spiral, thickening neck and especially the back side of the head, hiss for a long time, furiously attacking. Werner (1983) points out the similarity of *C. nummifer* and *Vipera palaestina* in Israel. Schätti and Agasian (1985) describe the mimicry of *C. ravergieri* and *C. nummifer* with *Vipera lebetina, V. palaestina, V. xanthina* and with *Agkistrodon halys intermedius*. The presence of black-headed specimens in Central Asian connect it with *Boiga trigonatum* (*melanocephala*) and *Naja naja* dwelling there.

In fact, we noted the similarity of these mountain racers with adder snakes in some regions of the former Soviet Union. In Armenia, in the Khosrov Reserve male of *C. ravergieri* were observed with zig zag dorsal patterns similar to *Vipera raddei*. In Razdan Canyon near Erevan (the village of Zovuni), we observed *C. nummifer* similar in appearance to

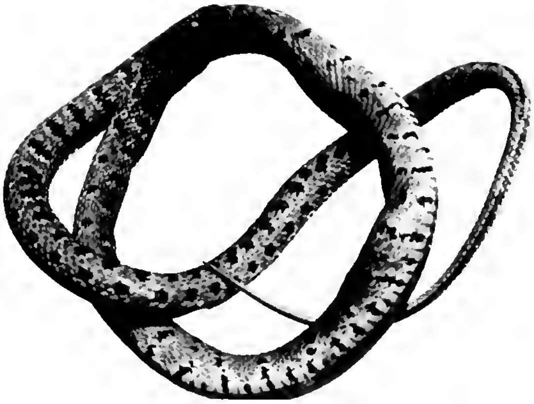

Figure 2. A blackheaded specimen of Coluber ravergieri with a contrasting coloration of the body (IZT, Keltechinar River, 1990; Coll. Atayev).

Figure 3. An uniform grey specimen of C. ravergieri with an unclear picture of the back side of the body and tail (IZT, village Sayvan, 1990; Coll. Atayev)

Figure 4. A melanistic specimen of *C. ravergieri* (IZT, Eastern Kopetdag, village Manysh, 04.06.1984; Coll. Atayev): general view from above.

Figure 5. A melanistic specimen of *C. ravergieri* (IZT, Manysh Village): general view from below.

Figure 6. The head and anterior part of the body of melanistic specimen of *C. ravergieri* from above (IZT, Manysh Village).

Figure 7. The head and the anterior part of the body of C. ravergieri, melanistic specimen from below (IZT, Manysh Village).

Figure 8. A young specimen of *Coluber nummifer* (IZT, Kugitang Mountains, 1981; Coll. Zakharova).

subadult *V. lebetina obtusa*, and this similarity extended to this species behavioral threat response. In Central Asian, young *C. nummifer* (Fig. 8) look like young *V. lebetina* (*turanica/chernovi*), but *C. ravergieri* may be only remotely similar to *Boiga trigonatum melanocephala*.

The problems of snake mimicry, including *C. ravergieri-nummifer*, have been considered by Werner (1983a, 1983b, 1984, 1986). Beside the likeness in coloration, Werner discusses the matters of behavior, triangular shape of the head of Colubrid snakes in Israel, postulating Batesian or Mullerian mimicry. The similarity of *C. nummifer* and *C. ravergieri* with venomous snakes in Central Asia is intriguing, especially if the ranges of the models and mimics are considered. Werner's (1983b) explanation that the evolution of protective coloration by all snakes in the area is a precursor to mimicry applies here. Earlier Lantz proposed (1916) that reptiles tend to match dominant environmental color. Sweet (1985) in analyzing the possible Batesian mimicry in *Pituophis melanoleucus* and *Crotalus viridis*, pointed out that phenotypic similarity in these two species may be a result of cryptic adaptation and not selection for mimicry or only additive because the importance of mimicry varies geographically.

In fact, the diurnal snakes of Turkmenistan (excluding the burrowing species or the species with limited surface activity; *Typhlops*, *Eryx*, *Eirenis*) are remarkably similar in appearance as are the nocturnal species similar to each other. The diurnal snakes (*Vipera lebetina*, *Coluber ravergieri*, *C. nummifer*, *Agkistrodon halis caucasicus*) distributed in the mountains and foothills are of gray to brown, rusty colors with black or dark-brown elements forming spots or a zig zag pattern. In more mesic areas of the mountains (mainly in the upper elevations), snakes are bright with contrasting colors, and in dry, bare foothills they are monochrome generally the color of burnt soil.

The nocturnal species (*Echis multisquamatus*, *Boiga trigonatum*, *Spalerosophis diadema*, *Lythorhynchus ridgewayi*) are characterized by contrasting coloration or with transverse light (almost white) stripes located in an irregular manner. The latter resembles burnt grass or brush and twigs, typical habitat where these snakes occur. The nocturnal species tend to be slow and sluggish in behavior.

We observed the triangular head shape described by Werner in *V. Lebetina* and *Naja oxiana* as well as other venomous snakes which we have observed in nature (Vipera *kaznakovi*, *V. dinniki*, *V. ursinii*, *V. aspis*, and *Agkistrodon halis*). When threatened these venomous snakes first try to hide and then take a defensive position characteristic for this species only if it is necessary. We can noted similar behavior for Colubrid snakes independent of coloration. We observed the triangular head shape character in Turkmenistan in 20 specimens of *C. rhodorhachis* not taking into account whether they were red-stripe animals (*forma typica*) or cross-banded snakes (*forma ladacensis*). We also observed triangular head shape in *C. karelini*, *C. atayevi*, *Boiga trigonatum*, and *Spalerosophis diadema*.

Triangular head shape, coiling, hissing and striking as well as protective coloration are the mechanisms for avoiding predation. However, in specialized snake predators such as *Circaëtus gallicus* attack is stimulated by the snake form, irrespective of the coloration and the shape of the head. One pair of *C. gallicus* on the Badkhyz Reserve eats about 1800 *V. lebetina* in one summer (pers. comm. L. Simakin).

In the case of the *C. ravergieri-nummifer* complex polymorphism (and other colubrid species of Turkmenistan) we believe that environmental background matching is the primary function of this coloration for diurnal snakes. And mimicry may only be considered as a secondary explanation. The presence of melanistic specimens of *C. ravergieri* in the mountains of Pamiro Alaj and the Eastern Kopetdag may be related to adaptive thermoregulation and these higher, cooler locations. The black-headedness of *C. ravergieri* in the Central Asia may be interpreted as a rudimentary state of ancestral melanistic coloration and it can also carry a more subtle physiological meaning as for example being a sensing element of daily and seasonal temperature changes. The black-headedness can increase the role of pineal complex as a sensing element of solar radiation (Ralph et al, 1979) and in controlling the thermoregulatory behavior. It was also noted that the head of black-headed forms of *C. ravergieri* emerging of holes were difficult to see in the shadow of the hole.

Appendix I

Physical and pholidotic characters of Coluber ravergieri from Turkmenistan.

Location	Ventr.	S.cd.	Sq.	Sex	Specimen location
Khatab Village, Amu Darya River	217	90	21	M	IZT
Anau Village, Eastern Kopetdag	201	92	21	M	IZT
Keltechinar River, Eastern Kopetdag	198	92	21	M	IZT
Keltechinar River, Eastern Kopetdag	198	88	21	M	IZT
Ack Village, Western Kopetdag	192	87	21	M	CBR, N 453
Sayvan Village, Western Kopetdag	200	89	21	M	CBR, N 450
Turkmenistan	201.1 (192-217)	89.7 (87-92)	21	MM	Our data
Turkmenistan	198.8 (194-206)	88.0 (86-90)	21	MM	Schätti & Agasian, 1985
Keltechinar River, Eastern Kopetdag	212	84	21	F	
Keltechinar River, Eastern Kopetdag	221	84	21	F	
Chaacha River, Eastern Kopetdag	208	84	21	F	CBR, N 447
Chaacha River, Eastern Kopetdag	217	84	21	F	CBR, N 448
Chandyr River, Western Kopetdag	199	90	21	F	CBR, N 449
Sayvan Village, Western Kopetdag	206	72	21	F	CBR, N 451
Western Kopetdag, Sayvan village	203	81	21	F	CBR, N 452
Turkmenistan	209.4 (199-221)	82.7 (72-90)	21	FF	Our data
Turkmenistan	211.0 (207-216)	84.5 (82-87)	21	FF	Schätti & Ahasian, 1985

Appendix II

Scale characters of Coluber nummifer from Turkmenistan

Location	Ventr.	S. cd.	Sq.	Sex	Specimen location
Kugitang, Svintsovyi rudnik	208	102	23 (17)	M	IZT
Tashauz	210	94	23 (15)	M	IZT
E. Kopetdag, Keltchinar R.	205	90	23 (17)	M	Our data
Turkmenistan	207.7 (205-210)	95.3 (90-102)	23 (15) 17	MM	Our data
Turkmenistan	205.6 (200-211)	98.0 (93-103)	23 (17) 15	MM	Schätti & Agasian, 1985
Kugitang	217	96	23 (17)	F	IZT
Central Kopetdag	216	98	23 (17)	F	IZT
Turkmenistan	215.3 (214-217)	100.0 (97-103)	23 (17) 15	FF	Schätti & Agasian, 1985

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Anomalies of Gonads in *Bufo viridis* from Uzbekistan

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Abstract.- Collected material of *Bufo viridis* inhabiting the Ferghana Valley, the city of Tashkent, Tashkent and Dzhizak regions of Uzbekistan in 1971, 1972, and 1992-1993 has revealed cases of hermaphroditism (0.8%) and anomalies (7.4%) in the gonads of male toads from areas with different levels of urbanization.

Key words: Amphibia, Anura, Bufonidae, Ranidae, *Bufo viridis*, *Rana ridibunda*, Uzbekistan, gonads, hermaphroditism.

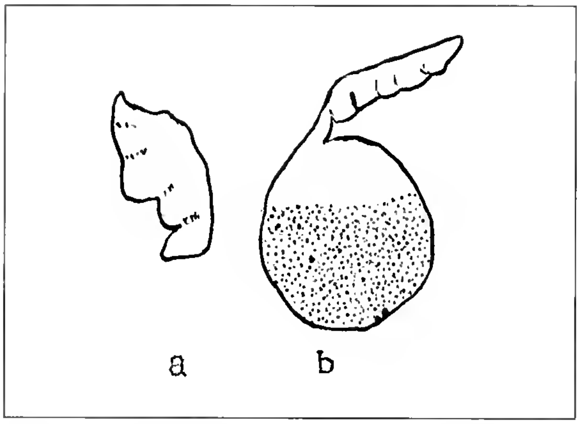

Figure 1. Underdeveloped ovary (a) and testis (b) in a hermaphrodite *Bufo viridis*.

Introduction

There is not much evidence in the literature, at least in the former USSR, of cases of hermaphroditism and anomalies in the inner organs of reptiles and amphibians. Terentyev (1950) reported the anomalies of the gonads in various frog species, which were recorded by other researchers. Yakovleva (1964) observed a combination of male and female sexual organs in *Vipera ursini* from the vicinity of the city of Frunze (currently Bishkek), Kyrgyzstan. Brushko (1968) and Radzhabov (1975(described cases of hermaphroditism in *Elaphe dione* and anomalies of the gonads in *Coluber ravergieri* and *Elaphe Dione*.

During the whole period of collection of the material on the ecology of tailless amphibians in Uzbekistan (1971-1995), the authors recorded the individuals of *Bufo viridis* showing anomalies in their gonads.

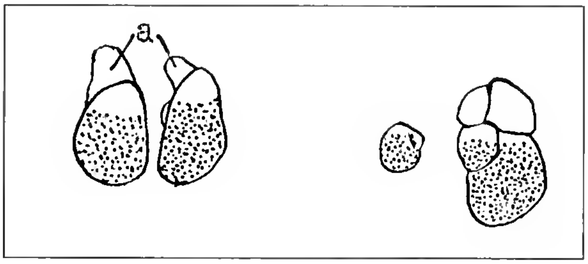

Figure 2. Normal testes (left) and lobular testes (right) of the male *Bufo viridis* (a- appendage).

Materials and Methods

The material was collected in the Ferghana Valley (vicinity of the village Yangikishlak, the foot of Mount Karatash, Lake Aidarkul), Tashkent region (stow Aksakata, the villages Urta-aul and Yangi-Bazar) and in the city of Tashkent, in the span from 1992-1995. The gonads (241 males) were measured (length x width, mm) and weighed (mg). The index of gonads was then calculated as a ratio of the gonad weight to body weight. If some anomalies were observed, the testes were drawn or photographed.

Results and Discussion

While collecting the material, we encountered two individuals of *Bufo viridis* that had testes at one side and underdeveloped ovaries and oviduct at the other (Fig. 1). The testes were well developed, with a high relative index (4.7 and 3.6%).

The testes of the toads are normally oval or spheric, slightly compressed in the direction "back-abdomen" (Fig. 2). Their lower part is often pigmented. There is a small appendix in the upper part.

The anomalies in the testes constituted 7.4% and concerned mainly those in the integrity of the latter

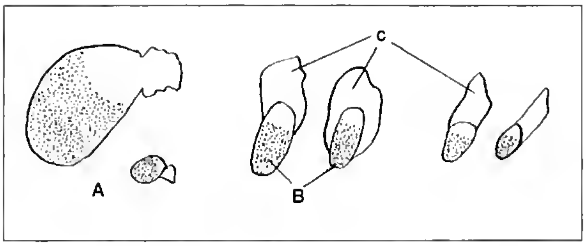

Figure 3. The ratio of the testes (a), testes (b), and appendages (c).

(Fig. 2), when one or both testes consisted of 2-4 in the lobes. In the collection of 1971, there was and individual whose both testes consisted of the lobes: the right lobe measuring 3x2.5; 3x2; 3.5x2.5 mm and the left one 3x2.5; 5x3 mm. The individuals that constituted 4.5% showed gonads significantly different in size (Fig. 3), one testis being bigger than the other (10x5.1 and 4.5x3; 12.5x3 and 7x3.5mm, etc.). In 0.8% of the cases the individuals had only one testis, relatively well developed (9x7 mm and 9x6 mm), and which well corresponded in weight and indices to the testes of the animals with the same sizes. So, two testes of a male, whose body length reached 68.5 mm, weighed 134 mg, and a single testis of a male measuring 67 mm was 176 mg. Besides, there were individuals whose gonad appendices were equal to or bigger than the gonad itself (Fig. 3). So, the length of the right testis was 8 mm and its appendix 7 mm. The length of the left testis was 6.5 mm and its appendix 6 mm.

Noteworthy, similar anomalies of the gonads have been recorded for *Rana ridibunda* from the Ferghana Valley as one testis of an individual was bigger than the other (8.5x4.5 mm and 4.5x2.5 mm); another individual's left testis consisted of three lobes (3x2; 2x1.5; 2x1 mm) and the right one measured 7x4 mm. Besides, the testes of another individual were unusually knobby and consisted of 5-8 lobes.

While analyzing the material collected from different areas, our attention was drawn to the fact that anomalous changes in the male gonads were characteristic of those individuals inhabiting areas with different levels of urbanization of their habitats.

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Egg Components and Utilization During Incubation in the Turtle, *Chinemys reevesii*

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Abstract. -The energy content, water content and ratios of egg components in the turtle, *Chinemys reevesii*, were determined during 0-55 days of incubation. The total water content of the egg took 65% of egg mass on preincubation and increased 5.66% during incubation time. The total water content of the egg on preincubation was found 60.7% in the yolk, 35% in the albumen and 4.3% in the shell. The ratios of those varied with the embryonic age (days) growth, and the greater portion the water in the egg had transferred to the embryonic tissues on 55 days of incubation when the water content of the embryo was 50.4% of the egg total water content. The dried mass of shell, yolk and albumen on preincubation were 35.3%, 61.0% and 3.1% of the egg dry mass, respectively. The component materials of those, except for a major portion of the remained shell, were transferred into the embryonic tissues with the incubation days as the total transferred rate was 79.3%, and the cost rate for 20.7%. The lipid content in dried yolk averaged 20.4% of the yolk's dried mass during incubation. The energy content of the yolk, albumen and embryo were relatively stable through the incubation period and averaged 6462.5, 5087.7 and 6291.4 cal/g, respectively.

Key words: Turtles, Chinemys reevesii, egg components, energy content, Incubation.

Introduction

Oviparous reptiles characteristically allocate the majority of their total reproductive investment to their eggs (Fischer et al., 1991). The eggs of the turtle, *Chinemys reevesii*, reflect the total reproductive investment in the offspring by females. This post-hatching yolk is the source of energy for the survival and growth of the hatchlings in some reptiles during the first days of life (Kraemer and Bennett, 1981; Congdon et al., 1983a, 1983b; Troyer, 1987; Wang et al., 1990, 1995). The component materials and energy in the turtle egg are first utilized for embryonic development and, secondarily, for hatchling maintenance after it leaves the egg. However, the utilability rates of the component materials, such as the shell, albumen and yolk of the *Chinemys reevesii* egg for embryonic development at the different stages of incubation are not clear. How many component materials of the egg are allocated and which are necessary for the embryonic development and hatchling? So far, only limited data are available on changes of the shell, albumen and yolk rations in the egg during the different stages of the incubation for reptiles.

In this paper, we report some component (albumen, yolk and shell) ratios and energy values in freshly laid egg of the turtles, *Chinemys reevesii*, and also the changes of the component ratios during the different stages of incubation.

Materials and Methods

One hundred eggs of the common turtle, *Chinemys reevesii*, were collected in the morning after the oviposition of the females in June 1987 and 1988 at a turtle farm near East China Normal University in Shanghai, China. Each egg was removed from the nest on the day of laying, marked and weighed with a torsion balance (±0.01 mg). Ten fresh eggs were used for the standard (normal) level of the egg component materials and the energy content. The remaining 90 eggs were incubated in an environmental temperature of 28±0.05° on a water-saturated substrate (sand), and the inside of the incubation chamber was periodically misted with water. Those hatching eggs were used for some analyses of the ratios of the component materials and the energy content during the different stages of incubation (Tables 1-6).

When the eggs for assay were cracked, the embryo, yolk, albumen and shell were carefully separated and each one was separately placed in a pre-weighed glass container and then weighed. The embryo was separated from the yolk and both were freed from the surrounding choriallantoic and viteline tissue, and then blotted dry and weighed. The albumen was cleaned away from the shell membranes, and the shell was rinsed with distilled water and blotted dry and weighed. The samples were then dried to a constant mass in an oven at 60°C. All the weighings were accurate to the nearest milligram. All of the dried materials were stored in a desiccator until assayed.

Water content was calculated as the difference in the net wet and dry mass of the egg materials. The energy contents of the dry embryo, yolk and albumen were then measured. Triplicates of each individual sample were assayed by combustion to determine the energy content with the microbamb calorimeter (JR-2000 type made in China) and benzoic acid standards. The results were corrected for free ash energy content.

The lipid content of the yolk was removed with petroleum ether from an aliquot off the dry yolk mass in a soxhlet extractor; each length of the extractive time lasted 5 hours. The amount of lipid was determined by subtracting the mass of the sample after extraction from the sample mass before extraction. The sample weighings were accurate to the nearest milligram.

Results

The changes of the egg components of *Chinemys reevesii* at the different incubation times are shown in Tables 1, 2 and 3.

Eggshell. During day zero of incubation, the fresh mass of the eggshell was 14.6% of the fresh egg (Table 1) and the dried mass of the eggshell was 35.3% of the dried egg (Table 2). The values of the shell declined as the time of incubation increased, and exhibited an age phase of incubation (Tables 1 and 2).

Yolk Content and Incubation Time. During the first days of incubation, the yolk contents took the majority of the egg components (Tables 1 and 2). But, those contents declined as the incubation time increased. When the hatchlings left their eggshells, the remaining yolk was only about 6-9% of the fresh yolk mass on the zero day of incubation.

Albumen Contents. The fresh albumen contents (%) of the egg were higher after than before 20 days of incubation (Table 1). But, dried albumen (%) of the egg mass expressed relative stability (Table 2).

Embryonic Mass. From 0-10 days of incubation. the embryos had not been determined because of a little tissue of each embryo. We found that the embryonic wet and dry mass of *Chinemys reevesii* increased with the time (days) of incubation (Tables 1 and 2). The recently emerged hatchlings averaged 4.8 g (SD=0.78, N=10) or 79.31% (SD=2.4) of the total content in the egg mass compared with day zero of incubation, so that, the rate of the material transferred to the tissues of the embryos was 79.31% (SD=2.4) and the rate of cost was 20.69% (SD=2.39).

Water Content in Eggs. The water content in eggs was determined by subtracting the dried mass from the fresh mass of the egg, and the results are shown in Table 3.

During 0 day of incubation, the water content of each egg averaged 65% (SD=6.3, N=10). The rates of those after 20 days of incubation raised with the incubation days slightly increased (Table 3) as the mean growth rate my reach 9.2% until 55 days of incubation.

The water content of the shell averages 16.1% (SD=1.3, N=76) throughout the incubation period. The water in the yolk on 0 day of incubation was 65.5% (SD=7.8, N=10), but the value of that declined as the incubation time increased (Table 3). The water in the embryos also declined as the incubation time increased. But, the water in the albumen kept in a range of 95.3-97.3% on 0-55 days of incubation (Table 3).

Lipid Content in Yolk. Table 4 shows that the lipid content (%) in the dried yolk on the first periods of incubation reduced slightly, and then, increased with the incubation time did as raised to 26.51% on 55 days on incubation.

Energy Values of Egg Contents. The energy values (cal/g) of the yolk, albumen and embryo throughout incubation time are shown in Table 5.

The caloric values (free-ash) of the wet-yolk increased with the incubation days and those data are fitted into the following equation: for wet yolk, cal/g=2356.52±31.43 days, r=0.9745, $P<0.01$. But, the caloric values (free-ash) of the dried yolk stabilized relatively in the range of 6343.9-6609.8 cal/g.

The caloric values of the embryonic mass also increased with the incubation time (Table 5) as the relation between caloric values (Y) and days (X) of incubation expressed a positive linear regression correlation for $Y=1306.32+97.44X$, $r=0.9820$, $P<0.01$. The caloric values of dried embryonic mass were stabilized in the range of 6257.7-6337.7 cal/g (free-ash).

The albumen energy values are the lowest among components of the egg (Table 5). Such as the total mean energy values of wet albumen is 204.8 cal/g and dried albumen is 5087.7 cal/g throughout the period of incubation, but only equal to 5.95% of wet and 76.7% of dried yolk energy, respectively.

Discussion

Type and Mass of Eggshell

The types of eggshell in the turtles were classified to be both fundamental patterns of the rigid-shell (or brittle-shelled) and the flexible-shelled; in the former, the shell mass take above 30% of the whole egg dried mass and below 21% of one in the latter (Congdon and Gibbons, 1985). The dried mass of shells averaged 35.3% of the total dried mass of eggs in *Chinemys reevesii* and should be classified as a type of rigid eggshell, and the mass of that is approximate to 36.44% of *Gopherus polyphemus* eggshell mass and is lower by 4-8% than those of *Kinosternon subrubrum, K. coloratus* and *Clemmys marmorata* (Congdon and Gibbons, 1985).

The shell mass in the egg in *Chinemys reevesii* declined as the incubation days increased (Table 1 and 2), declining a total of 37.8% in fresh eggshell and 6.2% in the dried mass of eggshell with a part of calcium in the eggshell that was possibly transferred into the developing embryo. We have determined the contents of calcium and magnesium in whole egg (Table 6) for tested the above hypothesis. The results (Table 6) show that (1) the calcium and magnesium contents were less in posthatching eggshells than in preincubation ones; (2) the calcium and magnesium contents of the egg contents (yolk and albumen) only equaled 45.93% and 87.74% of those in hatchlings, respectively. Obviously calcium and magnesium in the egg contents were not enough to provide the embryonic development. The other 54.07% of calcium and 12.26% of magnesium in the newly hatchlings may come from reserves in the eggshell. Some previous papers also support our results: the sources of calcium in embryos of sea turtles came 60-80% from stores in the eggshell (Simkiss, 1967; Bustard et al., 1969) and the 56% of calcium in embryonic snapping turtles, *Chelydra serpetins*, obtained also from the development required (Packard et al., 1984b).

Growth of Embryos and Consumption of Yolk. We found that the yolk content declined as the incubation time increased, the embryo mass increased as the incubation time did. Both reflect a potential relationship between yolk consumption and embryonic growth. Because the turtle egg is a semi-closed system, all course of material transference, energy flow and embryonic development is carried out in the system throughout the incubation period. The yolk of the turtle is the main sources of energy and materials for the embryonic development, so the yolk of *Chinemys reevesii* declined as the embryo grew during the incubation times.

The just newly hatchlings of *Chinemys reevesii* averaged 4.8 g (SD=0.78, N=10) for 68.41% of the fresh egg content (albumen and yolk) mass at 28±0.5°C of the incubation temperature. If all of the egg contents may provide for the embryonic development, the transferred rate from the egg contents into embryonic tissues was 68.41%, and the rate of cost was 31.59% at 28±0.5°C of the incubation temperature in *Chinemys reevesii* eggs. The transferred rate of the *Trionyx triunguis* egg contents is 75.21% (Leshem et al., 1991). But, the transferred rate is influenced by the temperature of incubation, at 30°C for 65.54% and at 33°C for 62.61% in *Chinemys reevesii* egg contents (Wang et al., 1990).

Movement of Water Inside Eggs. The total water content of each *Chinemys reevesii* fresh eggs at preincubation averaged 65% that the percent water approximates to 66.9-70% water of the *Alligator mississippiensis* egg (Fischer et al., 1991). The water content of the reptile eggs have been defined as the hydric condition necessary for successful completion of the incubation (Packard and Packard, 1988). We found that the total lost water about 20% laid egg mass in the Grass lizard (*Takydromus septentrionalis*) had failed to hatch. In addition, the egg must absorb much more water from its surrounding substrata for the embryonic development completion, and the mass of eggs may be increased 342.2% of the initial egg mass over the course of incubation (Wang et al., 1989). In this study, the total water content of the *Chinemys reevesii* egg increased only 5.66% (SD=2.61, N=76) of the initial egg mass during incubation. But, eggs of some species hatch successfully even declining appreciably in mass. The eggs of the snapping turtles (*Chelydra serpentina*) frequently hatch after declining in mass by 18% over the course of incubation (Morris et al., 1983); the eggs of soft-shelled turtles (*Trionyx triunguis*) may lose approximately 21% water of the egg without ill effect during incubation (Leshem et al., 1991).

The total water content of the *Chinemys reevesii* egg on the preincubation reserved 60.7% in the yolk, 35% in the albumen and 4.3% in the shell (Table 3). The ratios of those varied with the incubation times (Table 3). The changes of the ratios may cause the yolk consumption and the embryonic growth; for example, on 55 days of incubation, the wet mass of yolk was only 7.5% of egg mass and the wet embryonic mass had grown to 45.9% of the egg mass (Table 1) when the water of the yolk took only 4.9% of the egg total water content and the water of embryo took 50.4% of the egg total water content (Table 3). Secondarily, yolk is also the approximate source of water used by embryos (Morris et al., 1983), so a quantity of water was transferred to the embryo. The albumen and shell water content were apparently not changed (Table 3).

The water content of the *C. reevesii* embryo declined significantly with the embryonic age (Table 3) that the changes of the relative hydration are similar to previous reports for the embryos of Green iguana (*Iguana iguana*) (Ricklefs and Cullen, 1973) and Colubrid snake (*Coluber constrictor*) (Packard et al., 1984). The water content of the embryo may be an index to the maturity of the embryo and can be used to estimate embryonic age.

Lipid of Yolk. The rate of the lipid content in the dry yolk of *Chinemys reevesii* averaged 20.4% during incubation. The value of that is close to 21% of the egg lipid in pained turtles, *Chrysemys picta* (Congdon et al., 1983). The lipid in the yolk may play an important role through embryonic development. It provides an embryo with greater amounts of usable metabolic energy and water (Gutzke and Packard, 1987), and the most part of one is transferred to the hatchling for it cost in the first days after it leaves the egg (Fischer et al., 1991).

Energy of Egg Contents. The changes of the energy content (cal/g) in the wet mass of albumen, yolk and embryo of the *Chinemys reevesii* are affected by their water content. However, the energy content in those of dried mass are relatively stable through incubation (Table 5). The caloric value, 6291.4 cal/g (SD=31.8), of the dried yolk in *Chinemys reevesii* is close to the value of those in the snapping turtles, *Chelydra serpentina* (6.6 cal/g), and the slider turtles, Pseudemys scripta (6.7 Kcal/g), at the time of laying (Slobodkin, 1962). The total energy content of the dry yolk in the *Chinemys reevesii* increased as the lipid content of the yolk did. Both show positive correlation, r=0.6768 (P<0.01), and the correlation is significant.

Acknowledgments

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Appendix I

Tables 1-6

Table 1. The changes of wet mass of egg components in *Chinemys reevesii* during incubation.

Day	N	Egg Mass in g	Component % of egg mass					Age phase of each component (%)			
		(M±SD)	Shell	Yolk	Albumen	Embryo	Other*	Shell	Yolk	Albumen	Embryo
0	10	5.89±1.43	14.6	54.4	23.9	-	7.1[a]	100	100	100	-
10	8	5.67±0.97	12.5	47.3	22.9	-	17.3[a]	85.7	86.9	95.7	-
20	10	6.15±0.98	12.2	35.3	43.1	3.2	6.2	83.2	64.9	179.9	100
30	9	6.72±1.05	12.0	27.6	40.1	15.5	4.8	82.3	50.7	166.8	493.0
40	10	7.36±0.79	11.3	16.9	32.1	35.7	4.0	77.5	30.8	134.1	1133.7
45	9	7.10±1.02	11.3	16.5	30.6	37.1	4.5	77.6	30.2	127.9	1175.6
50	10	7.28±0.43	9.9	10.9	30.5	42.5	6.2	67.5	20.0	127.4	1340.6
55	10	8.16±0.96	9.7	7.5	31.7	45.9	5.2	66.2	13.7	132.4	1455.2

*The values of those indicate the remains inside the shell after the embryos are out of the shell.

[a] shows the estimated values which includes those of the embryonic membranes and embryos etc.

Table 2. The changes of dry mass of egg components in *Chinemys reevesii* during incubation.

Day	N	Egg Mass in g	Component % of egg mass					Age phase of each component (%)			
		(M±SD)	Shell	Yolk	Albumen	Embryo	Other*	Shell	Yolk	Albumen	Embryo
0	10	2.09±0.22	35.3	61.0	3.1	-	0.6[a]	100	100	100	-
10	8	2.12±0.42	35.0	60.7	3.5	-	0.8[a]	99.2	99.5	112.9	-
20	10	1.89±0.39	34.9	60.2	3.8	0.7	0.4	98.9	98.7	122.6	100
30	9	2.02±0.30	34.6	55.7	3.6	5.5	0.6	98.0	90.3	116.1	785.7
40	10	2.02±0.32	34.0	40.4	3.4	21.7	0.5	96.3	66.2	109.7	3100.0
45	9	2.04±0.31	34.0	36.5	3.5	25.6	0.4	96.3	59.8	112.9	3657.1
50	10	1.93±0.28	33.6	27.9	3.4	34.1	1.1	95.2	45.7	109.7	4871.4
55	10	2.07±0.36	33.1	18.7	3.4	43.2	1.6	93.8	30.7	109.7	6171.4

*The values of those indicate the remains inside the shell after the embryos are out of the shell.

[a] shows the estimated values which includes those of the embryonic membranes and embryos etc.

Table 3. The changes of water content of eggs in *Chinemys reevesii* during incubation.

Day	N	Total water in egg		Ratios of water (%)				% of each component water			
		G		Shell	Yolk	Albu-men	Embryo	Shell	Yolk	Albu-men	Embryo
		M (SD)	M (SD)	M (SD)	M (SD)	M (SD)	M (SD)	M (SD)	M (SD)	M (SD)	M (SD)
0	10	3.81	65.0	4.3	60.7	35.0	-	17.4	65.5	95.3	-
		(0.89)	(6.3)	(0.8)	(9.0)	(9.0)	-	(3.0)	(7.8)	(1.9)	-
10	8	3.57	63.1	3.6	55.2	41.2	-	14.9	59.6	95.5	-
		(0.86)	(5.4)	(0.5)	(8.4)	(8.7)	-	(2.5)	(6.4)	(1.1)	-
20	10	4.27	67.3	3.6	30.7	61.1	4.0	17.6	51.7	97.0	93.1
		(0.61)	(6.3)	(1.6)	(9.3)	(7.7)	(1.9)	(8.0)	(6.1)	(1.5)	(5.0)
30	9	4.69	70.6	2.6	18.7	57.8	20.7	15.7	45.2	97.3	90.0
		(0.95)	(2.7)	(0.4)	(2.7)	(4.3)	(5.6)	(1.5)	(2.0)	(0.4)	(0.7)
40	10	5.35	72.5	2.2	11.5	44.3	42.0	14.8	40.2	97.3	84.0
		(0.64)	(1.9)	(0.2)	(3.3)	(5.2)	(5.9)	(1.1)	(2.8)	(0.2)	(3.0)
45	9	5.06	71.3	2.4	9.4	43.2	44.7	14.6	38.9	96.5	82.4
		(0.72)	(1.1)	(0.3)	(1.7)	(5.2)	(6.3)	(1.9)	(0.9)	(0.5)	(2.2)
50	10	5.36	73.6	2.5	7.1	44.5	47.7	17.5	41.2	96.6	79.6
		(0.69)	(3.0)	(0.4)	(0.5)	(8.3)	(5.6)	(4.3)	(2.2)	(13)	(2.5)
55	10	6.06	74.2	2.4	4.0	43.8	50.4	15.9	40.8	96.6	77.1
		(0.76)	(2.1)	(0.6)	(0.3)	(4.9)	(4.2)	(1.4)	(2.1)	(0.6)	(1.3)

Table 4. The lipid contents in dry mass of yolk of *Chinemys reevesii* eggs during incubation.

Days	N (egg)	Lipid % of yolk (M±SD)
0	10	20.50±1.49
10	8	18.58±0.57
20	10	15.92±0.95
30	9	19.75±0.84
40	10	20.11±1.23
45	9	21.26±2.01
50	10	21.27±1.12
55	10	26.51±2.14

Table 5. The energy contents (cal/g) of albumen, yolk and embryo in the eggs of *Chinemys reevesii* during incubation.

Days	N (eggs)	Yolk		Albumen		Embryo	
		Wet	Dried	Wet	Dried	Wet	Dried
0	10	2331.4	6344.6	247.6	5313.5	-	-
10	8	2536.7	6372.7	240.3	5297.9	-	-
20	10	2967.2	6343.9	238.4	5281.2	199.6	6337.7
30	9	3549.8	6486.1	217.3	5188.3	956.1	6256.0
40	10	3674.6	6538.4	185.7	5144.8	2245.2	6287.4
45	9	3907.6	6397.5	173.8	4895.8	2331.2	6295.5
50	10	3831.7	6609.8	165.0	4853.5	2600.4	6257.7
55	10	3911.8	6606.7	170.2	4726.3	2894.3	6313.8
Mean		3338.9	6462.5	204.8	5087.7	1871.1	6291.4
SD		637.9	112.8	34.8	229.4	1054.7	31.8

Table 6. Calcium and magnesium contents (M±SD, in mg) of eggshell, egg content and hatchlings in *Chinemys reevesii*.

Contents	N	Eggshells		Egg contents	Hatchlings
		Preincubation	Posthatching		
Ca	5	227.10±19.20	183.30±29.05	15.67±4.67	34.12±1.04
Mg	5	1.63±0.14	0.99±0.15	2.02±0.14	2.30±0.55

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A Comparison of Embryonic Metabolic Rates in Two Lizards

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Abstract. -The metabolic rates of eggs in both the wall lizard *Gekko japonicus* and the grass lizard *Takydromus septentrionalis* were measured through incubation at 32°C. The ontogeny of embryonic metabolism in both species of lizards exhibits an exponential pattern, similar to that recorded for some squamates that develop in parchment-shelled eggs, but different from some crocidilians and chelonians that develop in parchment-shelled and brittle-shelled eggs.

Both the embryos and hatchlings of *T. septentrionalis* have higher metabolic rates than those of *G. japonicus*. An embryo of *T. septentrionalis* consumes more oxygen than that of *G. japonicus*, although the latter species has a much longer incubation period at 32°C.

Key words: Sauria, *Takydromus septentrionalis*, *Gekko japonicus*, Hatchling, Embryonic Metabolic Rate, Exponential Pattern, Incubation, Egg, Oxygen, Consumption.

Introduction

Embryonic metabolic characteristics of incubating eggs have been reported for at least 23 species of living reptiles, including seven species of snakes (Clark, 1953; Dim'el, 1970; Black et al., 1984), eleven species of chelonians (Lynn and Von Brand, 1945; Ackerman, 1981; Gettinger et al., 1984; Webb et al., 1986; Thompson 1989; Wang et al., 1990), one species of lizard (Wang et al., (1989), three species crocodilians (Thompson, 1989; Whitehead and Seymour, 1990), and one species of tuatara (Thompson, 1989). Three patterns of the ontogeny of embryonic metabolism in reptiles have been recognized in incubating reptilian eggs: peaked, sigmoid, and exponential (Thompson, 1989; Whitehead and Seymour, 1990; Wang et al., 1990). These patterns are very similar to those observed in birds (Vleck et al., 1980; Wang et al., 1991). However, it is still unclear whether patterns of metabolic ontogeny are species-specific, and whether patterns in lizards (especially in geckos) are different from those of other reptiles.

The two lizard species (*Gekko japonicus* and *Takydromus septentrionalis*) studied show distinct differences in activity patterns, foraging behavior, and microhabits (Liu and Hu, 1940; Wang, 1964, 1966). The wall lizard (*G. japonicus*) is a nocturnal, sit-and-wait predator found on the walls of old houses and temples. It remains immobile for more than half of its nocturnal period. One to three clutches two eggs each, are oviposited annually (Liu and Wu, 1940; Ji et al., 1991). In contrast, the grass lizard (*T. septentrionalis*) is a diurnal and active forager in high grasses (Wang, 1964). One or two, rarely three, clutches of two to five parchment-shelled eggs each, are laid annually in humid soil where they swell and become increasingly turgid during incubation (Wang, 1966). In this paper we compare the characteristics of the ontogeny of metabolism of the eggs of these species during incubation.

Materials and Methods

Gravid *Gekko japonicus* and *Takydromus septentrionalis* were collected on buildings in Shanghai and in fields on the Zhoushan Islands, respectively. The captured animals were taken to the laboratory, maintained in aquaria, and fed with mealworms (larvae of *Tenebrio molitor*). Eggs were laid at room temperatures of 24-28°C. Each freshly laid egg was numbered, the length and width were measured (nearest 0.1 mm), and the wet mass recorded (nearest 0.1 mg). Egg volume was calculated by using the ellipsoid equation $V=\frac{3}{4}\pi a^2 b$, where V=volume, $a=\frac{1}{2}$ of width and $b=\frac{1}{2}$ of length. The surface area of each eggshell was obtained by measuring the width and length axes of 2a and 2b, respectively, and substituting them in the equation for the area of ellipsoid,

$$2\left(b^2+\frac{a^2 b}{\sqrt{b^2-a^2}}\,\mathrm{in}\sqrt{\frac{b^2-a^2+b}{a}}\right)$$

Table 1. Egg and hatchling dimensions of *Gekko japonicus* and *Takydromus septentrionalis* during incubation at 32°C.

		Pre-incubation egg			Changes in egg dimension (pre-pipping)			Incubation days	Hatchlings		
		Species	N	mass mg(SD)	vol. mm^3 (SD)	area mm^2	mass %	Vol. %	area %		SVL mm (SD)
Gekko japonicus	69	681.8 (49.3)	700.2 (84.1)	7510	-14	0	0	42.9 (2.9)	25.9 (1.5)	468.3 43.4)	68.7
Takydromus septentriona	75	267.4 (32.6)	246.1 (35.0)	2510	280.9	298.9	283	26.3 (1.2)	24.0 (1.6)	309.2 (43.0)	111.6

The eggs were half buried in moistened sand substrates and placed at a nearly constant temperature of 32°C (SD=0.5°C). Relative ambient humidities were 80-85% for *G. japonicus* eggs and 99-100% for *T. septentrionalis* as indicated by an FC-1 Hydro Thermometer. Volume and wet mass of incubating eggs were recorded at five day intervals.

At five day intervals, oxygen consumption of incubating eggs was measured by using a small closed system respirometer (details of the apparatus are given in Wang, 1986). Oxygen consumption of hatchlings was measured in the same apparatus. All experiments were conducted at 32°C (SD=0.5°C) from 0830-1030 hr. Each experiment was completed within one hour and data were recorded every fifteen minutes. Carbon dioxide (CO_2) exhaled by animals was absorbed by 30% sodium hydroxide (N_aOH) solution. All rates of oxygen consumption were corrected to STPD, and expressed as volume of 0_2 per unit egg mass in grams or as volume 0_2 per egg at the time of collection (ml 0_2/g * h or ml 0_2/egg * h).

The total 0_2 consumption of each egg from initial incubation to hatching was derived by a stepwise regression of log $_{10}$ transformed data. A t-test was performed to test for statistically significant differences between means.

Results

Incubation Time

The mean duration of incubation to hatching of *Gekko japonicus* eggs was 42.9 days at 32°C, compared with 26.3 days in *Takydromus septentrionalis* eggs at 32°C (Table 1), so the latter is shorter 16.3 days than the former.

Changes in Eggs During Incubation

The surface area, volume, and wet mass to *T. septentrionalis* eggs during incubation increased to 283%, 280.9% and 298.9%, respectively, of initial values (Table 1). At hatching, the mean wet mass of *T. septentrionalis* was 309.2 mg or 111.6% of the initial egg mass (Table 1). In contrast, there were no changes in egg volume and surface area during incubation of *G. japonicus*, but egg wet mass at pre-pipping declined to 14% of the initial egg mass (Table 1), and the wet mass of hatchlings was only 68.7% of pre-incubation egg mass (Table 1).

Oxygen Consumption During Incubation. The rates of oxygen consumption of eggs in *G. japonicus* and *T. septentrionalis* are shown as a function of incu-

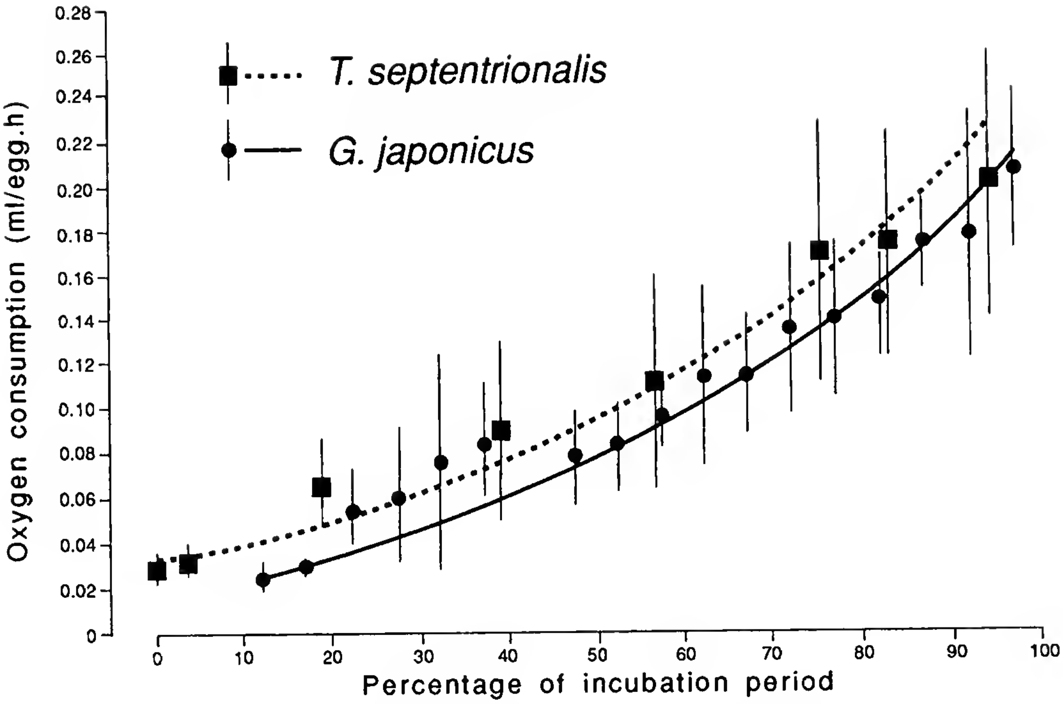

Figure 1. Relationship between oxygen consumption of eggs in two species of lizards (*Takydromus septentrionalis* and *Gekko japonicus*) and the percentage of incubation period at 32°C. Squares (*T. septentrionalis*) and circles (*Gekko japonicus*) represent mean values of oxygen consumption of eggs. Vertical lines indicate two standard deviations about the mean. The dashed lines indicate normalization curves of oxygen consumption per egg at different stages of incubation.

bation time in Fig. 1. The following semi-logarithmic regression equations are best fitted by those data. These equations are of the general form: log V= a + bT ± c, where V is oxygen consumption in ml 0_2/eggs * h, and T is time in days.

For *G. japonicus*:

log V = -1.5017+0.0087T ± 0.0768 (r=0.98, P<0.01).

For *T. septentrionalis*:

log V = -1.4340+0.0086T ± 0.0740 (r=0.95, P<0.01).

The slopes (b) of the regression equations of the two species lizards are nearly the same (b=0.0086 and b=0.0087). The two species had the same general patterns of exponential embryonic metabolic ontogeny as that usually observed in other squamate reptiles (Dim'el, 1970; Black, 1984) and in altricial birds (Vleck et al., 1979).

Embryonic metabolic rates of *T. septentrionalis* on the first and second days of incubation averaged 0.1179 ml 0_2g * h and 0.1196 ml 0_2/g * h for per gram mass egg respectively. Oxygen consumption of eggs of *G. japonicus* could not be detected until about the fourth day of incubation (12% of the incubation period). The average total oxygen consumed during embryonic ontogeny was 73.48 ml 0_2/egg or 274.79 ml 0_2/g per gram mass of initial egg mass, or 0.0293 ml 0_2/mm^2 per square millimeter of initial egg surface area in *T. septrionalis*, and only 104.42 ml 0_2/egg or 153.15 ml 0_2/g, or 0.0204 ml 0_2/mm^2 in *G. japonicus*, although the latter species had a much longer duration of incubation that averaged 42.9 days at hatching (Table 1).

Metabolic Rates of Hatchlings. The resting metabolic rate per gram mass of hatchlings averaged 0.6547 (SD=0.0870, N=16) ml 0_2/g * h for *T. septentrionalis* and 0.4603 (SD=0.0476, N=16) ml 0_2/g * h for *G. japonicus*. So that the resting metabolic rate of *T. septentrionalis* is 0.1944 ml 0_2/g * h, or 42% higher than that of *G. japonicus*. For *G. japonicus*, oxygen consumption of hatchlings and eggs just before pipping were 0.2144 (SE=0.0186, N-19) ml 0_2/lizard * h and 0.2139 (SD=0.0148, N=19) ml 0_2/egg * h, respectively. For *T. septentrionalis*, oxygen consumption of new hatchlings and eggs just before hatching were 0.2024 (SD=0.0069, N=16) ml 0_2/lizard * h and 0.2072 (SD=0.0300, N=16) ml 0_2/egg * h, respectively.

Discussion

To our knowledge, this is the first report on the embryonic metabolic ontogeny of lizards. Our results show that both these lizards have an exponential embryonic metabolic pattern. (Fig. 1). This pattern is similar to some snakes or lizards that develop in parchment-shelled eggs and those birds with altricial hatchlings, but differs from the peaked and sigmoid patterns observed in some crocodilians, sea turtles, and fresh water turtles (Vleck et al., 1979; Ackerman, 1981a, 1981B; Whitehead and Seymour, 1990).

Whitehead and Seymour (1990) showed that six species of reptiles with brittle-shelled eggs exhibited the peaked pattern, and ten of thirteen reptilian species with parchment-shelled eggs exhibited a non-peaked metabolic pattern, i.e., seven species snake for an exponential pattern, and three species sea turtles of those for a sigmoid pattern, and other three species fresh turtles of those are only a peaked pattern. Why does *G. japonicus*, with a non-parchment-shelled egg, also exhibit an exponential pattern? Unfortunately, there are few data dealing with the reasons for the observed patterns of embryonic metabolic ontogeny in reptiles, especially in lizards. Some data suggest that the patterns of embryonic metabolic ontogeny in reptiles may be species specific, but do not necessarily depend upon the type of eggshell. For example, there are three patterns of embryonic metabolic ontogeny among reptiles with parchment-shelled eggs, i.e., peaked, sigmoid, and exponential pattern (Whitehead and Seymour, 1990). However, all of seven snakes examined exhibited an exponential pattern of embryonic metabolic ontogeny, three sea turtles showed a sigmoid pattern, and three crocodilians and seven freshwater turtles exhibited a peaked pattern. Metabolic rates of developing embryos reflect the energetic demands of both growth and maintenance (Wang et al., 1991). Peaked and sigmoid patterns of embryonic metabolic rates are likely to be associated with defining embryonic growth rates late in incubation, and exponential patterns of metabolic rate in reptilian embryos is likely due to continuous increase of the embryonic growth rate through incubation.

Although *G. japonicus* had a longer incubation period than did *T. septentrionalis*, the former species consumed less oxygen through incubation. The total oxygen consumption during embryonic ontogeny at 32°C per gram or per square millimeter of initial incubation egg mass or surface area in *G. japonicus* was only 153.15 ml 0_2/g or 0.0204 ml 0_2/mm^2, compared to 274.79 ml 0_2/g or 0.0293 ml/mm^2 for *T. septentrionalis* i.e., 179.4% or 143.6% higher, respectively. In addition, Fig. 1 shows that the regression curve of oxygen consumption for *G. japonicus* was clearly lower than that of *T. septentrionalis*. Also, the standard rates of evaporative water loss in some gekko eggs are lower than other reptiles (Dunson and Bramham, 1981; Dunson, 1982). The low level of metabolism may be a characteristic of gecko eggs.

Besides this phylogenetic difference, another possible reason for the difference in embryonic metabolism between the two species may be related to the structural characteristics of the eggshells. The eggs of *T. septentrionalis* are parchment-shelled and when placed in suitable substrates, tend to become larger during incubation because of water absorption. The enlarged eggs of *T. septentrionalis* have a surface area at hatching that reached 282.7% of initial eggshell area (Table 1). This possible increase in pore diameter and shell permeability (Packard, 1980) may promote increased embryonic metabolism.

Both the metabolic rates per hatchling and egg at pipping were nearly the same. The resting metabolic rate of new hatchlings can be used to estimate metabolic rates of their eggs just before pipping. The resting metabolic rate of hatchlings of *T. septentrionalis* was about 29.7% higher than that of *G. japonicus*. The difference in resting metabolic rates of new hatchlings between the two species may be due to phylogenetic characteristics, as geckos have a low metabolism (Feder and Feder, 1981; Dunson and Bramham, 1982). To eliminate the effect of body mass on metabolic rate, we used the formula $M/W^{0.73}$ to correct the results, where M is metabolic rate, W is body mass, and 0.73 is close to the average of the interspecies coefficient and has the advantage of correcting for difference in mass. The corrected resting metabolic rates of hatchlings are 0.4768 ml $0_2/W^{0.73}$ * h for *T. septentrionalis* and 0.2942 ml $0_2/W^{0.73}$ * h for *G. japonicus*; the former species is 31.1% higher than the latter.

We conclude that the difference in metabolic rates of hatchlings between the two species is not primarily caused by difference in body mass. Instead, there must be an interspecific difference in metabolic rates between the two lizard species.

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Varied and Fluctuating Foraging Modes in Nocturnal Lizards of the Family Gekkonidae

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Abstract. -Heliothermic lizards have been used as model organisms in studies of foraging mode, although their behavior is generally complicated by thermoregulation. Tropical nocturnal gekkonid lizards could be better models than temperate diurnal lizards. In several recent reviews, gekkonids have been considered to be sit-and-wait (ambush) predators. Observation of *Gekko hokouensis, G. japonicus* and *Teratoscincus roborowskii* in the field on warm nights revealed that by the measure of moves-per-minute they are sit-and-wait (SW) predators but by the measure of percent-time-moving *G. hokouensis* is widely-foraging (WF), as is *Coleonyx variegatus*, according to the literature. The behavior of individuals of all three species combines to varying extent both SW and WF modes. This observation accords with recent reports of foraging behavior in *G. gecko* and *Stenodactylus doriae*. Reexamination of the original literature sources quoted in recent reviews showed that these sources had already qualitatively described many geckos as either WF or mixed strategists. The fluctuating foraging mode of geckos presumably enables these noctural visual predators to locate stationary prey and, without wasting locomotor energy, to locate mobile prey. The option to employ both SW and WF modes may depend on the absence of competition. Although geckos as a group had been believed to be SW predators, their relative clutch mass (RCM) had often been believed to be as small as in WF lizards. More recently, several geckos were shown to have larger RCMs. Hence geckos, rather than having a paradoxically low RCM, are in fact intermediate between SW and WF lizard groups in both RCM and foraging mode.

Key words: Reptilia, Lacertilia, Gekkonidae, *Gekko hokouensis, Gekko japonicus, Teratoscincus roborowskii,* China, Japan, foraging mode, nocturnality, relative clutch mass.

Introduction

Ever since they were first coined by Pianka (1966), the terms "sit-and-wait" (SW) and "widely foraging" (WF) have been used extensively to describe foraging behavior. Often they have been considered alternative states of a dichotomy (Pianka, 1986; McLaughlin, 1989; Etheridge and Wit, 1993; and references in Pietruszka, 1986), while some authors have viewed them as extremes of a continuum (Pianka, 1974:203; Pietruszka, 1986; Perry et al., 1990). Although Vitt and Congdon (1978) and Vitt (1990) recognized the possibility of a continuum of foraging modes, their papers highlight differences between SW and WF lizards. Implicit in the use of these terms (or the equivalent "ambush" and "active" foragers) are the assumptions that there is little intraspecific or intra individual variation in foraging behavior.

Lizards have been used often as models for studying the foraging behavior of animals in the field. The two commonest coins for quantification and comparison have been the "percent time moving"(PTM) and "movements per minute" (MPM, see below) (Huey and Pianka, 1981; Perry et al., 1990).

Going by such yardsticks, the foraging mode, either SW or WF, is usually considered typical of a whole lizard family. Thus, Agamidae, Anguidae and Iguanidae (s.l.), unless herbivorous, are SW foragers, whereas almost all Lacertidae, Scincidae, Teiidae and Varanidae are WF (Huey and Pianka, 1981; Dunham et al., 1988; Green and King, 1993; Cooper, 1994a, b).

The studies underlying this classification obviously presuppose that the observations quantified had been free of socially-motivated (Regal, 1983:116) and of thermoregulation-related (Anderson, 1993) behavior. Whereas it is relatively easy to account for the former (Kingsbury, 1989), it is often difficult to completely exclude the latter when observing diurnal poikilotherms such as lizards. Nocturnal lizards such as geckos can thus provide superior models of foraging mode if observed in a climate with stable night temperatures approximating those preferred by the lizards.

The Gekkonidae have traditionally been considered SW predators (Pianka, 1986:48; Dunham et al., 1988:513), and this view appears somewhat supported by recent observations on *Gekko gecko* (Stanner et al., in press). However, *Coleonyx variegatus* employs an intermediate stragtegy (Kingsbury, 1989) and some others have recently been counted as active foragers (Cooper, 1994a,b). Thus it remains unclear whether the Gekkonidae are characterized by a given foraging mode, as are other lizard families, and, if so, what that foraging mode is.

This issue is of particular interest because whereas SW lizards usually have greater relative clutch masses (RCMs) than WF lizards (Vitt and Congdon, 1978), geckos tend to have RCMs similar to those of WF Lizards (Vitt and Price, 1982: figs. 1 and 3). This putative paradox cannot be explained fully as an adaptation of geckos to life in crevices (Vitt, 1981): small RCMs occur also in cursorial, arenicolous species of geckos (Vitt and Price, 1982; Werner, 1989); in some of these this could be a phylogenetic constraint (Vitt, 1986; Stearns, 1992) but presumably at least in the primitive group of Eublepharinae (Kluge, 1967; Werner, 1972) this would not be the case. Hence additional data on the foraging modes of geckos are needed.

Therefore, we report here on the foraging behavior of three nocturnal geckos in the eastern Asian summer, *Gekko hokouensis*, *G. japonicus*, and *Teratoscincus roborowskii* . We pay particular attention to intraspecific variation, which has been reported in the foraging behavior of some other lizards (Pianka et al., 1979; Kingsbury, 1989; Perry, 1996), and to intra-individual variation, a topic which has not been addressed previously.

Materials and Methods

Abbreviations and Definitions

CV, coefficient of variation (standard deviation as percent of mean); FM, foraging mode; MPM, "movements per minute", the average number of times, during one minute, that a lizard changed its locomotory state from "stationary" to "moving"; PTM, "percent time moving" percentage of the total time, that the animal spent locomoting; percra, percents of ra; ra, rostrum-anus ("snout-vent") length (Werner, 1971); RCM, relative clutch mass, ratio of total clutch mass to total maternal mass, including the clutch (Vitt and Price, 1982); SD, standard deviation; SW, "sit-and-wait" predator; WF, "widely ranging forager".

Data Collection

Environmental factors such as illumination can affect the activity of nocturnal geckos (Frankenberg, 1979; Frankenberg and Werner, 1979; Bouskila et al., 1992; Petren et al., 1993). We therefore detail the circumstances of the observations.

Observations were made at night by one observer carrying an electric torch with a removable cover of red cellophane paper (two layers). When the torch was held on the observer's forehead, *Teratoscincus* could be located on the ground by their reflecting reddish eyeshine. With both *Gekko* species, which were observed mainly on walls, this method was superfluous. Searching began at a distance (>20 m for *Teratoscincus*; less for the *Gekko* species) with white light. The main observations were made from 3-10 m, depending on species and situation, with red light. We endeavoured to observe each individual for 30 minutes; finally the gecko was approached and examined. In all three species, some of the locomotion of the individuals was towards the observer, hence presumably the observer did not affect them (following Anderson, 1993).

To enable prompt photography, the observer carried a ready camera (Leica M3 with 135 mm lens) with flash and mostly Agfachrome Professional 200 ASA film. Air temperature was recorded with a Miller-Weber mercury thermometer ("Schultheis" type) 1 m above ground (for *Teratoscincus* also 1 cm above ground, and substrate temperature was also taken). Illumination was recorded with a Lunasix-3 (Gossen) light meter.

Observations and environmental data were recorded into a microcassette recorder (Panasonic RN-102). When the information was transcribed on paper, detailed time data were derived from a clock synchronized with recorded times. Because the speeds of recording and playback varied with battery strength, care was taken to use equivalent batteries.

Figure 1. Study site for *Gekko hokouensis* at the Chinen Castle ruins, near Chinen, Okinawa Island, Japan (4 August 1992).

Data Processing and Presentation

Geographical grid references of towns, for macroecological evaluation, are from the Times Atlas of the World (1967).

Observations suspected of reflecting social interactions or observer effect were excluded. The proximity of an observer may suppress the activity of lizards (Sugerman and Hacker, 1980) or stimulate excessive activity (Regal, 1983).

To enable comparison with previous data (Huey and Pianka, 1981; Perry et al., 1990), we use MPM and PTM to assess FM. These depend on the definition of discrete locomotor states, although the activity of the animals may constitute a continuum of patterns (Regal, 1983:115). We coarsely classified all postures and actions as "stationary" or "moving". "Stationary" included the time during which the gecko remained in the same place, perhaps moving its head, jaws, tongue, limbs or tail, or even shifting its posture by 180°, as long as it did not move towards another location. "Moving" included crawling, walking, running, jumping and jerking forwards.

A complication arose from frequent brief pauses during locomotion in *Gekko hokouensis*. We found a precedent in Avery et al. (1987a, b), who analyzed the locomotion of four lacertid species by videotape. "Standard" locomotion (neither fleeing nor chasing), presumably representing foraging behavior, comprised 88-143 bursts of movement per minute, each of 0.25-0.56 sec. The intervening pauses lasted 0.12-0.17 sec, and occupied 18-40% of the time. In the FM of female *Podarcis sicula* in nature, Avery (1991) defined as 'movement' a bout of locomotion separated from others by pauses of >1 second. Thus defined, movement duration in *P. sicula* averaged 10.9 sec; pause duration averaged 22.4 sec (MPM= 1.8; PTM= 32.7). We followed this methodology for approx. half the data of *Gekko hokouensis*, which included appropriate time statements.

In the remainder of *G. hokouensis* data, the observations had been grouped per half-minute periods, leaving precise durations unknown. These records were scanned automatically by the NOTITA computer program (N. Werner & H. Dreher, in MS) which constructed a quantitative table, from which some summarising statistics were derived by the Microsoft Excel program.

We do not use velocity as a descriptor of FM (Huey and Pianka, 1981; Magnusson et al., 1985; Anderson, 1993) because velocity is generally affected by body size (Avery et al., 1987b).

Species, Environments and Observations

***Gekko hokouensis* Pope, 1928.** *Gekko hokouensis* males attain 59.8 mm ra (mean53.9) and females 65.4 mm ra (mean 54.8) on Okinawa Island (Ota, unpublished data).

Study site. *G. hokouensis* was studied at the Chinen Castle ruins near Chinen (26° 07'N, 127° 49'E), southern Okinawa Island, Japan (. 1). Most observations were made on geckos on and in a small modern but uninhabited concrete-block building among large trees (fig. 1); few observations were made on geckos on the trees. None of the other gecko species occurring on Okinawa (Ota, 1989) was encountered in the study site.

Procedure and conditions. On five nights between 28 July and 4 August 1992, observations started between 1850 h (at which time the illumination was down to 700 lux) and 2015 h (sunset was approx. at 1915 h), and lasted as long as geckos were active on the building. Throughout the observations, the sky was mostly at least half overcast, hiding the moon which was waxing, in its first quarter. Air temperature varied only between 26.0 and 28.1° C. On the first night, observations were made by a team of two; on the later nights, the two observers functioned as separate teams. Observations were made from distances of 3-5 m, so that behaviour was seen in detail. Observation time totalled 27.25 team-hours.

Observations. Of 63 geckos recorded, only 12 could be followed for >30 min. These showed varied movement patterns.

Bouts during which the geckos were stationary, lasted from <1 min to >15 min. While stationary, geckos often turned their head (to one side or another, or back to the straight position, up to twice per minute),

Table 1. Measures of foraging mode in the geckos studied. Species means are based on samples described or quoted in the text.

Species	Minutes observed		Moves/minute		% of time moving	
	X	SD	X	SD	X	SD
	(Range)		(Range)		(Range)	
Gekko hokouensis n=12	37.8	7.15	0.35	0.15	25.5	14.7
	(30.5-53.5)		(0.18-0.65)		(5.1-51.5)	
G. japonicus n=12	25.44	12.32	0.15	0.2	8.94	9.7
	(4-43)		(0.00-0.75)		(0.0-50.0)	
Teratoscincus roborowskii	*11.97*	*8.81*	*0.44*	*0.8*	*8.83*	*14.8*
	(1.5-36.03)		*(0.00-2.82)*		*(0.0-50.0)*	
	Duration (seconds) of a single-					
	Stationary pause		*Move*			
Gekko hokouensis n=12	150.2	74.1	50.2	29.9		
	(5-1050)		(1-375)			
G. japonicus n=12	856.6	818.7	34.7	38.6		
	(2-2580)		(1-150)			
Teratoscincus roborowskii n=11	385.0	296.3	13.2	23.0		
	(1-1800)		(1-150)			

turned the whole body to another direction (up to once per four minutes), or waved or vibrated the tail (up to once in seven minutes). Licking the lips could occur at any time (usually up to once per minute).

Gecko movements between stationary bouts took three major forms: (a) Normal walking or running, usually for a distance of 5-100 cm at a time.

(b) Crawling: the geckos sometimes advanced, with or without pauses, by a slow "crawl", at a speed of about 1 cm/min. We saw no evidence that this was consistently related to the gecko having detected a prey item.

(c) Interrupted locomotion: a sequence of forward movements by 1-2 cm each ("micromoves"), at a rate of usually 2-12 (rarely up to 72) "micromoves" per minute. Following Avery et al. (1987a, b; see Materials and Methods) we classify each sequence of locomotion by "micromoves", including its brief pauses, as one bout of moving, or "move". But "micromoves" could also occur singly or widely spaced, and then were reckoned separately.

On the basis of these definitions of "moves", their statistics are summarized in Table 1.

The sex of twelve females was verified by capture or was evident due to obvious gravidity but the sex of only four males was ascertained by capture. Males appeared to be a little more active than females but the difference was not statistically significant (MPM: males, X=0.46; females, X=0.32; t-test p=0.06).

***Gekko japonicus* (Duméril et Bibron, 1836).** *Gekko japonicus* males reach 65 mm ra (mode 60 mm), and females reach 70 mm ra (mode 61 mm) (Tokunaga 1984:fig.1).

Study site. *G. japonicus* was studied on the Hakozaki campus of Kyushu University, Fukuoka (33° 39'N, 130° 21'E), Kyushu Island, Japan, where the investigations of Tokunaga (1984) had been conducted. The geckos were on various buildings and sheds, especially in portions of walls or passage ceilings lit by incasndescent or fluorescent lamps or by nearby street lamps. *G. japonicus* is the only gecko species in this study site (Nakamura and Uéno, 1963; Tokunaga, 1984), and no other reptiles were encountered during the observations.

Procedure and conditions. During three nights, 9-11 August 1992, observations by one observer started between 1915 h, when the illumination was 44 lux, and 2030 h (sunset, approx. 1910 h; end of twilight, approx. 2040 h), but had to be ended for logistic reasons by 2300 h, while geckos were still active. Throughout the observations the sky was overcast; sometimes a slight drizzle rained. The mostly-hidden moon was waxing in its second quarter. Light intensities where most geckos were observed ranged from 0.35 to 1000 lux. Some geckos were in the lit areas and others in nearby shaded situations. At the times the daily observations were conducted, air temperatures ranged from 27.2°C down to 24.5°C. These three nights followed two very rainy nights, when the site had been on the margin of a typhoon. The geckos were observed from distances of 5-8 m, so that fine details were missed. Observation time totalled 7.5 h.

Observations. Of 20 geckos recorded, only 7 could be followed for >25 min; the 12 observed for >4 min behaved variably: three remained stationary throughout (up to 43 min) whereas others alternated moving and pausing, usually moving less frequently than once every ten minutes, and spending up to 10% of their time in locomotion; but one spent 50% of the time moving (Table 1). There appeared to be some intra-individual variation; for example gecko no. 13 was once stationary for 15 min, whereas its other 7 stationary bouts all lasted <4 min.

The individuals were not sexed because most were high on walls.

Comment. The geckos may have been less active than usual during these observations due to the rainy weather and the cool season - in summer 1992 the mean daily temperatures were 2-3°C below the 30-year average (Fukuoka Meteorological Observatory records).

Teratoscincus roborowskii Bedriaga, 1905

Teratoscincus roborowskii was synonymized by Pope (1935:458) with *T. scincus* but is in the process of being validated by J. R. Macey et al. (see Autumn and Han, 1989). The species is arenicolous and its toes lack adhesive pads; males up to 87 mm ra, females up to 80 mm ra (from 30 adults in the California Academy of Sciences, courtesy J. Vindum).

Study site. *T. roborowskii* was studied near Turpan (42°55'N, 89°06'E), Xinjiang Uygur Autonomous Region, People's Republic of China (on the Turpan-Jiaohe road, approx. 4.5 km W of the Turpan SixMinarets Mosque; 3 km E of Jiaohe Ancient City).

Located on the margin of the Turpan Depression (-150 m), this area has a total annual precipitation average of 16.6 mm (Turpan Weather Bureau data). The daily maximum air temperature ranged up to 45°C in September 1987 (Autumn & Wang, 1988) but averaged only 40°C during the study period.

The study site comprised long-abandoned fields of blackish sand at the foot of hills with undisturbed vegetation described by Autumn & Wang (1988). The sand was soft in some places, hard packed in others, and retained remnants of furrows, ditches and wells. Plant coverage comprised only two small shrub species and by estimate varied between patches from 2% to 80%. Rainfall had exceeded the average - during the first half of the year (1.I.-9.VII.92), 21.8 mm had already acummulated (Turpan Weather Bureau data). In addition to the trees lining the road, some small stands of small *Tamarix* sp. trees occurred in the area.

Other than the *Teratoscincus* encountered at night, the only reptiles seen on the site were the diurnal lizards *Phrynocephalus axillaris* (Agamidae) and *Eremias velox* (Lacertidae). Some individuals of both species, especially of *Eremias*, were still active in the last daylight after sunset. According to Autumn & Wang (1988) *Psammophis lineolatus* (Colubridae) may also occur on the site. These authors pointed out the simplicity-in-principle of flora and herpetofauna on the site and in Chinese deserts in general.

Procedure and conditions. On four nights, 6-10 July 1992, observations (by one observer) started at 2125-2200 h (Beijing time; sunset, 2135 h), i.e., before the geckos emerged for their nocturnal activity on the surface; but had to be ended for administrative reasons at 0001-0030 h, while the geckos were still active. The moon was about 1/2 full (waxing), the sky mostly 4/8 cloudy; when gecko activity was high, the illumination was of the order of magnitude of 1 lux. Temperature differed little between sand surface, air 1 cm above ground and air 1 m above ground; the over-

Figure 2. *Teratoscincus roborowskii*, half-grown individual, scouting from the entrance of its burrow (Turpan, 2235 h, 8 July 1992).

all range during observations was 26.5-34.4°C. The wind varied from absent to fairly strong for short times, commonly blew from the north, and sometimes was noticeably warm. In the darkness, at distances of mostly approx. 10 m, gecko behavior was assessed from their returned eyeshine. Observation time totalled 10h 20' but as the torch became effective only at approx. 2210 h, the effective observation time approximated only 8h 20'.

Observations. On each night, the earliest gecko was spotted 40-65 min after sunset, after a search of 10-60 min. Thereafter, the finding of each successive individual usually required 0.5-5 min.

One individual, caught at 2310h on 9.VII.92 with sand temperature 30.5°C and air temperature (1 cm) 31.3°C, had a rectal temperature of 30.2°C.

Time budgets were calculated for the 11 animals observed (despite the vegetation) for > 90 sec and not suspected of having been affected by the observer (Table 1). Of 28 individuals discovered at a distance, only three were moving when spotted. This value of 10.7% of the animals moving when discovered is close to the 8.8 PTM calculated for the species (Table 1).

Individual foraging behavior was highly variable but two extreme patterns appeared to be dominant: several animals remained stationary throughout an observation period of 10-15 min; others kept alternating between standing and walking at intervals of 1-7 sec (rarely <1 or >60 sec).

Two individuals (a half-grown individual spotted on 8.VII at 2231 h and a subadult spotted on 9.VII at 2327 h) were sitting with only their fore-parts out of the openings of their burrows (fig. 2). One retained this position for 36 min, then ran out and away (the other was disturbed by the observer after 14 min, and retreated down its hole). When looking out from the burrow, these geckos may have been SW scouting like *Ptenopus* (Huey and Pianka, 1981).

Individuals were not sexed because this species autotomizes the skin when held, as described for *Teratoscincus scincus* by Bauer et al. (1993).

Comment. Thus these geckos are not simply "active foragers" as has been described for *Teratoscincus przewalskii* (Semenov and Borkin, 1992).

Discussion

The Foraging Mode of Gekkonid Species

For lizards, SW and WF appear to be the extremes of a FM continuum: (1) Both SW and WF are practiced differently by different lizard species, which combine different MPM and PTM values; (2) Some lizard species vary their FM during the day or during the year (Pietruszka, 1986); (3) the intermediate FM, repeatedly shifting the position for stationary scanning for prey, called "cruising" by Regal (1983:113-114), or, more aptly, "saltatory" by O'Brien et al. (1989), occurs also in lizards (Moremond, 1979). Nevertheless, SW and WF are definite foraging techniques: *Sceloporus merriami* and *Urosaurus ornatus* (Iguanidae) switched from distinct WF to distinct SW when food was scarce (Dunham, 1983). Indeed, generally SW is the optimal strategy for motile prey, and WF the optimal strategy for stationary prey (Gerritsen and Strickler, 1977).

In lacertid lizards the two FM measures, MPM and PTM, usually yield the same verdict as to whether a species is SW or WF, i.e., MPM values of <1-2 and PTM values of <15 indicate SW; MPM of >1.5-2 and PTM of >30 indicate WF (Huey and Pianka, 1981; Perry et al., 1990). By either index the species averages of *Gekko japonicus* and of *Teratoscincus roborowski* (Table 1) indicate that these geckos are SW foragers. The observations of Stanner et al. (in press) of *Gekko gecko* also are compatible with the suggestion of this species being a SW predator (0.04 MPM, 4.37 PTM). However, the third species studied here, *Gekko hokouensis*, is SW only in its MPM mean, and is WF, or nearly so, in its PTM. The situation in *Coleonyx variegatus* is very similar, with 0.57 MPM but 34 PTM (Kingsbury, 1989).

Thus by the index of MPM, all five gecko species for which at least some quantitative data exist, are SW predators. But the index of PTM is probably ecologically more significant, because it partly reflects energy investment in foraging, and by this index three species are SW, whereas two are WF. Moreover, the diet of *Ptyodactylus guttatus* indicates that this species forages more widely than previously believed (Perry and Brandeis, 1992), and Semenov and Borkin (1992) have stated that *Teratoscincus przewalskii* is a

Table 2. Coefficients of variation (CV) of measures of foraging mode in some lizards.

Family and Species	FM	CV of MPM	CV of PTM	Source
Lacertidae				
Acanthodactylus boskianus	WF	72.6	89.2	Perry et al., 1990
Acanthodactylus schreiberi	WF	56.5	67.5	Perry et al., 1990
Acanthodactylus scutellatus	SW	74.3	92.5	Perry et al., 1990
Eremias lineoocellata	SW	105.8	81.1	Huey and Pianka, 1981
Eremias lugubris	WF	36.4	25.6	Huey and Pianka, 1981
Eremias namaquensis	WF	55.7	48.6	Huey and Pianka, 1981
Ichnotropis squamulosa	WF	10.0	32.4	Huey and Pianka, 1981
Lacerta laevis	WF	84.5	81.0	Perry et al., 1990
Meroles suborbitalis	SW	40.4	45.9	Huey and Pianka, 1981
Nucras tessellata	WF	42.4	10.4	Huey and Pianka, 1981
Gekkonidae				
Gekko hokouensis	SW/WF	42.9	57.6	This report
Gekko japonicus	SW	133.3	107.5	This report
Teratoscincus roborowskii	SW	186.0	167.8	This report

WF species. This situation prompted us to trace some of the sources for the generalization that geckos are SW predators.

Dunham and Miles (1985) listed three gecko species, *Gehyra variegata*, *Heteronotia binoei* and *Oedura ocellata*, as SW predators, and quoted Vitt and Price (1982) as the source. Vitt and Price (1982) indeed listed 18 species of geckos, all as SW; this list included *G. variegata* and *H. binoei* but no *Oedura*. As sources for 16 species Vitt and Price (1982) quoted Pianka and Pianka (1976) and Pianka and Huey (1978) who, however, had described their stomach contents and not their FM. For the 17th species, *Coleonyx variegatus*, Vitt and Price (1982) quoted Tinkle and Hadley (1975) who had not dealt with FM, and Vitt and Congdon (1978), who had in fact listed the species, from their observations, as "sit and wait, limited foraging". The source for Vitt and Price's (1982) 18th species, *Lepidodactylus lugubris*, was an undated personal communication of Tinkle; he could have observed this species in trees, in rocks, or on houses having lights at night (Werner, 1990).

Dunham et al. (1988) gave the FM for nine species of geckos as SW, "based on literature descriptions": For three species they quoted Bustard (1968a,"1969"(=1968b), 1970, 1971), who, however, had said of *Gehyra variegata* (1968a), "Orthoptera ... fourth and fifth in numerical importance ... are the only items not found in the microhabitat. Presumably these are taken at night by foraging geckos when the grasshoppers are asleep;"of *Heteronotia binoei* (1968b), "grasshoppers ... most are presumably taken at night by foraging geckos when the grasshoppers are asleep;" and of *Oedura ocellata* (1971), "Most food eaten does not occur in the homesite and must be captured on the ground", indicating WF tendencies for all three (Bustard (1970) did not mention food or feeding). For two *Lygodactylus* species, Dunham et al. (1988) quoted Greer (1967) who, however, had intimated WF behavior, with ambushing only on opportune occasions. For the four remaining species they quoted How and Kitchener (1983) and Vitt (1986), though neither paper had dealt with FM.

Recently Arnold (1993) listed the forgaing modes of seven gecko taxa: he considered four species of *Pristurus* and *Quedenfeldtia trachyblepharus* passive feeders, *P. celerrimus* a cruising forager, and *Gonatodes* active foragers, although he provided no quantitative data by either of the two indices mentioned above. Hence by the criteria developed for other lizards (especially Lacertidae), of the seventeen gekkonoid species whose FMs have been quantified or described, only eight are strict SW predators: nine tend in varying degree to WF strategies. This agrees in principle with the recent survey of Cooper (1994a,b) who counted 52 species as SW and 8 as having WF or mixed strategies.

The Structure and Sources of the Variable FM of Geckos

Previous studies of lizard FM have found intraspecific variation, which varied in extent even among the species within a family in one region. Among Lacertidae in the Kalahari, the CV of MPM ranged from 10.0% in *Ichnotropis squamulosa* to 105.8% in *Eremias lineoocellata* and that of PTM ranged from 10.4% in *Nucras tessellata* to 81.1% in *Eremias lineoocellata* (Table 2; Huey and Pianka, 1981). In the gecko *Coleonyx variegatus*, males in an enclosure moved a greater distance per hour (17.6 m/hr) than did females (9.4 m/hr), although MPM were equal (0.57) (Kingsbury, 1989). In *Anolis polylepis*, Perry (1996) found significant differences in foraging behavior between males, females and juveniles. But we are unaware of any attention given to intraindividual variation in FM.

The three species reported here share great behavioral variability, as shown also (in two of them) by the high CVs of MPM and of PTM (Table 2). In each species, some individuals appeared to be very stationary, sometimes throughout the whole observation time (Table 1). Other individuals were so active that they could not be observed throughout the intended period. Single consecutive movement (or bouts of rapid alternations of standing and moving) lasted several minutes at the most (Table 1) but the maximum PTM observed in individuals approximated 50% in two of the species (Table 1).

Similar variability occurs in three other geckos for which some data are available. (1) The arenicolous *Stenodactylus doriae* in the 'Arava Valley, Israel: during 30 min observation periods, some individuals remain stationary throughout, whereas others move about actively (Werner, pers. obs.; Bogin, 1993). (2) The adult *Gekko gecko* individual briefly observed by Stanner et al. (in press) near Bangkok also behaved variably: In the first night it perched itself on a vantage point in the dark, and during 280 min of observation moved only 8 times, within only 40 cm (0.03 MPM, 2.5 PTM). In the second night it stationed itself at an illuminated window and was more active: during 640 min it moved 29 times (10 of these, eating); by these movements, which totalled 40 min, it locomoted nearly 50 meters (0.05 MPM, 6.25 PTM). (3) Preliminary observations of *Hemidactylus turcicus* (Perry, unpublished) also show great variability in FM.

No similar variability has been reported by Kingsbury (1989) from *Coleonyx variegatus*, so currently the combination of SW and WF behaviors is known only from gekkonine geckos.

This heterogeneity resembles that reported in *Lacerta laevis* (Lacertidae), in which during observation periods of five minutes, most individuals were either completely stationary or rather active (Perry et al., 1990).

Unless random, such heterogeneity could result from three factors, which are not mutually exclusive. (1) FM may change with age: in two species of *Ichnotropis* (Lacertidae), as well as in *Varanus komodoensis*, the juveniles are WF whereas the adults partly adopt SW behavior (Broadley, 1979; Auffenberg, 1981). But all the data discussed above were derived from adults and subadults.

(2) There are precedents for a sexual difference in the FM of lizards of other families, usually with males more active than females, by one measure or another (Pietruszka, 1986; Anderson, 1993; Perry, 1996). In *Coleonyx variegatus*, Kingsbury (1989) found that, although males and females moved equally frequently, males moved longer distances each time. This confirmed the earlier observation by Cooper et al.(1985), that males were more active (exposed) than females.

A reverse sexual difference occurs in *Phrynocephalus mystaceus* (Agamidae): males scout SW while perched in presumably territory-guarding situations, whereas females are WF (Polynova and Lobachev, quoted by Ananjeva and Tsellarius, 1986). Perry (1996) found a similarly reversed sexual difference in *Anolis polylepis*.

Of the geckos reported here, *Gekko hokouensis* males may have been a little more active than females. As explained above, *G. japonicus* and *Teratoscincus roborowskii* individuals were not sexed. In *Lacerta laevis* it is likewise unknown whether the different behavior patterns were related to sex (Perry et al., 1990).

(3) Species averages of MPM and PTM always mask intraspecific variation. With the usual short

observation bouts per individual, it remains unknown whether the variation is inter- or intra-individual. The longer observation bouts applied here, revealed individuals that switched from stationary to active behavior or vice versa. Because of the variations in the style and speed of the active behaviour, it seems that the animals were then foraging and not shifting to new SW stations; i.e., this was not saltatory foraging (O'Brien et al., 1989). But conceivably the brief pauses during WF in *G. hokouensis*, and also in the *Lacerta* spp. (Avery et al., 1987a, b; Avery, 1991), indeed serve for "snapshot scanning" as suggested by O'brien et al. (1989), so that in these species the WF periods are actually saltatory foraging. As the data now stand, the three species reported here, as well as *G. gecko* and *S. doriae*, seem to methodically practice a fluctuating FM, alternating SW and WF bouts.

Function of the Fluctuating FM in Geckos

Huey and Pianka (1981) summarized theoretical predictions and observations to the effect that an increase in food availability should result in an increase in foraging velocity, in SW as well as WF species. Moreover, Dunham (1983) found that *Sceloporus merriami* and *Urosaurus ornatus* switched from a WF to a SW foraging tactic during periods of low resource abundance.

If this principle were applicable to the fluctuating FM of geckos, a reversed "giving-up time" principle (Green, 1987) would be indicated: a gecko forages actively, till the lack of prey causes it to switch to the energetically cheaper SW strategy. When its patience is rewarded with prey, it "can afford to try its luck" and resumes the WF strategy.

We suggest that some geckos fluctuate between the two FMs irrespective of momentary success. Geckos are visual hunters despite the poor light in which most operate. They seem to cope with this handicap by (1) having larger eyes if nocturnal and also (2) if foraging cursorially, without scouting from vantage points (Werner, 1969); (3) by foraging in erect, stretch-limbed, posture (if cursorial), the better to view their surroundings (Werner and Broza, 1969); and (4) by being more active, WF, in the better-illuminated times of night (at least in some species) (Frankenberg and Werner, 1979; Bouskila et al., 1992). The last phenomenon seems to parallel the observation of Dunham (1983) quoted above: when food is more apparent, foraging becomes more active.

We hypothesize that (5) by alternatingly employing SW and WF strategies, some geckos, foraging when the range of vision is short, increase their probability of encountering stationary as well as mobile prey while reducing the costs associated with locomotion (e.g., energy expenditure and detection by predators). This would parallel the behavior of other animals which vary their foraging tactics at times of food shortage or increased food requirements (Curio, 1976:20, 27).

The employment of both SW and WF modes by these geckos may be related to lack of competition: The segregation of diurnal lizards in a community into SW and WF species presumably aids in resource partitioning (Pianka et al., 1979:87-88; Huey and Pianka, 1981:995). This dimension of resource partitioning comes in addition to the many reviewed by Schoener (1974). The species reported here, *Gekko hokouensis*, *G. japonicus* and *Teratoscincus roborowskii*, were each the sole nocturnal lizard species observed in the area. Where *G. gecko* was observed (Stanner et al., in press) it was associated only with *Hemidactylus frenatus*, two orders of magnitude smaller (>100g and <10g, respectively). Where *Stenodactylus doriae* was observed (Bogin, 1933) the area carrying its dense population (Bouskila, 1987) contains very few individuals of other cursorial geckos. It would be instructive to observe FM where a number of gecko species forage together. The comparison should be made within the Gekkonidae so as to minimize the confusion of ecological and phylogenetic factors (Dunham and Miles, 1985; Huey and Bennett, 1986).

FM and Relative Clutch Mass

It has been stated that geckos, believed to be SW predators, have small RCM, compared to SW lizards of other families (Vitt and Price, 1982; Vitt, 1986). However, on the one hand, Werner (1989) has already pointed out that the RCM of geckos is actually somewhat larger than generally believed, being intermediate between those typical of WF and SW lizards. On the other hand, we have shown here that the FM of geckos is not as strictly SW as generally stated but contains WF components to varying extent. Hence geckos, rather than having a paradoxically low RCM, are in fact intermediate between SW and WF lizard groups in both their FM and RCM.

Werner and Frankenberg (1989) have shown that among lizard species, the correlation of the RCM to the relative body size of the female (female ra as percent of male ra), depends on the FM of the species: in SW predators (Agamidae, Chamaeleonidae, Iguanidae), the larger the female is compared to the male, the greater the RCM. But in WF species (Lacertidae, Scincidae), the larger the female (relative to the male), the smaller the RCM. Interestingly, the relationship among gekkonidae tends to be as among

WF species (Werner, 1996). Moreover, Vitt (1990) has pointed out that among sympatric caatinga lizards, geckos differ from typical SW species in possessing continual rather than seasonal reproduction. The last two observations seem to further support the notion that geckos should not be considered strict SW predators.

Conclusions

By the statistical measure of MPM (as used for lacertids), the geckos *Coleonyx variegatus, Gekko gecko, G. hokouensis, G. japonicus* and *Teratoscincus roborowskii* are SW predators.

Gekko gecko, G. japonicus and *Teratoscincus roborowskii* are SW predators also by the statistical measure of PTM (as used for lacertids); but by this measure *Coleonyx variegatus* and *G. hokouensis* are WF. Most other gekkonine species, whose foraging has been verbally described in literature, also appear to have at least partial WF tendencies.

The foraging behavior of *Gekko gecko, G. hokouensis, G. japonicus, Stenodactylus doriae* and *Teratoscincus roborowskii* is sometimes SW and sometimes WF; at least in *G. hokouensis, G. japonicus* and *T. roborowskii* individuals appear to fluctuate between these two predation tactics.

The variable, often fluctuating, FM of these gekkonines probably serves to increase the variety of accessible prey for these nocturnal visual hunters.

The employment of both SW and WF tactics by these gekkonines may depend on the absence of other, competing nocturnal lizards.

Geckos are intermediate between SW and WF lizards, in both foraging mode and relative clutch mass.

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A New Species of *Rhabdophis* (Serpentes: Colubridae) from Hainan Island, China

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Abstract.- After detailed examination of a population of colubrine snakes previously identified as *Natrix* (sensu lato) *chrysarga* (Schlegel), from Hainan Island, China, it is now considered an undescribed species. This paper describes this new species and names it as *Rhabdophis adleri*.

Key words: Serpentes, Colubridae, *Rhabdophis adleri* sp. nov., China.

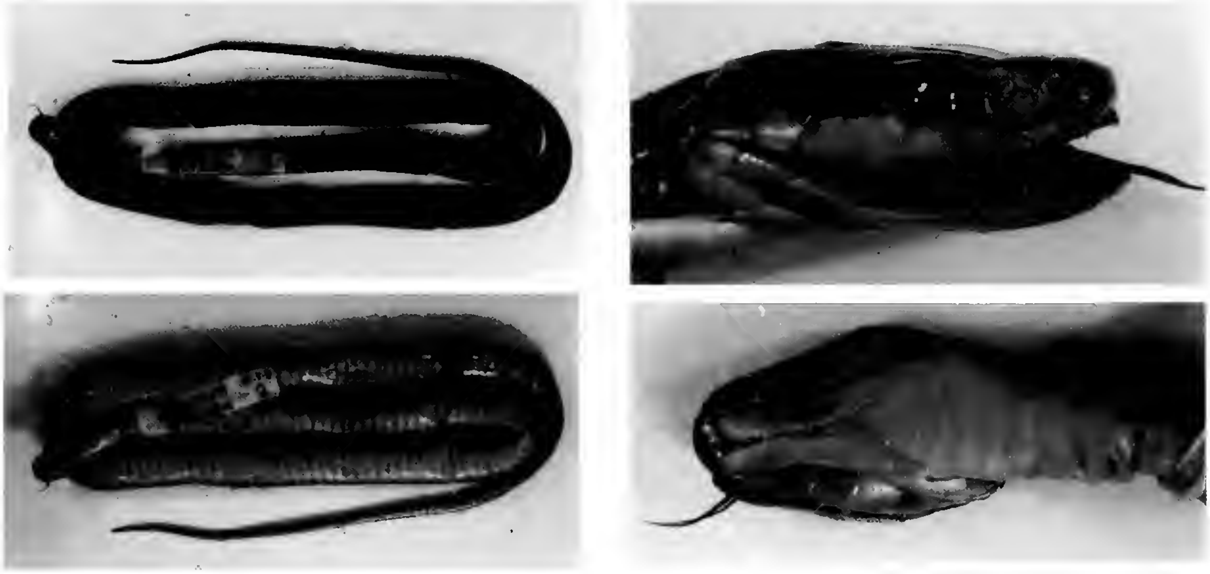

Figure 1. Allotype of Rhabdophis adleri.

Introduction

G. A. Boulenger ("1899," 1900) reported *Tropidonotus chrysargus* Schlegel from Wuchih Mts. (= Mt. Wuzhi), Hainan. M. A. Smith (1923) reported one specimen of *Natrix chrysarga* (Schlegel) from Kaphao (near Mt. Wuzhi), Hainan Island, which had 154 ventrals and 83 pairs of subcaudals, 8 supralabials, 4th and 5th touching the eyes. C. H. Pope (1935) reported two specimens from Hainan and two from Hong Kong as *Natrix chrysarga* (Schlegel). His description is abstracted from De Rooij (1917:89), but he noted that "Hainan examples seem to lack the dark spots usually present laterally on the ventrals" (loc. cit., p. 102). R. Bourret (1934) described *Natrix chrysarga callichroma* from Ba-vi, Tong King, Vietnam. M. A. Smith (1938) described *Natrix auchenia* based on specimens from Five Finger Mountain (Mt. Wuzhi), Hainan Island. M. A. Smith (1943) indicated under *Natrix chrysarga* that "the Himalayan and Hainan records of this snake are not correct," and considered his *Natrix auchenia* to be a synonym of *Natrix callichroma* Bourret, 1934. Thus, the Hainan specimens were referred to the latter. Recently, M. Toriba (1994), following M. A. Smith, also stated that the Hainan records of *Rhabdophis chrysargus* "should be replaced by *R. callichromus*." Z. X. Li (1962) recorded *Natrix himalayanus* as new to Hainan Island. I have examined one of his specimens (FDUA162), and actually it belongs to the new species described in this paper. A herpetological survey was carried out on Hainan Island in 1964 by a combined team of Sichuan Medical College (now West China University of Medical Sciences) and Southwest Institute of Biology (now Chengdu Institute of Biology), Academia Sinica. Nine specimens of *Natrix* (sensu lato) were

Table 1. Dimensions and scale counts of *Rhabdophis adleri* sp. nov.

Number	Locality (All Hainan Is.)	Sex	SVL	TL	Supra-labials	Infra-labials	Oculars	Ocu/temp	V	Sc	Bars
CIB64III5245	Mt. Wuzhi	M	505	205	2-3-3	10(5)	2-3	2+2+3/2	153	82	57+29
CIB64III5112	Mt. Wuzhi	F	445	125	2-3-3	10(5)	2-3	2+2+3	164	40+	69+18
CIB64III5114	Mt. Wuzhi	F	573	138	2-3-3	10(5)	1-3	2+2+3	157	52+	45+?
CIB64III5115	Mt. Wuzhi	F	600	200	2-3-3	10(5)	2/1-3	2+1/ 2+2/3	157	81	66+18
CIB64III5228	Mt. Wuzhi	F	687	240	2-3-3	10(5)	1-3/4	2+2+3	154	83	56+26
CIB64III5883	Mt. Diaoluo	M	515	180	2-3-3	10(5)	2/1-3	2+2	152	85	62+9
CIB64III5917	Mt. Diaoluo	M	595	195	2-3-3	10(5)	2-3	2+2+3/2	151	82	59+15
BIZ742	Mt. Diaoluo	M	—	—	2-3-3	10(5)	2-3	2+2	152	85	46+14
BIZ789	Mt. Diaoluo	M	—	—	2-3-3	10(5)	2/1-3	2+2	150	—	55+23
FDU-A162	Mt. Diaoluo	F	530	185	2-3-3	10(5)	2-3	2+2/3	155	82	—
BIZ757	Mt. Diaoluo	F	—	—	2-3-3	10(5)	2-3	2+3	153	76	64+30
BIZ787	Mt. Diaoluo	F	—	—	2-3-3	10(5)	1-3	2+2	157	65+	57+27 +
BIZ792	Mt. Diaoluo	F	—	—	2-3-3	10(5)	1-3	2+3/2	156	79	49+7
BIZ801	Mt. Diaoluo	J	—	—	2-3-3	10(5)	2-3	2+2	151	83	39+3
BIZ1021	Mt. Jianfengling	M	—	—	2-3-3	10(5)	1-3	2+3	155	88	55+21
BIZ641	Mt. Jianfengling	F	—	—	2-3-3	—	1/2-3	1+2	156	87	61+32
BIZ646	Mt. Jianfengling	F	—	—	2-3-3	10(5)	1-3	2+2	157	79	56+30
BIZ655	Mt. Jianfengling	F	—	—	3-2-3	—	2/1-3	2+2	154	60+	51+6+
BIZ659	Mt. Jianfengling	F	—	—	3-2-3	10(5)	1-3	2+3/2	155	63+	65+19
BIZ1013	Mt. Jianfengling	F	—	—	2-3-3	10(5)	1-3	2+2	156	81	62+18
—	Hainan Is.	F	—	—	2-3-3	10(5)	1-3	2+2	153	84	59+29

BIZ: Institute of Zoology, Academia Sinica (Beijing)

CIB: Chengdu Institute of Biology, Academia Sinica

FDU: Fudan University (Shanghai)

caught that are referable to the new species. I also examined specimens belonging to the same species from Hainan Island collected by Institute of Zoology, Academia Sinica. All the specimens examined by me were originally identified as *Natrix chrysarga* (as in B. Q. Hu et al., 1980:67) or *Rhabdophis chrysargus* (as in Zhao and Adler, 1993:256). After detailed examination, I now believe that it should be a new species which has never been described before.

Rhabdophis adleri sp. nov.

Tropidonotus chrysargus: Boulenger, "1899" (1900): 957.

Natrix chrysarga: Smith, 1923: 201; Pope, 1935: 101 (part); Hu et al., 1980: 67.

Natrix himalayanus: Li, 1962: 432.

Rhabdophis chrysargus: Zhao and Adler, 1993: 256.

Holotype: CIB 64III5917, adult male, 10 June 1964, Dali Village in Mt. Diaoluo, Lingshui Co., Hainan Prov., China, 225 meters.

Allotype: CIB 64III5228, adult female, 10 May 1964, Mt. Wuzhi, Qiongzhong Co., Hainan Prov., China, 500 meters (Fig. 1).

Paratypes: CIB 64III5112, 5114-5, females, 24-25 April 1964, CIB 64III5245, male, 11 May 1964, Mt. Wuzhi, Qiongzhong Co., Hainan Prov., China, 500-610 meters; CIB 64III5883, male, CIB 64III5441, juvenile, 1-9 June 1964, Mt. Diaoluo, Lingshui Co., Hainan Prov., China, 82-217 meters; CIB 64III6612, juvenile, 25 August 1964, Mt. Yinggeling, Baisha Co., Hainan Prov., China, 670 meters.

All the type series, but one (CIB 64III5245) which was presented to Fujian Medical College, are preserved in Chengdu Institute of Biology, Academia Sinica.

Diagnosis: A *Rhabdophis* with a nuchal groove and the last two maxillary teeth abruptly enlarged, but without a nuchal gland. Upper labials 8, the third to fifth (rarely fourth and fifth) touching the eye; 19 dorsal scale rows at midbody, all strongly keeled; olive green above with short dorso-lateral, yellowish transverse bars 39-69 +3-32 pairs.

Description of Holotype: Preocular 2, postocular 3; anterior temporal 2, posterior temporal 2; supralabial 8, the third to fifth touching the eye; infralabials 10, the first pair in contact with each other behind the mental, first five pairs in contact with the anterior chin-shields. Dorsal scales in 19 rows at neck and midbody, 17 rows before vent, the anterior dozen scales just behind parietals of two median rows small and arranged in parallel rows in formation of a nuchal groove, all the dorsal scales strongly keeled, the outer most ones slightly keeled; ventrals 151; anal divided; subcaudals in 82 pairs.

Total length 790 mm, tail length 195 mm, tail 0.25 of the total length.

Olive green above, with short yellow transverse bars on D_5 and D_6 at an interval of 1.5-2.5 scales, the dorso-lateral yellow transverse bars 59 pairs on body and 15 pairs on tail. Lower parts light yellow. Top of head olive green, a reverse "V" -shaped mark in light color upon the nape, upper lip light yellow with partial sutures grayish brown; ventral surface of head yellowish white.

The hemipenis is forked at 9th subcaudal plate and extends to the 13th subcaudal plate, bi-lobed type. It is spinous throughout and has a single very large basal spine or hook. The spines are small and relatively uniform in size but more dense on the tip of the organ and become larger on the base. The skin of the base forms cup-like depressions. The sulcus spermaticus is prominent and forked at the forked point of the organ (Zhang et al., 1984, based on holotype and 64III5883).

Variation of Allotype: The allotype (Fig. 1), an adult female, 1 preocular, 3 postoculars on left and 4 on right; ventrals 154; subcaudals in 83 pairs; yellow transverse bars 56+26 pairs; total length 927 mm, tail 240 mm, tail 0.26 of the total length.

Variation: I examined, excepting the type series, two males, four females, and one juvenile from Mt. Diaoluo, one male and five females from Mt. Jianfengling, Luodong Co., Hainan Island, and another female from Hainan Island, totally six males, fourteen females, and one juvenile (see Table 1). The variation is as follows: 2 preoculars (rarely 1), 3 postoculars (1 to 4); 2 anterior temporals (rarely 1), 2 posterior temporals (rarely 3); 8 supralabials, 3rd to 5th touching the eye, only two females from Mt. Jianfengling with only 4th and 5th touching the eye; 10 infralabials, 5 in contact with anterior chin-shield. Ventrals in males (n=6) 150-155 (mean 152.2), in females (n=14) 153-164 (mean 156); anal divided; subcaudals in males (n=5) 82-88 (mean 84.4), in females (n=9) 76-87 (mean 81.3). The yellow transverse bars are 39-69 + 3-32 pairs.

All the specimens examined have a nuchal groove. All specimens in the type series were dissected and no type of nuchal gland either sacculated or non-sacculated or naked area of skin could be found.

Comparisons: This new species differs from *Natrix callichroma* Bourret, 1934 and *Natrix auchenia* Smith, 1938 and in the latter "the scales of the neck are not altered in shape or size, but on stretching the skin of that part, two parallel longitudinal areas of naked skin are exposed," and "beneath the naked areas lies the gland (sacculated type); the coloration is "grayish-olive above, with indistinct narrow black, transverse bars, intersected on the dorso-lateral line by short whitish bars" (M. A. Smith, 1943:309). The scales of the neck of the new form are altered in shape and size in formation of a nuchal groove, but lack a nuchal gland; and the coloration is much different because black transverse bars intersected on the dorso-lateral line by short, whitish bars is never found (as in *auchenia*). This new species differs from *Tropidonotus chrysargos* Schlegel, 1937 by the latter having "1 preocular;...9 supralabials, 3rd to 5th touching the eye; usually six infralabials touching the anterior genials," and "hemipenis to the 8th caudal plate, forked near the tip" (loc. cit., p. 308). This new form has 2 (vary rarely 1) preoculars; 8 supralabials, 3rd to 5th touching the eye; only five infralabials touching the anterior chin-shield; and hemipenis to the 13th subcaudal plate and forked at 8th subcaudal plate. This new species differs also from *Tropidonotus himalayanus* Günther, 1864 by the latter having "1 preocular; 8 supralabials, 4th and 5th touching the eye" and "hemipenis extending to the 7th caudal plate, not forked" (loc. cit., p. 300), and the coloration is different.

Biological Data: Widely distributed over entire island at an altitude from 82 to 670 meters. It was found in the plains, hills, and low mountains. It is often found on the ridges between rice fields, among grass along small paths in hilly regions, and also is found at the border of forests. Our specimens were collected during the end of April and the middle of June. Most of them were collected around ten o'clock in the morning on fine days. It feeds on small frogs and fishes. No dates are available on its reproduction.

Etymology: I take great pleasure in naming this new species for Prof. Kraig Adler of Cornell University in Ithaca, New York, USA, in honor of his devotion to the study of Chinese amphibians and reptiles. He collaborated with me to prepare the book entitled "Herpetology of China."

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Infraspecific Classification of Some Chinese Snakes

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Abstract-Infraspecific classification of some Chinese snakes was carried out by calculating both coefficient of difference (C. D.) and mean value comparison. Four new subspecies were described in number 4, volume 14 of Sichuan Journal of Zoology, Chengdu (Zhao, 1995). The following is a condensed version of these descriptions.

Key words: Reptilia, Ophidia, *Xenopeltis hainanensis jidamingae* ssp. nov., *Psammodynastes pulverulentus papenfussi* ssp. nov., *Ovophis monticola zhaokentangi* ssp. nov., *Trimeresurus stejnegeri chenbihuii* ssp. nov., China.

Xenopeltis hainanensis jidamingae ssp. nov.

Holotype: ZM73002, adult male, July 1973, Puyun Xiang, Longquan Co., Zhejiang Province, China, altitude about 700 meters. The holotype is preserved in Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China.

Diagnosis: This new subspecies has higher ventral counts, 159-164 (mean 161.6; Table 1), than that of the nominate subspecies, which has 152-157 (mean 154.7).

Distribution: Mainland China, including Zhejiang, Fujian, Jiangxi, Hunan, and Guangdong provinces, and Guangxi Zhuang Autonomous Region.

Etymology: This new subspecies is named after Professor Da-ming Ji of Liaoning University in honor of her devotion to the study of ecology of *Agkistrodon shedaoensis* Zhao.

Psammodynastes pulverulentus papenfussi ssp. nov.

Holotype: MVZ 23857, an adult female, 5 May 1934, Kuraru (=kueitzuchiao), Koshun District (=Henchun Town), Takao-shu Province (now Pintung Hsien), Taiwan, China, 150 meters, collected by J. Linsley Gressitt. The holotype is preserved in the Museum of Vertebrate Zoology, University of California, Berkeley, California, USA.

Diagnosis: This new subspecies has higher ventral and subcaudal counts (Table 2). Ventral plus subcaudal counts range from 214-245, mean 234.2, while that of the nominate subspecies is 201-245, mean 219.5.

Distribution: Taiwan Island, China.

Etymology: I take great pleasure in naming this new subspecies for Dr. Theodore J. Papenfuss of the Museum of Vertebrate Zoology, University of California at Berkeley. He has collaborated with us to study desert amphibians and reptiles in northwestern China since 1987 and got a lot of achievements.

Ovophis monticola zhaokentangi ssp. nov.

Holotype: KIZ730093, adult male, 11 December 1973, Bapo, Gongshan Co., Yunnan Province, China, altitude 1400-1500 meters.

Allotype: KIZ730018, adult female, 23 May 1973, the same locality as the holotype.

Paratypes: KIZ730096, male; KIZ730024 and 730032, females, 29 May-26 December 1973, the same locality as the holotype; and CIB740003, male, 17 March 1974, Pianma, Lushui Co., Yunnan Province, China, altitude 1980 meters.

The specimens examined are preserved in the Kunming Institute of Zoology (KIZ) and the Chengdu Institute of Biology (CIB). Both institutes belong to Academia Sinica.

Diagnosis: This new subspecies has higher ventral plus subcaudal counts, 215-225 (mean 217.5±5.28; Table 3) than that of all the other known subspecies. The coloration of the head is similar to the nominate subspecies.

Distribution: Gaoligong Shan north of Pianma, Lushui Co., extreme western Yunnan Province, China.

Etymology: This new subspecies is named after Professor Ken-tang Zhao of Suzhou Railway Normal College in honor of his contributions to the study of the lizard genera *Phrynocephalus* and *Eremias*.

Trimeresurus stejnegeri chenbihuii ssp. nov.

Holotype: CIB64III5599, adult male, 6 June 1964, Diaoluo Shan, Lingshui Co., Hainan Province, China, altitude about 250 meters.

Allotype: CIB641115945, adult female, 11 June 1964, the same locality as the holotype.

Paratypes: CIB641115906, 5944, 5978-9, 6013, 6043-4, 6069, 6101, 6104, 6107, males; CIB641115600, 5735, 6014, females, 6-15 June 1964, Diaoluo Shan, Lingshui Co., Hainan Province, China, altitude 225-290 meters. CIB641115110, 5181, 5261-2, males, 23 April to 12 May, 1964, Wuzhi Shan, Qiongzhong Co., Hainan Province, China, altitude 500 meters.

Diagnosis: This new subspecies has higher ventral counts, 169-178 (mean 172.6; Table 4) in males and 168-174 (mean 172) in females, while the nominate subspecies has 154-170 (mean 162.6) in males and 154-172 (mean 162) in females.

Distribution: Hainan Island, Hainan Province, China.

Etymology: This new subspecies is named after Professor Bi-hui Chen of Anhui Normal University in honor of his contributions on research and protection of the endangered Chinese Alligator.

Acknowledgments

The data for Taiwan specimens of *Psammodynastes pulverulentus* and *Trimeresurus stejnegeri* (including *formosensis* and *kodairai*) is taken from M. Maki (1931), and the data for Philippine specimens of *P. pulverulentus* is taken from E. H. Taylor (1922). I express my cordial appreciation to these authors. I also express my sincere thanks to the Kunming Institute of Zoology, Academia Sinica and the Zhejiang Museum of Natural History for permission to examine specimens.

Appendix I

Tables 1-4

Table 1. Comparison of *Xenopeltis h. hainanensis* Hu and Zhao, 1972 and *X. h. jidamingae* Zhao, 1995.

Subspecies		*X. h. hainanensis*		*X. h. jidamingae*
n		7		7
Ventral Counts:	Range	152-157		159-164
	M±S. D.	154.7±2.14		161.6±2.07
ΔM			6.9	
C. D.			1.64 (>1.28)	
S. E.d			1.12	
ΔM/S. E.d			6.16 (>3)	

Table 2. Comparison of *Psammodynastes p. pulverulentus* (Boie, 1927) and *P. p. papenfussi* Zhao, 1995.

Subspecies		*P. p. papenfussi*		*P. p. pulverulentus*
n		22		37
V+Sc	Range	214-245		201-245
	M±S. D.	234.2±6.62		219.5±9.87
ΔM			14.7	
C. D.			0.89 (<1.28)	
S. E.d			2.37	
ΔM/S. E.d			6.16 (>3)	

Table 3. Comparison of three subspecies of *Ovophis monticola* (Günther, 1864).

Subspecies		*O. m. monticola*		*O. m. zhaokentangi*		*O. m. orientalis*	
n		40		6		25	
V+Sc	Range	172-203		215-225		*169-182*	
	M±S. D.	188.6±7.38		217.5±5.2		*176±3.48*	
ΔM			28.9		41.5		*12.6*
C. D.			2.28 (>1.28)		4.74 (>1.28)		*1.16* *(<1.28)*
S. E.d			3.13		1.77		*1.58*
ΔM/S. E.d			9.23 (>3)		23.45 (>3)		*7.97 (>3)*

Table 4. Comparison of *Trimeresurus s. stejnegeri* Schmidt, 1925, *T. s. chenbihuii* Zhao, 1995, and Taiwan population.

Subspecies		*T. s. chenbihuii*		*T. s. stejnegeri*		Taiwan Population	
n		18		175		26	
V+Sc	Range	236-256		199-246		*213-236*	
	M±S. D.	245.9±5.54		229.3±6.86		*227.5±5.71*	
ΔM			16.6		1.8		*18.4*
C. D.			1.34(>1.28)		0.14 (<1.28)		*1.64* *(>1.28)*
S. E.d			1.67		1.42		*1.73*
ΔM/S. E.d			9.94 (>3)		1.27 (<3)		*10.64* *(>3)*

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Journal article from a journal that uses year instead of volume

Gatten, R. E. Jr. 1974. Effect of nutritional state on the preferred body temperatures of turtles. Copeia 1974(4):912-917.

Journal article, title translated, article not in English

Ananjeva, N. B. 1986. [On the validity of *Megalochilus mystaceus* (Pallas, 1776)]. Proceedings of the Zoological Institute, Leningrad 157:4-13. (In Russian).

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Cai, M., J. Zhang, and D. Lin. 1985. [Preliminary observation on the embryonic development of *Hynobius chinensis* Guenther]. Acta Herpetologica Sinica 1985, 4(2):177-180. (In Chinese).

Book

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Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25-91. In C. Gans and F. H. Pough (eds.), Biology of the Reptilia, Vol. 12, Physiological Ecology. Academic Press, New York.

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United States Environmental Data Service. 1968. Climatic Atlas of the United States. Environmental Data Service, Washington, D. C.

Abstract of oral presentation

Arnold, S. J. 1982. Are scale counts used in snake systematics heritable? SSAR/HL Annual Meeting. Raleigh, North Carolina. [Abstr].

Thesis or dissertation

Moody, S. 1980. Phylogenetic and historical biogeographical relationships of the genera in the Agamidae (Reptilia: Lacertilia). Ph.D. Thesis. University of Michigan. 373 pp.

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