KOREAN JOURNAL OF ZOOLOGY
Vol. 22, No. 4, 153—164 (1979)

Biochemical Variation and Systematic Status of the Genus *Agkistrodon* (Crotalidae) in Korea

Nam Keuk Paik, Yung Jin Kim* and Suh Yung Yang**
(Dept. of Biology, Gangneung College, *Korea Atomic Energy Research Institute, and **Dept. of Biology, Inha University)

韓國產 살모사 屬에 關한 遺傳的 變異 및 系統學的 硏究

白 南 極·金 英 眞*·梁 瑞 榮**
(江陵大學 生物學科, *韓國原子力硏究所, **仁荷大學校 生物學科)
(Received September 5, 1979)

적 요

한국산 살모사 속의 분류학적 재 검토를 위하여 352개체의 표본을 재료로 형태학적 및 유전학적 조사를 한 결과 다음과 같은 결과를 얻었다.

형태학적 조사

1. Gloyd의 분류법에 준하여 분류한 결과 한국산 살모사 속은 3종 임을 확인하였고 분류가 애매한 중간 형태의 개체는 하나도 발견되지 않았다.

2. 강원도 설악산과 전라북도 덕유산에서는 이들 3종이 모두 채집 되었고 살모사와 쇠살모사는 경기도 광릉 및 용문산에서 공서함을 확인하였다. 이들 지역에서도 잡종 개체는 발견되지 않음을 미루어 보아 이들 3종은 생태적으로 완전히 격리된 종들이라 사료된다.

3. 모든 종들은 뚜렷한 성적이형을 나타내었다.

4. 까치살모사는 다른 두 종에 비하여 미장의 상대비가 적었고 복린의 수는 많았다.

5. 살모사와 쇠살모사는 복린의 수, 미하린의 수 및 미장의 상대비에 유의한 차이가 없었다.

유전적 분석

1. 전기영동법을 이용하여 26개의 유전자를 분석한 결과 12개의 유전자 (46.1%)는 종 사이에 차이가 없었고 4개의 유전자 (15.4%)는 거의 동일하였으나 유전자 빈도에 약간의 차이가 있었으며 나머지 10개 유전자 (38.5%)는 종 사이에 뚜렷한 차이가 있었다.

2. 종평균 유전적 다형형의 빈도는 9.03%로서 이 값은 다른 척추동물

에 비하여 훨씬 적은 값이었다.

3. 종간의 유전적 근연치는 평균 S=.695 및 D=.342로써 이 값으로 미루어 이들은 뚜렷이 독립된 종이라고 여겨진다.

4. 쇠살모사는 유전적으로 까치살모사와 유연한 관계가 더 크고 까치살모사와 살모사와는 유연관계가 제일 적었다.

이상의 결과로 볼 때 한국산 살모사 속은 Gloyd가 주장한 바와 같이 살모사 (*Agkistrodon bromhoffii brevicaudus*), 쇠살모사 (*A. caliginosus*) 및 까치살모사 (*A. saxatilis*)의 3종으로 분류함이 타당하다고 사료된다.

INTRODUCTION

For more than a century there has been a great deal of confusion in the systematics of *Agkistrodon* in Korea, mainly due to the morphological close similarity of the species within the genus, limited materials, wide range of individual variability and improper choice of taxonomic characters. Several species names (Halys-intermedius-blomhoffii complex) of Korean *Agkistrodon* appear in the literature (Strauch, 1868: Stejneger, 1907, 1925: Thompson, 1916: Slevin, 1925: Emelianov, 1929, 1937: Sowerby, 1930, Maki, 1931: Rendahl, 1933: Tanner, 1953: Stewart, 1954: Dixon, 1956: Shannon, 1956: Hahn, 1960: Webb *et al.*, 1962: Klemmer, 1963: and Terentév and Chernov 1965).

Recently Gloyd (1972) gathered over one hundred forty specimens of this genus in Korea and carried out an intensive morphological analysis and described three species including a new species: *Agkistrodon blomhoffii brevicaudus, A. saxatilis* and *A. caliginosus*. Kang and Yoon (1975) lumped these species into one single species, *A. halys*, followed by Pope (1935).

The purposes of this report were to classify them based on Gloyd's criteria of morphological characters and to compare the genetic relationship among them by means of electrophoresis.

MATERIALS AND METHODS

Morphometric analysis

The specimens for the morphometric analysis were collected during 1954—1977 period and preserved in 10% Formalin. A total of 352 specimens from 17 localities was classified into three species categories by external morphology according to Gloyd's criteria (Fig. 1. A, B, and C). Among them 233 adult specimens were used for morphometric analysis. The number of ventrals and subcaudals in each specimen was counted and tail to body length ratio (in percentage) calculated. Because ontogenetic and sexual variation can observe interspecific differences, we used only adult specimens and males and females were treated separately.

Electrophoresis

Live specimens of *A. b. brevicaudus* (n=6), *A. caliginosus* (n=5) and *A. saxatilis* (n=6) were collected at Mt. Seolag, Kang Won Do in 1977 and shipped to the lab. Blood samples were obtained by nicking the aorta and collecting blood in a heparinized pipette. The sample was centrifuged at 2,500 g for 10 minutes to separate plasma from the red blood cells and the plasma fraction was stored at −40° C until use. The red blood cells were suspended and washed twice in 10 volumes of 0.85% saline and lysed by freezing in a volume of deionized water. Stroma and lipids were removed by centrifuging the hemolysate at 49,500 g for 30 minutes at 4° C, and the extracted hemolysates were stored at −40° C. Liver and kidney were individually homogenized using the methods of Selander *et al.* (1971). The supernatant was pipetted and stored in a glass vial. Plasma, hemolysate and tissue extracts were subjected to horizontal starch-gel electrophoresis as described by Selander *et al.* (1971) and Kim *et al.* (1976). The following gel buffer systems were used: (1) lithium hydroxide: general proteins (GP-1, 2, 3 and 4) in plasma, general proteins (GP-5 and 6), esterases (Es-1 and 2), glutamic oxaloacetate transaminases (GOT-1 and 2), phosphoglucose isomerase (PGI), and peptitase (Pept) in liver: (2) discontinuous triscitrate (Poulik): hemoglobin (Hb) in hemolysate and mannose-6-phosphate isomerase (MPI) in kidney: (3) continuous triscitrate (pH 8.0): isocitrate dehydrogenases (IDH-1 and 2), lactate dehydrogenases (LDH-1 and 2), malate dehydrogenases (MDH-1 and 2), and α-glycerophosphate dehydrogenase (α GPD) in kidney: (4) tris-versene-borate (pH 8.5): alcohol dehydrogenase (ADH) and indophenol oxidases (IPO-1 and 2) in liver: and (5) tris malate-EDTA: 6-phosphogluconate dehydrogenase (6PGD) and xanthine dehydrogenase (XDH) in liver.

Proteins, as represented by bands on starch gels, were designated by their mobility from the origin. One allele, farthest away from the origin, was designated as a and b, c *etc.* in descending order. If an enzyme was encoded by two or more loci, the one with the highest mobility towards the anode was designated as 1. Genetic interpretations of allozymic variation are based on criteria elaborated by Selander *et al.* (1971).

Genetic relationships among species were assessed by calculating Rogers' coefficient of genic similarity (Rogers, 1972) and Nei's genetic distance, D (Nei, 1971): the formula used for D was that presented by King and Wilson (1975). Using the Rogers' similarity values, clustering technique was utilized to analyze relationships among them. The unweighted pair group and the complete linkage methods (Sneath and Sokal, 1973) were performed on a CDC6400 computer using the NT2 program of the Numerical Taxonomy Program, University of California, Berkeley (developed by W.W. Moss).

Specimens examined

Sample localities and collection date are listed by species. Sample sizes for each analysis are indicated (N=total number of specimens collected: G=genetic: M=morphological). Species designations used here are from Gloyd (1972).

Agkistrodon blomhoffii brevicaudus Stejneger.

Gyeonggi-do: Gwangneung, June 1955-July 1960 (N=25, M=23). Mt. Yongmun, July 1957 (N=2). Deogjeog Isl., Aug. 1959 (N=6). Anmin Isl., July 1960 (N=2).

Gangwon-do: Mt. Seolag, June 1967 and July 1977 (N=9, G=6). Gwangpan-ri, Chunseong-gun (from local store), Aug. 1970 (N=26, M=26). Hwangchon-gun (from local store), Aug. 1971 (N=16).

Gyeongsang-bugdo: Andong, June 1965 (N=7).

Jeonra-bugdo: Mt. Deogyu, Aug. 1954-Aug. 1962 (N=47, M=43).

Jeonra-namdo: Geoje Isl., July 1953 (N=3). Jindo Isl., Aug. 1960 (N=5).

A. caliginosus Gloyd.

Gyeonggi-do: Gwangneung, June 1955-May 1960 (N=23, M=23).
Mt. Yongmun, July 1957 (N=1).

Gangwon-do: Mt. Seolag, June 1967 and July 1977 (N=9, G=5).

Jeonra-bugdo: Mt. Deogyu, Aug. 1954-June 1977 (N=92, M=86).

A. saxatilis Emelianov.

Gangwon-do: Mt. Seolag, June 1967 and July 1977 (N=9, G=6). Mt. Odae, Aug. 1973 (N=2). Mt. Palbong, Hongcheon-gun, July 1977 (N=1), Chunchon (from local store), Aug. 1970-June 1977 (N=25). Gohan, Chunseong-gun, Sept. 1977 (N=1). Deogyuwon, Chunseong-gun, Sept. 1977 (N=1). Jeongseon, June 1964 (N=4).

Jeonra-bugdo: Mt. Deogyu, July 1954-Aug. 1959 (N=36, M=32).

RESULTS AND DISCUSSION

Morphometric analysis

All specimens examined were well fit to the Gloyd's criteria to classify them into either one of three species categories and no specimen was doubtful to classify correctly. For this reason we conclude that Gloyd's morphological characters are good criteria to distinguish each species.

Three species are sympatric at two localities (Mt. Seolag, Gangwon-do and Mt. Deogyu, Jeonra-bugdo) and *A. caliginosus* and *A. b. brevicaudus* are sympatric at Gwangneung and Mt. Yongumn, Gyonggi-do. No intermediate form or "Hybrid like" was found at these sympatric localities. Therefore, it seems likely that they are ecologically well isolated species.

The results of morphometric analysis based on 233 adult specimens from three large sample sizes are presented in Table 1, 2 and 3.

Table 1. Variation in number of ventrals.

Species	Locality*	Males				Females			
		N	Range	Mean	SE	N	Range	Mean	SE
A.b. brevicaudus	1	9	142—150	146.4	0.86	14	144—159	148.4	0.91
	2	10	143—149	145.8	0.65	16	144—150	147.6	0.46
	3	20	142—151	145.9	0.60	23	140—152	146.8	0.57
A. caliginosus	1	10	146—150	148.1	0.48	13	144—150	146.7	0.62
	3	42	142—150	146.7	0.36	44	142—151	147.3	0.58
A. saxatilis	3	13	152—160	156.1	0.60	19	153—167	158.8	0.87

* 1. Gwangneung, Gyeonggi-do
2. Gwangpan-ri, Chunseong-gun, Gangwon-do
3. Mt. Deogyu, Jeonra-bugdo

Table 2. Variation in number of subcaudals.

Species	Locality*	Males				Females			
		N	Range	Mean	SE	N	Range	Mean	SE
A.b. brevicaudus	1	9	39—51	45.0	1.26	14	32—45	40.3	0.84
	2	10	47—52	48.4	0.51	16	39—47	42.4	0.56
	3	20	32—52	43.7	1.24	23	34—46	39.7	0.68
A. caliginosus	1	10	40—48	46.1	0.76	13	35—47	41.2	1.12
	3	42	40—51	45.6	0.40	44	31—46	40.8	0.67
A. saxatilis	3	13	41—47	44.3	0.54	19	37—48	40.9	0.62

* Localities are same as in Table 1.

Table 3. Relative length of tail-in percentage.

Species	Locality*	Males			Females		
		N	Range	Mean	N	Range	Mean
A.b. brevicaudus	1	9	11—16	14.2	14	10—14	12.4
	2	10	14—17	15.4	16	12—14	12.6
	3	20	10—16	14.1	23	11—16	13.0
A. caliginosus	1	10	8—16	14.0	13	11—16	13.2
	3	42	8—16	13.7	44	11—16	13.2
A. saxatilis	3	13	11—14	12.8	19	6—14	11.8

* Localities are same as in Table 1.

Notable sexual dimorphism was found. Males of all species have on the average fewer number of ventrals than females except Gwangneung population of *A. caliginosus* (Table 1) but the number of subcaudals (Table 2) and relative tail to body length (Table 3) of males tend to exceed those of females.

A. saxatilis has significantly more number of ventrals and relatively shorter tail to body length than *A. caliginosus* and *A. b. brevicaudus*. There were no marked difference in the number of subcaudals among all species. No distinct meristic character difference in the number of ventrals, the number of subcaudals and relative tail to body length was found between *A. caliginosus*. and *A. b. brevicaudus*. This is not concordant with the data presented by Gloyd (1972).

Genetic variation and genetic relatedness

Since breeding tests have not been conducted with these species, it is not absolutely certain that the observed bands on the gels represent allelic variation at a given locus. However, heterozygote band patterns were generally the same as those described in organisms for which breeding tests have been made. Therefore, it was assumed that electrophoretic variation represented allelic variation.

A total of 16 structural proteins encoded by 27 presumptive genetic loci were examined in all individuals. Allele frequencies in polymorphic loci, type of alleles in each species, and proportion of polymorphism are given in Table 4. Twelve loci out of 26 (46.1%) were identical in all three species. These were GP-2, GP-4, GP-5, GP-6, GOT-2, PGI, IDH-2, LDH-1, LDH-2, MDH-1, MDH-2, and AD H. Four loci (15.4%) were nearly identical with minor frequency differences

Table 4. Allele frequencies at 14 polymorphic loci in three species of the genus *Agkistrodon*.

		A. caliginosus	*A.b. brevicaudus*	*A. saxatilis*			*A. caliginosus*	*A. b. brevicaudus*	*A. saxatilis*
GP-1	a		.16		Pept	a	1.00	.75	1.00
	b	1.00	.50			b		.25	
	c		.33	1.00	MPI	a	.20	1.00	
GP-3	a	1.00		.17		b	.80		1.00
	b			.83	αGPD	a			.08
	c		1.00			b	1.00	1.00	.92
Hb	a	1.00	1.00	.92	IPO-1	a	1.00		
	b			.08		b		1.00	1.00
Est-1	a		1.00		IPO-2	a			1.00
	b	1.00		1.00		b	1.00	1.00	
Est-2	a		1.00		6PGD	a			1.00
	b	1.00		1.00		b	1.00	1.00	
GOT-1	a	.10			XDH	a			1.00
	b	.90	1.00	1.00		b	1.00		
IDH-1	a	1.00				c		1.00	
	b			1.00	% Polymorphism		7.8	7.8	11.5
	c		1.00						

(Hb, GOT-1, Pept, and αGPD). Rest ten loci (38.5%; GP-1, GP-3, Est-2, MPI, IDH-1, IPO-1, IPO-2, 6PGD, and XDH) were either monomorphic or polymorphic yet with notable interspecific mobility difference.

The average proportion of polymorphic loci is 9.03%. This is considerably less than the average polymorphism found in other vertebrates (see Selander and Johnson, 1973). Probably this is partially due to the small sample size. Electrophoretic data can be used to measure the genetic relatedness among different organisms (Avise, 1974, Yang *et al.*, 1974). Two methods are commonly used, Rogers' coefficient of genic similarity (S) and Nei's genetic distance (D). Table 5 presents a matrix of both genic similarities and genetic distances among three

Table 5. Genetic relationships among three species of *Agkistrodon*. Rogers' coefficient of genic similarity (S) is given above the diagonal and Nei's genetic distance (D) is given below.

	A. caliginosus	*A.b. brevicaudus*	*A. saxatilis*
Agkistrodon caliginosus	—	.708	.720
A. b. brevicaudus	.319	—	.656
A. saxatilis	.308	.399	—

species examined. Genetic similarity phenogram based on Rogers' S value for three species of the genus is given in Fig. 2. Their average S and D values are .695 and .342 respectively. These values fall within good species level (Avise, 1974). Mean S value of .695 among *Agkistrodon* species is lower than the value between two congeneric species of Sceloporus lizards (S=.790) reported by Hall and Selander (1973). The S value between two Korean snakes, *Elaphe schrenckii* and *E. dione*, is .690 and this value is about same as that of *Agkistrodon* species (Yang *et al.*, 1980). These data provide us to believe that three taxa of *Agkistrodon*

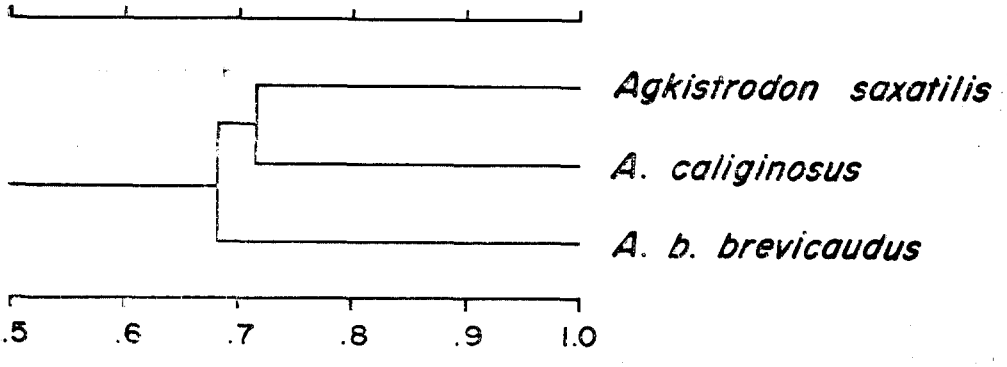

Fig. 2. Genetic similarity phenogram for three species of *Agkistrodon* based on allele frequencies at 26 loci. Clustering by the complete linkage method.

in Korea are distinct species. As shown in Fig. 2 and Table 5, *A. caliginosus* is genetically more related to *A. saxatilis* than to *A. b. brevicaudus*. *A. saxatilis* and *A. b. brevicaudus* show least genetic similarity (S=.656). Far from being mere morphological variants, as suggested by Kang and Yoon (1975), *Agkistrodon caliginosus*, *A. b. brevicaudus*, and *A. saxatilis* are highly distinctive evolutionary units.

SUMMARY

A total of 352 specimens of congeneric species of *Agkistrodon* was collected and morphometric analysis and starch-gel electrophoresis were carried out in order to investigate the taxonomic status of this genus.

The results obtained in this study are as follows:

Morphometric analysis

1. Three species are recognized based on Gloyd's criteria. There was no specimen that was doubtful to classify correctly. Therefore, it seems that Gloyd's morphological characters are good criteria to identify each species.

2. All three species are sympatric at two localities (Mt. Seolag, Gangwon-do, and Mt. Deogyu, Jeonra-bugdo) and *A. caliginosus* and *A. b. brevicaudus* are sympatric at Gwangneung and Mt. Yongmun, Gyonggi-do. No hybrids were found in these sympatric localities.

3. Notable sexual dimorphism was found in meristic characters.

4. *A. saxatilis* has significantly more number of ventrals and shorter tail ratio than other two species.

5. There were no significant meristic character differences between *A. caliginosus* and *A. b. brevicaudus*.

Genetic analysis

1. Among 26 loci investigated, 12 loci (46.1%) were identical in their mobility, 4 loci (15.4%) were nearly identical with minor frequency differences, and 10 loci (38.5%) showed interspecific mobility difference.

2. The average proportion of polymorphic loci was 9.03%. This is considerably less than that of other vertebrates.

3. The average S and D values between species are .695 and .342 respectively. These values indicate that three taxa are distinct species.

4. *A. caliginosus* is genetically more related to *A. saxatilis* than to *A. b. brevicaudus*.

The above results led us to conclude that there are three species of *Agkistrodon*, namely *A. b. brevicaudus*, *A. caliginosus* and *A. saxatilis*, as proposed by Gloyd. Far from being mere morphological variants, as suggested by Kang and Yoon (1975), they are highly distinctive evolutionary units.

ACKNOWLEDGMENTS

We are greatly indebted to Chai Hyeock Yu for his skilled assistance in photographing the live snakes and the illustration. Miss Ssang Sook Lee assisted in the statistical analysis and preparation of the manuscript.

REFERENCES

Avise, J.S., 1974. Systematic value of electrophoretic data. *Syst. Zool.* **23**: 465—481.

Dixon, J.R., 1956. A collection of amphibians and reptiles from west central Korea. *Herpetologica* **12(1)**: 50—56.

Emelianov, A.A., 1929. Snakes of the Far Eastern District. *Zapiski Vladivostokskogo Otdela Russkogo Geograficheskogo Obschestva* [*Mem. Vladivostok Section, Russian State Geograph. Soc.*] **3(1)**: 1—208.

Emeliaonv, A.A., 1937. On a new species of *Ancistrodon* (Ophidia) in the Far East. *Bull. Far Eastern Branch of the Acad. of Sci. USSR* **24**: 19—40.

Gloyd, H.K., 1972. The Korean snakes of the genus *Agkistrodon* (Crotalidae). *Proc. Biol. Soc. Wash.* **85(49)**: 557—578.

Hahn, D.E., 1960. Collecting notes on central Korean reptiles and amphibians. *J. Ohio Herpet. Soc.* **2(4)**: 16—24.

Hall, W.P., and R.K. Selander, 1973. Hybridization of karyotypically differentiated populations of the *Sceloporus grammicus* complex (Iguanidae). *Evolution* **27**: 226—242.

Kang, Y.S. and I.B. Yoon, 1975. *Illustrated encyclopedia of fauna and flora of Korea. Vol.* **17**, Amphibia and reptilia. Ministry of Education, Korea pp. 190.

Kim, Y.J., Y.I. Sunwoo, and K.S. Rhee, 1976. Isozymes and karyotypes of *Bufo* species. *Kor. J. Zool.* **19(3)**: 123—141.

King, M.-C., and A.C. Wilson, 1975. Evolution at two levels: molecular similarities and biological differences between humanas and chimpanzees. *Science* **188**: 107—116.

Klemmer, K., 1963. Liste der rezenten Giftschlangen. *In* Die Giftschlangen der Erde, N.G. Elwert, Marburg/Lahn pp. 255—464.

Maki, M., 1931. A monograph of the snakes of Japan. Tokyo Dai-Ichi. 245pp.

Nei, M., 1971. Interspecific gene differences and evolutionary time estimated from electrophoretic data on protein identity. *Amer. Nat.* **105**: 385—398.

Pope, C.H., 1935. The reptiles of China. Nat. Hist. Central Asia X. *Amer. Mus. Nat. Hist.*, New York, pp. 1—604.

Rendahl, H., 1933. Die Unterarten des *Ancistrodon halys* Pall. nebst einigen Bemerkungen zur Herpetologie Zentralasiens. *Arkiv for Zoologi, Stockholm* **25(8)**: 1—33.

Rogers, J.S., 1972. Measures of genetic similarity and genetic distance *Univ. Texas. Publ.* **7213**: 145—153.

Selander, R.K. and W.E. Johnson, 1973. Genetic variation among vertebrate species. *Ann. Rev. Ecol. Syst.* **4**: 75—91.

Selander, R.K., M.H. Smith, S.Y. Yang, W.E. Johnson, and J.B. Gentry, 1971. Biochemi-

cal polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics VI. *Univ. Texas Publ.* **7103**: 49—90.

Shannon, F.A., 1956. The reptiles and amphibians of Korea. *Herpetologica.* **12(1)**: 22—49.

Slevin, J.R., 1925. Contributions to oriental herpetology. II. Korea or Chosen. *Proc. Calif. Acad. Sci.* **14(5)**: 89—100.

Sneath, P.H.A., and R.R. SoKal, 1973. Numerical taxonomy. W.H. Freeman and Co., San Francisco 573 pp.

Sowerby, A.C., 1930. The reptiles and amphibians of the Manchurian Region. *In* The Naturalist in Manchuria. Tientsin, Tientseu Press, Ltd. 4—5: 3—41.

Stejneger, L., 1907. Herpetology of Japan and adjacent territory. *U.S. Nat. Mus. Bull.* **58**: 1—577.

Stejneger, L., 1925. Chinese amphibians and reptiles in the United States National Museum. *U.S. Nat. Mus. Proc.* **66(25)**: 1—115.

Stewart, G.D., 1954. A small collection of reptiles from central Korea. *Copeia* **1954(1)**: 65—67.

Strauch, A., 1868. Concerning poisonous snakes found in Russia. *Trudy Russkikh Estestvo-ispytatelei v. St. Petersborge* [*Transactions of the Russian Naturalists Society, Trudy Russk. Estestv.*], **1**: 271—297.

Tanner, V.M., 1953. Pacific islands herpetology. NO. VIII, Korea. *Great Basin Natul.* **XIII**: 67—73.

Terentév, P.V., and S.A. Chernov, 1965. Key to amphibians and reptiles. Ed. **3**: 1—315 [Translation of work of 1949] *Israel Program for Sci. Transl., Jerusalem. IPST* **1255**: 65—50104.

Thompson, J.C., 1916. The variation exhibited by *Ancistrodon halys* (Pallas), a pit-viper inhabiting the Far East. Trans. *San Diego Soc. Nat. Hist.* **2(2)**: 61—76.

Webb, R.G., J.K. Jones Jr., and G.W. Byers, 1962. Some reptiles and amphibians from Korea. Univ. Kansas Publ. *Mus. Nat. Hist.* **15(2)**: 149—173.

Yang, S.Y., Y.J. Kim, and N.K. Paik, 1980. Biochemical systematics of Korean snakes. *in preparation.*

Yang, S.Y., M. Soulé, and G.C. Gorman, 1974. *Anolis lizards* of the eastern Caribbean: a case study in evolution. I. Genetic relationships, phylogeny, and colonization sequence of the *roquet* group. *Syst. Zool.* **23**: 387—399.

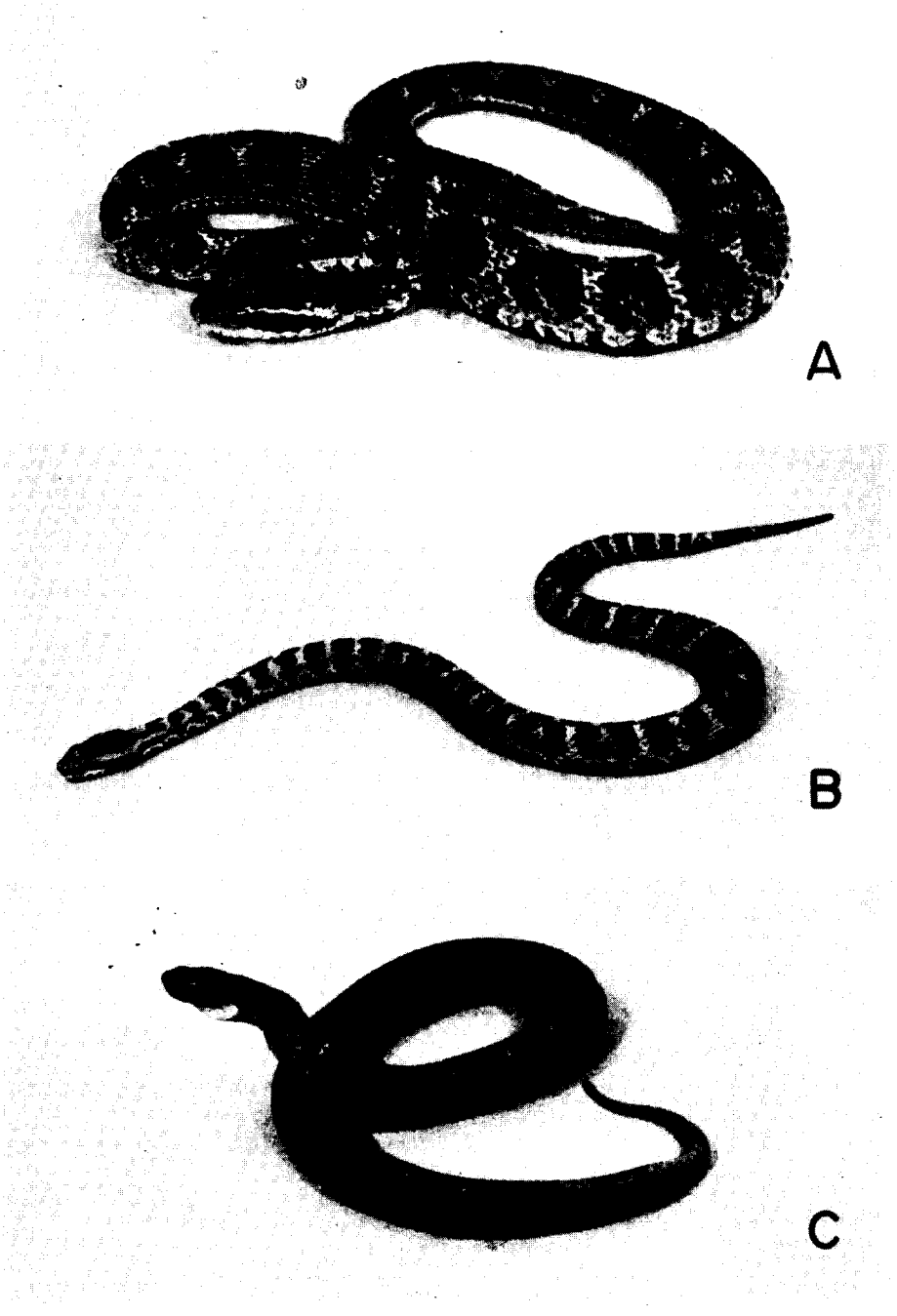

Fig 1. Photographs of Korean *Agkistrodon*.

A. ***Agkistrodon bromhoffii brevicaudus*** Stejneger, SYY 3218.

B. ***Agkistrodon saxatilis*** Emelianov, SYY 3219.

C. ***Agkistrodon caliginosus*** Gloyd, SYY 3220.