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James A. Peters

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ON THE BIOLOGY OF THE GIANT INDONESIAN MONITOR LIZARD
(Varanus komodoensis Ouwens)

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In the half century that has passed since the day of the discovery of the largest of contemporary lizards, the giant Indonesian monitor lizard (Varanus komodoensis Ouwens), this relict reptile has repeatedly attracted the attention of zoologists (Burden, 1927, 1928; Dunn, 1927; Mertens, 1930, 1959; Tänzer and Heurn, 1938; Lederer, 1942; de Jong, 1944; Hoogerwerf, 1948, 1954, 1958; Pfeffer, 1959; and others). However, despite the investigations carried out, the basic question of the biology of the giant monitor, including propagation, postembryonic growth, and population dynamics, are all still in the initial stage of study.

The materials collected by the authors in July and August, 1962, at the time of the work of the First Indonesian-Soviet Expedition on the islands of Komodo, Padar, and Rintja in the Lesser Sundas Archipelago, have served as the basis for the present work, which supplements the information in a number of areas of the biology of the monitor lizard. The authors express gratitude to all their comrades in the work, who took part in the collection of the materials used by the authors. In general form, some of the results of the investigations made by the expedition have been published earlier (Darevskii and Maleev, 1963).

Propagation and postembryonic growth

The data in the literature on the propagation of the giant monitor are based exclusively on observations of the animals in captivity.

For the purpose of clarifying the actual breeding periods of the monitors in nature, at the time of work on the Komodo [dragon] we dissected two sexually mature males, 157 and 238 cm. long, and a female, 171 cm. in length, the gonads of which have been subjected to microscopic study. (The microscopic investigation of the gonads has been done by V. N. Kulikova of the Institute of Cytology of the Academy of Sciences, U.S.S.R.) For both males, dissected August 3 and August 5, the testes were found in a state of rest, being loose, wrinkled bodies 4 cm. and 6 cm. in length. Microscopic study revealed small ducts, chiefly in initial stages of spermatogenesis, passing in the walls and complete cut-off of production of mature spermatozoa, which were also lacking in the collapsed appendages of the testes. Judging from the state of the

gonads, sexual activity of males had already been interrupted in extreme measure by mid-July and, consequently, mating could occur no later than this period. It is interesting that in the smaller female, with a length of 157 cm., well developed fat bodies with a weight of 120 g were observed, while in the adult specimen fat deposits were lacking. Inasmuch as the deposition of shaped fat bodies usually begins in lizards only at completion of the breeding period, it is possible to assume that in the young female the interruption of sexual activity set in correspondingly earlier, obviously already at the end of June.

In the female studied, dissected August 26, the oviducts were empty, but in the ovaries numerous white oocytes were found, some of which attained 8 to 10 mm. in diameter. Furthermore, in the left ovary eight and in the right ovary seven well-defined corpora lutea with distinct cicatrices were found which indicate that the output of 15 ova in the oviduct had occurred no more than a month ago and, consequently, oviposition might have occurred at the end of July or at the very start of August. The well-developed fat bodies in the female also speak in favor of such a conclusion, the lobes of which have reached 27 cm. in length with a weight of 220 g. The fact that the female studied laid only 15 eggs is apparently connected with her relatively small size, 171 cm., 74 of which are for the torso and head. According to the data of Pfeffer (1959), the number of eggs per clutch for large females reaches 25 to 26.

It may be noted that in many Palearctic reptiles a state of the gonads similar to that which was observed for the monitors under study usually is found in the fall of the year in the period preceding hibernation. Evidently for the giant monitor, as also for a number of other tropical reptiles, the dry season that lasts on the islands for more than three months is such a period of repose.

Thus, the studies made by us showed that in natural conditions the breeding of the monitors occurs 2 to 3 weeks earlier than in the zoological gardens of Java and at entirely different periods than in the zoological gardens of Europe. (In 1963 for the females captured by us, which had already mated in conditions of freedom on Komodo, egg-laying at the Surabaja Zoological Garden [eastern Java] was observed throughout July).

Assuming that the length of the incubation period on Komodo is the same as in the zoological gardens of Java and is equal to 8 to 8.5 months, it must be thought that the young monitors make their appearance here as early as March and the start of April, shortly after completion of the rainy season, i.e. in very favorable periods biologically.

As has already been mentioned, the period of work on Komodo of our expedition coincided with the periods of egg-laying and, consequently, the smallest of the specimens encountered by us might

be no older than four months; if one accepts their hatching as having been in the March-April period of this year. Such small specimens have been observed several times by the members of the expedition. However, the youngest of the monitors caught by us have attained a length of 115 to 125 cm., i.e., they have been 16 to 18 months old and probably hatched in March and April 1961. The measurement and marking of the young monitors which we did (see table 1) will permit in subsequent captures obtaining data on migrations and intensity of their growth in nature. The marking of the animals has been done by a standard method, by cutting off the terminal phalanges of the digits. The sites of release of the marked monitors on the Island of Komodo are indicated in the figure.

Judging from the data that are to be had, males make up a considerable part of the monitor population on the island of Komodo. Of the 17 specimens acquired here by Americans in 1926, 14 were males, and there were only 3 females (Dunn, 1927). Judging from the measurements of this author, two skeletons found in abandoned traps set by local residents belonged to males. Proceeding from the dimensions of the body (females of the mammoth monitor do not exceed 2 m. in length), six of the nine skins from the Island of Komodo examined by us at the Bogor Zoological Museum on Java also belonged to males. Two males from Komodo were delivered in 1935 to the zoological garden of the city of Surabaja (Tänzer and Heurn, 1938). Finally, among the 26 specimens caught on Komodo by our expedition, 22 were males and 4 females. Thus, at least 46 of the 56 monitors acquired on the Island of Komodo at various times, i.e., more than 80 percent have been males. In other words, the ratio between the sexes on this island is approximately 6:1. It may be noted that chiefly males have been acquired in different zoological gardens, the same as on the islands of Rintja and Flores. The clear predominance of male specimens in the island population of monitors apparently is no accident, but rather reflects the actual ratio of the sexes existing in nature. It is possible that the sharp reduction in number of females is the manifestation of a special mechanism of regulation of the number which prevents overpopulation of the monitors on the island. The small territory of the island, together with the limited amount of food (carrion), as well as the great length of life of the monitors themselves, might fully play the role of factors that have produced in the process of evolution the selection of such a mechanism.

Feeding Habits

The feeding habits of the giant monitor have been studied rather fully. According to the data of Burden (1927, 1928), Hoogerwerf (1954, 1958), and Pfeffer (1959), and also according to the observations of our expedition, the monitor's food is composed primarily of the carrion that appears more or less regularly on the islands as a result of the natural death of the red deer that have been guided here (Cervus rusa timorensis), of the wild hogs (Sus scrofa subsp), and of wild buffaloes and horses. The specialized sense of smell, together

with the highly developed Jacobson's organ, permits the animals to discover the food quickly, which they, in distinction from other reptiles, do not swallow whole but tear apart with their teeth, remindful in this respect of the carnivorous mammals. It should be emphasized that, with the exception of crocodiles, giant monitors are the only present-day reptiles that act in such way, which permits speaking of a definite skip in character which, at greater morphological comparison, distinguishes it from the other representatives of the genus Varanus.

In devouring the carrion the monitor, like a number of other carnivores, first rips open the abdomen, swallowing the entrails. In addition, it often buries its head in the abdominal cavity of the host, to which the long neck of the reptile contributes much.

The predator plays with the host, usually standing on stretched-out legs, and by this its abdomen is quite visible which, as it is filled with food, sags more and more, gradually reaching the ground.

While eating chiefly carrion, the mammoth monitors are capable of also attacking live prey, up to wild hogs and deer inclusively. Table 2 give some concept of their ration on the Island of Komodo, which was compiled on the basis of the selection of 18 specimens of dry droppings, collected in the first half of August. It may be noted that these specimens, in the majority of cases, have been collected on open summits of hills, at the edge of wooded areas, and at other sites apparently favored by the monitors as lookout points.

To this should be added that in the stomach of one of the monitors dissected by us a large rat was found, Rattus sp, and in another the skull of an adult boar, partly digested. As our observations on Komodo and Rintja indicate, the monitors regularly appear on the shore after high tide, where they pick up the fish and invertebrates thrown up by the sea. It is interesting to note that the majority of the pit clusters of the brush turkeys (Megapodius freicineti), observed by us on the islands, were dug by the monitors in searches for eggs, which was easily established by the tracks in the sand.

It is puzzling to note that monkeys and deer, which are regularly subjected to the attack of the monitor lizards on the islands, fearlessly permit them to come close to them, discovering the danger only at the very last moment when it is already practically impossible to be saved from the teeth or a blow of the tail of the carnivore. Similar observations in regard to monkeys (Macaca irus) have been made on the Island of Rintja by Hoogerwerf (1958) and in regard to deer by our expedition on the Island of Komodo (Darevskii and Maleev, 1963). It is suggested that such an astonishing lack of caution of the victim is explained in considerable measure by the method of hunting of the monitor, which approaches the prey slowly and completely noiselessly, reminiscent in this respect of snakes.

Body temperature

Date on body temperature of monitors in natural setting were obtained for the first time by our expedition on the Island of Komodo. The cloacal temperature was measured by deep insertion of a mercury thermometer, calibrated to an accuracy of 0.5°, into the cloaca. The measurement was usually done in the morning at the withdrawal of the monitors from the cage snares placed in the shade into which they had fallen the day before. As a rule, the temperature of the air at a height of 0.5 m from the ground was also observed simultaneously. (see Table 3.)

From the table it is seen that the body temperature of active monitors, depending on the temperature of the medium, fluctuates between 26 and 33°[C] i.e., it is found within limits that are customary for many other tropical lizards. These data agree well with the observations of G. Lederer (1942), according to which the optimal temperature of the medium for keeping monitors in captivity lies within the range of 25 to 30° [C]. Our observations showed that at a temperature of the air of over 30° [C], the monitors try to keep in the shade and, in case of an obligatory stay in the sun, for instance at the devouring of a prey that lies out in the open, from time to time they open their mouths wide and breathe out repeatedly, thus contributing to the cooling of the body like mammals devoid of sweat glands.

Table 1.

Marking of monitors trapped on the Island of Komodo in August 1962

No.	Animals Marked	Sex	Date Marked	Length Torso with Head	Tail	Total	Site of Release
1	10	male	Aug. 1	46 mm.	69	115	Vic of base camp (see fig.)
2	11	female	Aug. 4	51 mm.	73	124	" "
3	12	male	Aug. 4	58 mm.	80	138	" "
4	13	male	Aug. 4	66 mm.	88	154	" "
5	14	female	Aug. 19	50 mm.	75	125	" "
6	15	male	Aug. 19	61 mm.	84	145	" "
7	16	male	Aug. 22	55 mm.	--	--	" "
8	17	male	Aug. 26	62 mm.	89	151	" "
9	18	male	Aug. 26	80 mm.	105	185	" "
10	19	male	Aug. 26	67 mm.	93	160	" "
11	20	male	Aug. 26	76 mm.	93	170	" "
12	30	male	Aug. 25	81 mm.	103	184	Vic.upper camp (see fig.)

Table 2.

Composition of 18 specimens of dry droppings of the mammoth monitor, collected on the Island of Komodo

Key:	Number of Encounters	
Components of the Droppings	Absolute	Percent
fur of ungulates	18	100
deer hooves	5	2.8
scales of lizards	9	50
scales of snakes	4	2.2
scales of fish	2	1.1
bird feathers	4	2.2
chitinous parts of insects	4	2.2
remnants of plants	7	3.8

Table 3.

Body temperature of monitors on the Island of Komodo

Serial No.	Date of measurement	Cloacal Body Temperature, ^{o}C	Temperature of Air in Shade, ^{o}C
1	Aug. 4	33	33.5
2	Aug. 4	31	---
3	Aug. 4	29	---
4	Aug. 4	29.5	---
5	Aug. 4	32	---
6	Aug. 1	28	29
7	Aug. 19	25.5	27.5
8	Aug. 19	30	30
9	Aug. 22	27	27.5
10	Aug. 22	27	---
11	Aug. 22	30	30
12	Aug. 22	29	33
13	Aug. 26	29.5	31.5

Legend to Figure 1: Islands of Komodo,Podar, and Rintja

1 - Expedition camps; 2 - routes through marsh of the Indonesian-Soviet expedition; 3- central peaks of the islands; 4 - region of release of the marked monitors on the Island of Komodo at the upper camp; 5 - region of release of the marked monitors on the Island of Komodo in the environs of the base camp.

Reading from left to right: Island of Komodo, Komodo jungle; Sea of Flores; Pada Island; Rintja Island; Flores Island.

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INDEX TO THE SCIENTIFIC NAMES
IN
"CLASSIFICATION OF THE LIZARDS"

by

CHARLES LEWIS CAMP

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A LIST OF INSTITUTIONS OFFERING COURSE WORK AND DEGREE PROGRAMS IN HERPETOLOGY

Prepared by

James A. Peters

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The list that follows has been prepared from forms filled out by the professors in charge of herpetological course work at the respective institutions, and thus represents the most current information available. The material is, for the most part, self-explanatory, but a few words of explanation are necessary. The word "yes" or "no" in the column marked "U.G. Res." indicates whether or not the institution has some type of undergraduate research participation program. This is often sponsored by the National Science Foundation, although each school is likely to be different. When offered, further information is available from the department concerned.

An "X" in the columns marked "M.A.-M.S." or "Ph.D." means that the institution offers that graduate degree for herpetological research. If these columns are not marked a student cannot take an advanced degree in herpetology in that institution. The columns marked "Grad" and "Undergrad" indicate the level at which each course is presented by the instructor. The address given under the column "institution" is sufficient to reach the proper place, if the state name is added. Revisions in the list will be welcome and an attempt will be made to keep it up-to-date.

STATE	INSTITUTION	DEPARTMENT	MA-MS	Ph.D	COURSEWORK OFFERED number	title	INSTRUCTOR	FREQUENCY	Grad.	Und.Grad	PRE-REQUISITES	U.G. Res.
ARIZONA	Ariz.State College, Tempe	Zool.	X	X	Zoo 210	Problems in Herp.		yearly		X		yes
					Zoo 499	Ind.Study		yearly		X	Superior students	
					Zoo 270	Vert Zool	M.Fouquette	yearly		X	Gen.Bio.	
					Zoo 474g	Herp	" "	yearly	X	X	Anim.Ecol.	
					Zoo 590	Read/Conf. in Herp.		yearly	X			
					Zoo 592	Research in Herp.		Semester	X			
	Univ.of Ariz. Tucson	Zool.	X	X	Zoo 232	Herp.	C.A.Lowe	yearly	X	X		
					Zoo 299	Sp.problems	" " "	yearly		X		
ARKANSAS	Ark.State Coll.,State Coll., 72467	Biol			Zoo 303	Herp.	Wm.Byrd	yearly		X	Gen.Zoo	no
CALIFORNIA	Calif. State College Fullerton 92631	Biol	X		Bio 400	Ind.Study	B.Brattstrom	Semester	X	X		yes
					Bio 471	Nat.Hist. of Vert.	" "	yearly		X	Gen.Bio.	
					Bio 560	Seminar	" "	yearly			Comp.Anat.	
	Calif.State College, Long Beach 90804	Zool.	X		Zoo 110	Herp.	R. Loomis	spring		X		
					Bio 119	Inv.in Bio	Loomis;Hardy	Semester		X		yes
					Zoo 210	Adv.Herp.	R.Loomis	Alt.yrs.	X		Zoo 110	
					Bio 299	Inv.in Bio	Loomis;Hardy	Semester	X			
	State College San Diego	Biol.	X		Zoo 115	Herp.	Etheridge	yearly		X	Comp Anat	
					Zoo 200	Seminar in Herp.	Etheridge; Jameson;Hunsaker	irreg.	X		Nat Hist of Vert	yes

STATE	INSTITUTION	DEPARTMENT	MA-MS	Ph.D.	COURSEWORK OFFERED Number	Title	INSTRUCTOR	FREQUENCY	Grad.	Und.grad	PRE-REQUISITES	U.G. Res.
CALIFORNIA (Cont.)	St.Polytech. College San Luis Obispo	Bio Sc.	X		Zoo 329	Vert.Fld. Zoo	R.Pimentel	yearly		X		yes
					Bio 461-2	Sr. Proj.		yearly		X		
					--- -----	Herp.('66?)						
	U. Calif. Berkeley	Zool	X	X	Zoo 137	Herp.	R.Stebbins	alt yrs	X	X	Vert.Nat. Hist.	yes
					Zoo 199	Sp.study				X		
	U.Calif. Los Angeles	Zool	X	X	Zoo 133	Herp	K. Norris	yearly		X		
					--- ---	Seminar in Rept-Amph problems	K. Norris	yearly	X			
	U.Calif. Riverside		X	X	Zoo 146	Field Zoo	W.Mayhew	yearly		X		yes
					Zoo 254	Vert Zool Seminar	R.Ruibal	yearly	X			
	St. Coll. Fresno	Biol	X		Zoo 137	Herp.	Hadrall	alt.yrs.		X	Gen Zoo	no
	L.A.St.Coll., Los Angeles	Biol	X		Zoo 472	Herp.	V.Vance	alt.yrs.		X	Vert Zoo	no
	San Jose St. College San Jose	Biol	X		Zoo 113	Vert Zoo	Hendricks;Smith	yearly			Bio Zoo (113)	yes
					Zoo 171	Herp	Smith;Harrington	yearly			Vert Zoo (171)	
	Univ.So.Calif. Los Angeles	Biol	X	X	Bio 543L	Herp	Savage	alt.yrs.	X		Grad.Status	yes
	Stanford Univ. Stanford	Bio.	X	X	Bio 139	Herp I	Leviton;Myers	yearly		X		yes
					Bio 140	Herp II	Leviton	yearly		X		
					Bio 199	Sp.prob.	Leviton;Myers or Twitty	yearly		X		

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COLORADO	Col.State Univ. Ft. Collins	Zool	X	X	Zoo 129	Herp	D. Pettus	alt.yrs	X	X	Intr.Zoo-Vert.Zoo	yes
	U.Colo. Boulder	Biol	X	X	Zoo 432	Herp	Maslin	yearly		X	Gen.Bio Comp.Anat	yes
FLORIDA	U. Fla Gainesville	Zool	X	X	Bio 652	Herp	Auffenberg	alt.yrs	X		Vert.Nat. Hist.	no
GEORGIA	U. Ga. Athens	Zool	X	X	Zoo 404	Herp	J. Kerr	yearly	X	X	Vert Zoo and others	yes
IDAHO	U. Idaho Moscow				Zoo 219	Sp.studies (Herp)	P. Dumas	yearly	X		Gen Zoo	
		Bio Sc	X	X	Zoo 129	Herp	P. Dumas	yearly	X	X	Gen Bio	
ILLINOIS	U.Chicago	Anat	X	X	Anat 339	Evol.Biol.of Low.Tetrap.	D. Wake	alt.yrs	X	X	Int.Zoo Vert.Zoo	yes
	U.Illinois Urbana	Zool	X	X	Zoo 338	Herp	H.M.Smith	alt.yrs	X	X	Elem Zoo	yes
	S. Ill. U. Alton	Zool			Zoo 408	Herp	R. Axtell	yearly		X	One year Zoo	yes
	S. Ill. U. Carbondale	Zoo.	X	X	Zoo 408	Herp	R. Brandon	yearly	X	X	One year Zoo	yes
INDIANA	U.Notre Dame Notre Dame	Biol	X	X	Bio 161-62	Int.to Res.in Bio	Tihen-Gordon	Each Sem.		X	Comp.Anat Ecol-Genet.	yes
					Bio 364-65	Sp.prob. in Herp	Tihen-Gordon	Each Sem.	X			
KANSAS	U. Kansas Lawrence	Zool		X	Zoo 182	Herp	W. Duellman	yearly	X		Nat.Hist. Vert.,Comp Anat	yes
					Zoo 304	Sp.Topics in Herp.	W. Duellman	Irreg	X			

STATE	INSTITUTION	DEPARTMENT	MA-MS	Ph.D.	COURSEWORK OFFERED		INSTRUCTOR	FREQUENCY	Grad.	Und.grad	PRE-REQUISITES	U.G. Res.
					Number	Title						
KENTUCKY	U. of Ky. Lexington	Zool	X	X	Zoo 522	Herp	R. Barbour	Alt yrs	X		Gen.Zoo	yes
LOUISIANA	La.St.U. Baton Rouge	Zool	X	X	Zoo 146	Herp	D. Rossman	yearly	X	X	Gen.Zoo Comp.Anat	
	N.E. La.St. College Monroe	Biol	X		Zoo 164	Herp	N. Douglas	yearly	X	X	Int.Zoo Comp.Anat (preferred)	yes
	Tulane U. New Orleans	Zool		X	Zoo 656	Herp	H. Dundee	Alt yrs	X	X	Comp.Anat Ecol., N.H. of Verts,or similar	
MARYLAND	U.of Md. College Pk.	Zool			Zoo 129	Vert.Zoo	- ---------	yearly	X	X	2 yrs.Zoo	
			X	X	Zoo 399	Thesis Research	J.Crenshaw; R.Highton	yearly	X			yes
MASSACHUSETTS	Harvard U. Cambridge	Zool	X	X	Bio 133	Bio.Amph Rept.	E.Williams	Alt yrs	X	X	Gen.Bio	yes
	Williams Coll. Williamstown	Biol	X									yes
MICHIGAN	Andrews U. Berrien Springs	Biol			Bio 454	Herp	A.Thorsen	Alt yrs		X	Gen Zoo or apprv.	yes
	Mich.St.U. E.Lansing	Zool	X	X	Zoo 484	Herp	M.Hensley	yearly	X	X	Gen.Bio., Bio of Vert	
	U.of Mich Ann Arbor	Zool		X	Zoo 555	Herp(Rept)	D.Tinkle	alt yrs	X		Evol and Syst.of Vert or equiv. and perm. of instru	
					Zoo 556	Herp(Amph)	C.F.Walker	Alt yrs	X		(same)	

STATE	INSTITUTION	DEPARTMENT	MA-MS	Ph.D.	COURSEWORK OFFERED Number	COURSEWORK OFFERED Title	INSTRUCTOR	FREQUENCY	Grad.	Und.grad.	PRE-REQUISITES	U.G. Res.
MISSISSIPPI	Miss.St.U., St.College	Biol	X	X	Zoo 554	Herp	D.Ferguson	yearly	X	X	Gen.Zoo	no
MISSOURI	U.of Mo. at Kansas City 64110	Biol	X	X	Zoo 415	Herp	Milstead	Irreg	X	X	Perm.Instr	yes
					Zoo 530	Vert.Zoo	Milstead	yearly	X	X	Perm.Instr	
MONTANA	Mont.St. Coll., Bozeman	Zool	X	X	Z-E 426	Herp	C.Davis	yearly	X	X	Comp.Anat	yes
NEVADA (See addenda)	U.Nevada Reno	Biol	X		Zoo 333	Fishes,Amph. and Rept.	I.LaRivers	yearly		X	Intro.Zoo	yes
NEW MEX. (See addenda)	New Mex. State U. Univ.Park	Wildlife Mngmt	X		AnSc 486 ---- ---	Herp Probl.Course		alt. years	X	X	Gen.Biol other	yes
NEW YORK	U.Buffalo Buffalo	Biol	X	X	Bio 433	Herp	C.Gans	Irreg.	X	X	Elem.Bio Comp.Anat	yes
	St.Bonaventure U. St.Bonaventure 14778	Biol	X	X	531-532	Herp	R.Bothner	Alt yrs	X		Comp.Vert Anat	
OHIO	Ohio State Univ. Columbus 43210	Zool Entoml	X	X	Zoo 656	Herp	N.Green (summer schl., Put-In-Bay only)	Alt yrs	X	X	Gen.Bio or Zoo and 10 Hrs.Biol	yes
					Zoo 701	Research, Sp.Prob.		Quarterly	X	X	Perm.of Instr.	
	Ohio U. Athens	Zool	X		Zoo 113	Bio of Vert	H.Seibert	Alt yrs		X	Intro.Zoo	yes
					Zoo 343	Bio studies		Each Sem		X	Adv.Zoo	

STATE	INSTITUTION	DEPART-MENT	MA-MS	Ph.D.	COURSEWORK OFFERED		INSTRUCTOR	FREQUENCY	Grad.	Und.gra	PRE-REQUISITES	U.G. Res.
					Number	Title						
OKLAHOMA	Okla.St. U. Stillwater	Zool	X	X	Zoo 464	Herp	B.Glass	Alt yrs	X	X	Vert Anat.	no
	U. of Okla. Norman	Zool	X	X	Zoo 208	Herp	A.Bragg	Irreg	X	X	8 Hrs Zoo Permission	no
	U. of Tulsa Tulsa	Zool	X		Zoo 143	Fld.Zoo	H.Lindsay	yearly		X	One Sem. Bio	yes
OREGON	Oregon St. Coll. Corvallis	Zool	X	X	Zoo 473	Herp	R.Storm	yearly	X		2 Yrs.Zoo	yes
PUERTO RICO	U. Puerto Rico Rio Piedras	Biol	X		Bio 541	Sem. in Syst.	H.Heatwohl	Irreg	X			yes
RHODE ISLAND	U. of R.I. Kingston	Zool	X	X	Zoo 166	Vert.Bio	V.Hutchison	Alt yrs	X	X	Comp Anat	yes
					-- ---	Herp [proposed '66]						
SOUTH DAKOTA	U.of S.Dak. Vermillion	Zool	X	X	Zoo 104	Herp	D.Dunlop	yearly	X	X	Gen Zoo	no
TEXAS	Baylor Univ. Waco	Biol	X		Bio 421	Herp	B.C.Brown	Irreg	X		Comp.Anat 14 Sem.Hrs Bio	yes
	Lamar Tech. Beaumont	Biol			Bio 430	Undergrad. problems		Quarterly		X		yes
	No.Texas U. Denton	Biol	X		Bio 405	Anim.Ecol	J.Silvey	yearly	X		12 Sem.Hrs Bio	no
					Bio 534	Herp-Ichth	J.Silvey					
	Sam Houston St.College Huntsville	Biol	X		Bio 346	Herp	F.Potter	Alt yrs	X	X	Gen.Zoo	yes
					Bio 563	Bio.Probl. (Res.in Herp)		yearly	X			
					Bio 568	Adv.Ecol [Herp]		Irreg	X		Perm of Instructor	
					Bio 569	Adv.Taxon.[Herp]		Irreg	X			

STATE	INSTITUTION	DEPARTMENT	MA-MS.	Ph.D.	COURSEWORK OFFERED		INSTRUCTOR	FREQUENCY	Grad.	Und.grad.	PRE-REQUISITES	U.G. Res.
					Number	Title						
TEXAS (Cont.)	Texas A-M University College Sta.	Wldlife Sci.	X	X	WS 315	Herp	R.Baldauf	yearly	X	X	Gen Zoo	yes
					WS 316	Fld.Herp	R.Baldauf	yearly	X	X		
	Texas Tech College Lubbock	Biol	X	(X)	Zoo 533	Herp		yearly	X	X	Evol.theory Vert.Zoo Comp.Anat	yes
	U. of Texas Austin	Zool	X	X	Zoo 384L	Syst-Envr. Zoo (sec.3) Herp	W.Blair	Alt yrs	X	X		yes
UTAH	Brigham Young Univ. Provo	Zool	X	X	Herp 345	Herp	W.Tanner	yearly		X	Gen Zoo-Ichth.	yes
	U.of Utah Salt Lake City	Zool	X	X	Zoo 124	Herp	J.Legler	Irreg	X	X	Gen Zoo or Gen Bio	yes
VIRGINIA	Coll. of William-Mary Williamsburg	Biol	X		Bio 403	Probl. in Bio	Brooks;Terman	Alt yrs		X	Gen Bio	yes
					Bio 413	Vert Bio	Brooks;Terman	Alt yrs	X	X		
	U. of Virginia Charlottesville	Biol	X	X		Herp		Alt summ at Biol. Stat. Mt.Lake	X			no
WASHINGTON	Pacific Luthern Coll. Tacoma 98447	Biol			Bio 324	Nat.Hist. of Vert	J.Knudsen	yearly		X	Gen.Bio	no
	U. of Wash. Seattle	Zool	X	X	Zoo 362	Nat.Hist of Vert	R. Snyder	yearly		X	Gen.Zoo or Gen.Bio	yes

STATE	INSTITUTION	DEPART-MENT	MA-MS	Ph.D.	COURSEWORK OFFERED Number	COURSEWORK OFFERED Title	INSTRUCTOR	FREQUENCY	Grad.	Und.grad.	PRE-REQUISITES	U.G. Res.
WEST VIRGINIA	Marshall U. Huntington 25701	Biol	X		Zoo 402-502	Vert.Nat. Hist.	N. Green	Yearly			Gen Zoo	Yes
					Zoo 450-52	Special	N. Green	Yearly		X		

ADDENDA

Nevada	Nev.Sthrn. Univ. Las Vegas	Biol			Zoo 203	Vert.Zool	Deacon;Bradley	Yearly		X	Gen Zoo	
					Zoo 332	Herp.	Deacon	Alt.yrs	X	X	Gen Zoo	yes
					Zoo 491	Spec.Prob.	Deacon;Bradley	Yearly	X	X	Jr-Sr. Status	
New Mex.	Univ.N.Mex Albuquerque	Biol	X	X	Biol 488	Herp.	Degenhardt	Yearly	X	X	1 yr.Biol	no
					Biol 551	Spec.Prob.	Degenhardt	Sem.	X	X	Herp	
					Biol 599	Masters thesis	Degenhardt	Sem.	X		B.S.degree	
					Biol 699	Dissertation	Degenhardt	Sem.	X		M.S.degree	

A

INDEX TO SPECIES FOR WHICH HEMIPENES ARE DEPICTED IN "CROCODILIANS, LIZARDS, AND SNAKES OF NORTH AMERICA"

MPHIBIANS

by

E. D. COPE

ANNUAL REPORT UNITED STATES NATIONAL MUSEUM
for 1898, pp. 155-1294

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ICES

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The names used in this index are those used by Cope, and a few of the species were erroneously identified or names were perhaps transposed, but no attempt has been made to bring the names up to date or to correct errors. In some instances Cope omitted the terminal lobes of the hemipenis, particularly when they were long, slender extensions of the much broader basal part. The plate on which the hemipenis appears is given immediately after the name, followed by the figure number in parentheses.

The index is trimmed to fit into the back of Cope's book.

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CONSIDERATIONS CONCERNING THE VARIABILITY OF AMPHIBIANS AND REPTILES

by Bogdan Stugren

Stuii și Cercetări de Biologie (Cluj)

volume 13, number 1
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1962

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Almost forty years ago, in 1928, Robert MERTENS and Lorenz MÜLLER published their first check list of European amphibians and reptiles. Thanks to this work the concept of geographical races (subspecies), and the corresponding trinomial nomenclature, became commonplace in herpetological literature published in Europe. This process paralleled the development of herpetology in the United States, where STEJNEGER and BARBOUR, and then Karl P. SCHMIDT, introduced the concept of geographical races into the study of amphibians and reptiles. The trend of herpetological research toward the study of geographical races was greatly stimulated by Bernhard RENSCH's synthesis of views on the subject (1929). Finally, the second edition of MERTENS and MÜLLER's check list (1940), and the comprehensive works of TERENTJEV and CHERNOV (1940, 1949) on the amphibians and reptiles from the U.S.S.R., were events in European herpetology which definitely established the concept of geographical race instead of the old Linnean expression "variety," which lacked precision.

The utilization of the theory of geographical races in the systematics of amphibians and reptiles (and of vertebrates generally) was valuable. Being methodologically efficient, this theory contributed to a better understanding and to a more realistic view of the species of amphibians and reptiles, got rid of a chaotic situation which then existed in taxonomy, and freed systematics from a lot of names without content. But soon this theory itself became a source of extreme formalization in taxonomy. The old systematics, with its typological theories, pressed living things into the procrustian bed of the species concept metaphysically interpreted. The theory of geographical races, although free from that viewpoint, led often to unjustified description of new geographical races, which were very doubtfully real. In addition, the variability of species was implicitly restricted to the process of genesis of new geographical races.

I do not contest a priori the background of the subspecies concept in reality. But I intend to discuss some facts which cannot be explained by the theory of geographical variability in the sense given by RENSCH.

With some species, students were unable to discover geographical races by means of old classical methods based on the observation and detailed description of a few specimens. A new hope arose when mathematical methods were applied to the study of large samples of specimens. But often even the most detailed statistical analysis did not substantiate geographical races. So it was clear that there were species with intense population and individual variability; but this variability did not always permit the definition of geographical races. This was established, for instance, in the case of the Eurasiatic viviparous lizard (*Lacerta vivipara* JACQ), by TERENTJEV (1948) and WERMUTH (1955). WERMUTH established that geographical variation of some morphological features was independent of other characters. The theory of geographical races includes an implicit correlation between the trends in the geographical variation of the species characters. STUGREN and VANCEA (1961) established similar evidence for the viviparous lizard from Rumania, in a study of populations from the Eastern and Southeastern Carpathian Chains and from the Western Mountains (Apuseni Mountains in Rumanian). Even in this last massif where the populations of *L. vivipara* have been entirely isolated from the main area of the species since the warmer postglacial period, no geographical race has developed. The authors noticed that morphological differences between males and females in a population are (statistically considered) more significant than those between individuals belonging to the same sex but living in different areas. With regard to the correlation between the variation of morphological characters, STUGREN and VANCEA observed three groups of traits, using the Chi square - test:

1. Characters which vary independently (density of squamae temporalia versus constellation of squamae praefrontalia, and versus the index of density of squamae dorsalia (Schuppendichte-Index).

2. Characters which apparently vary independently from each other, but the hypothesis of an independent distribution has a low probability (constellation of squamae praefrontalia versus the index of density of squamae dorsalia).

3. Characters which are correlated (density of squamae temporalia versus the conformation of the scutellum massetericum[1])

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[1] As defined by SCHREIBER in the scond edition of his work "*Herpetologia europaea*" (1912), the scutellum massetericum is a larger central scale in the temporal region of the head of some lizards.

These observations, together with other details discussed by STUGREN and VANCEA, confirm the peculiar nature of the variability in the viviparous lizard. It may be designed as clinal variability in the sense of J. HUXLEY.

In a second example, *Eremias arguta* PALL. did not evolve in Rumania by the way of allopatric speciation. The species reaches its westernmost point of distribution in Rumania where it occurs in small isolated populations only. The isolated colonies in the Danube Delta and in the typical steppe habitat of southeastern Moldova, at Hanu Conachi, do not present any differences of subspecific, taxonomic value (BĂCESCU, 1937). Utilization of statistical methods (FUHN and VANCEA, 1961; STUGREN, 1961a), did not show significant differences between populations. It is obvious that geographical and genetical segregation between the populations of *E. arguta* did not lead to evolution by means of allopatric speciation. Despite the favourable conditions for the evolution of separate geographical races, the event did not take place. Therefore I suggest that the mechanisms of natural selection have a reduced action in the isolated colonies of *E. arguta*, from Rumania. The populations are small, their variability is uniform. It seems that non-selective forces (such as the Sewall Wright effect) are directing the evolution of those populations. I consider these facts contradictory to the theory of geographical races and to the theory of allopatric speciation also. An objection might be raised that the isolation of populations of *E. arguta* in Rumania is a recent one, dating probably only from the holocene age. But according to the theory of geographical races, 8,000 years - and the isolation is probably not more recent than this - are quite enough for the development of subspecies.

In my opinion, in other species of Lacertidae, there are also some characteristics which show a clinal variability. The color pattern of *Lacerta agilis exigua* EICHW., a subspecies inhabiting a large area east of the Dnieper, gradually fades towards the west. But some specimens of *L. agilis* from the Danube Delta still present a distinct color pattern. Since this opinion is based on the examination of only a few specimens from the Danube Delta and the Southern Ukraine, it was not possible to use statistical methods. I consider also the variation in the pholidosis of the temporal region of the head in *Lacerta viridis* (LAUR.) to be clinal. For instance, a big scutellum massetericum, which reaches the supratemporalia and the supralabialia, is generally considered as a differential characteristic of *L. viridis meridionalis* CYRÉN. There are no available data on the frequency of this feature in the Balkan Peninsula. Among populations of *L. viridis* from the Dobrudgea region of Southeastern Rumania, there are some individuals which present this feature. I found few such individuals in the nothern parts of the Dobrudgea, in the Măcin Mountains. But in the Southern Ukraine and, much more in the north, in Bassarabia, there are some lizards which present the typical massetericum of *L. viridis meridionalis.* These facts were not tested by statistical methods, and we cannot be sure that there is a real cline. But these data lead us to the hypothesis that the massetericum changes in a clinal fashion from larger in the south to smaller in the north.

A distinctive mode of variability is to be found in *Lacerta praticola* EVERSM. This species is found in the Caucasus, in the Balkan Peninsula and in the south of Rumania, being absent from Asia Minor (MERTENS, 1952). The species has been split into geographical races: *L. praticola praticola* EVERSM. in the Caspian basin of the Caucasus, and *L. praticola pontica* LANTZ and CYRÉN in the pontic basin of the Caucasus and in the Balkan Peninsula. In an earlier paper (STUGREN, 1961), I suggested that the populations from the Banat province in south-western Rumania, belong to a peculiar geographical race, described by SOBOLEWSKY (1930) as *L. praticola hungarica*, and I suggested the revalidation of the name *hungarica*. To my mind, the populations in the neighborhood of Bucharest represent an intermediate form between *hungarica* and *pontica*. Other Rumanian herpetologists (FUHN and VANCEA, 1961), do not recognize the validity of the *hungarica* race, and neither did MERTENS and WERMUTH (1960). But the taxonomic status of the population from south-western Rumania is not the main problem to be discussed here. Whether we accept the validity of the *hungarica* race or not, we must recognize the fact that the populations from south-western Rumania have a distinctive pholidosis, which closely resembles that of the remote *L. praticola praticola*. In this case, two population-groups, situated at the geographical extremities of the species range (Eastern Caucasus and Banat), present common traits. *L. praticola hungarica* and *L. praticola praticola* are much closer to each other than to *L. praticola pontica*. According to the "rules" of clinal variability, and according to the theory of RENSCH as well, populations situated at the geographical extremes of the species-range are usually very differentiated from each other. The variability of *L. praticola* follows an opposite trend. I suggested the term *anticlinal* for this pattern of variability.

Facts concerning amphibians not in conformity with the theory of geographical races have been reported by many investigators. TERENTJEV (1949, 1960) discussed an independent variability of measurable features in Bombina variegata (L.), B. bombina (L.), and B. orientalis (BLGR.), as well as a typical clinal variability with Hyla arborea arborea L. The same trends of variability were observed by KAURI (1959) in Rana esculenta L. CURRY-LINDAHL (1956) has shown that the distribution of the so-called varieties "maculata" and "striata" of the moor frog (Rana arvalis NILSS.) is not in agreement with that expected of geographical races. Investigations made by LAC (1956) on moor frogs from eastern Slovakia have shown that there are intermediate populations between R. arvalis arvalis and R. arvalis wolterstorffi FEJ. The same author (LAC, 1957), also noticed intermediate populations between Triturus cristatus cristatus (LAUR.) and T. cristatus dobrogicus (KIR.). This intermediacy was earlier noted by FUHN (1953), in populations in the neighborhood of Bucharest.

My investigations have confirmed such statements. I have especially studied the variability of the European species of Bombina. Examining large samples of individuals, I stated (STUGREN, 1959, STUGREN and POPVICI, 1961), that in the area where the red bellied toad (B. bombina (L.) and the yellow bellied toad (B. variegata (L.) live together, heterogeneous populations, with some characteristics of both species, are often to be found. The distribution of these characteristics in the populations studied follows the rule of POISSON. But no intermediate subspecies between the two European species of Bombina have developed. Every population can be determined as belonging to B. bombina or to B. variegata. I suggested that the "mixture of traits" is not a consequence of a mass-hybridization, because the populations are ecologically segregated. But no mechanism able to explain these facts are so far available. These phenomena being at the limit between two clines, I suggest the term of interclinal variability.

Rana arvalis is represented in Rumania by isolated populations. Some of them are reported as belonging to R. arvalis arvalis, while the others to R. arvalis wolterstorffi. But no clear morphological differences have been found between them. STUGREN and POPOVICI (1960), described an intermediate population between the two races. Yet unpublished data (manuscript in print), lead to the conclusion that R. arvalis cannot be split into geographical races.

Some striking phenomena were noticed in Triturus vulgaris (L.). FUHN (1951) described an endemic race from Transylvania - T. vulgaris ampelensis. But intermediate populations between this and the nominate race were found as well (STUGREN and POPOVICI, 1961a). In addition T. vulgaris borealis from Sweden, based on the description given by GISLÈN and KAURI (1959), closely resemble ampelensis. I have examined a few specimens from the Central Ukraine which also have some traits of ampelensis. No definite statement can be given as yet, because of the lack of sufficient information for statistical tests. In Triturus cristatus (LAUR.), STUGREN and POPOVICI (1960) have found an intermediate population between the nominate race and T. cristatus dobrigicus (KIR.).

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It is apparent that our data do not contradict the theory of geographical races. This theory does not exclude such phenomena as gradual transitions between geographical races, intermediate populations, and the existence of species that do not split into geographical races. The theory does emphasize that geographical races are the main forms in which variability appears. But, I believe, the very numerous facts concerning the existence of intermediate populations allow us to have certain doubts on the validity of geographical races within some species. Some races are described and differentiated only by means of statistical methods, by average values (averages of certain measurable characteristics). But are statistical criteria sufficient to form the basis for differentiation of geographical races? Some distinguished zoologists, like CAIN (1958) and MAYR (1957), consider as valid both races and species differentiated only by average values or statistical indexes. Other zoologists, for instance PFAFF (1935) and WERMUTH (1955), feel that a race, like a species, must be distinctive enough to be recognized by the eye ("nach dem Augenschein"). I think that populations which differ from one another only by typical biometrical values should not be considered as geographical races. Only when a population bears certain qualitative characteristics, not subjected to intense variability, would I regard it as a valid subspecies. My opinion is that only such features are useful to be differential ones between races which are not expressed by statistical values, but by classical morphological diagnoses.

Some years ago, TERENTJEV (1957), proposed the hypothesis that the concept of geographical races does not express a biological reality, and he regarded it as methodologically out of date. The above published data are not sufficient as arguments to support his hypothesis. They do it only in part. In conclusion, study of the amphibians and reptiles of Rumania indicates that there are four kinds of variability: geographical (sensu RENSCH), clinal, anticlinal, and interclinal. It seems that geographical races are not frequent in nature. On the contrary, they are restricted, because many traits characteristically vary independently of each other.

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7

NEW SPECIES OF SCINCID LIZARDS FROM THE ISLANDS OF THE LESSER SUNDA ARCHIPELAGO (EAST INDONESIA)

by I. S. Darevskii

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The species and subspecies of the lizard family Scincidae described below were obtained by the author in July-August 1962 during his work with the first Indonesian-Soviet Zoological Expedition on the islands of the Lesser Sunda Archipelago. In addition to the main task - the study of the biology of the Giant Indonesian Monitor (Varanus komodoensis Ouwens), the expedition investigated the fauna of the islands inhabited by it: Komodo, Padar and Rintja, which lie in the southern part of the Flores Sea, east of Sumbawa Island. The herpetological collection consists of more than 200 specimens of lizards and snakes and is deposited at the Zoological Institute of the Academy of Sciences of the USSR and at the Bogor Zoological Museum in Java, where the holotypes of the new species have also been deposited.

The author expresses his debt of gratitude to the head of the Indonesian-Soviet expedition, Dr. Sampurno Kadarsan, the director of the Bogor Zoological Museum, who was kind enough to put at my disposal the rich collection of his Museum for comparative studies and for identification.

SPHENOMORPHUS MERTENSI sp. n. (Figures 1 and 2)

Diagnosis. A short-legged lygosome of medium size with 5 supraocular scutes, 26 to 28 rows of smooth scales around midbody and several enlarged preanals. A tendency towards the formation of an undivided transparent disc is observed in the structure of the lower eyelid.

Holotype. The Bogor Zoological Museum (Indonesia), No. 975, 1 female, adult, Island of Padar in the Lesser Sunda Archipelago, 8 August 1962, I.S. Darevskii.

Paratypes. The Zoological Institute of the Academy of Sciences of the USSR (Leningrad), No. 17597, 2 specimens, adult, same locality.

Description. Head obtuse anteriorly. Lower eyelid covered with unequal scales, with central scales markedly enlarged, forming a slightly distinct semitransparent disc (Figure 2). Ear opening oval, with 3 slightly distinct scale lobules in its anterior part. Nostril in nasal scute, supranasal absent. Frontonasal markedly wider than long, meeting with rostral anteriorly and in close contact with frontal posteriorly, separating the two prefrontals. Frontal not longer than frontoparietals and interparietal together. Five supraoculars, second of which is largest. First two supraoculars in contact with frontal. Parietals in contact with each other posterior to interparietal. Nuchals slightly distinct. Seven supralabials. Twenty-eight rows of smooth scales equal in size around midbody (27 and 26 respectively in the 2 paratypes). Two somewhat enlarged preanals. Tail thickened in its anterior third, somewhat longer than body with head. Limbs relatively short; do not meet when appressed to the body. Hindlimbs somewhat shorter than distance from tip of snout to base of forelimbs, distance between limbs 1.5 times the distance between snout and base of forelimbs. Fourth digit of hindlimb longer than third and covered ventrally by 23 lamellae (22 and 23, respectively, in the paratypes). Yellow-brown color above. Narrow dark-brown stripe along spine passing to the end of the tail interrupted in some places and broken into separate elongated spots. One row of small spots of similar color lateral to dorsal stripe, in places doubled or fused into small stripes. A wide dark-brown temporal stripe passing from nostril through eye and on sides of back, edged by slightly distinct light dotted lines. Sides of body below temporal stripes densely covered by small speckles and spots, gradually disappearing towards abdomen. Mat white color below with brown marks on inframaxillary scutes. Length of body with head 60 mm, unautotomized tail 76 mm. In the paratypes 55 and 94 mm and 52 and 88 mm, respectively. Named after the German herpetologist R. Mertens, who dedicated many of his works to the herpetofauna of Indonesia, and of the Lesser Sunda Archipelago in particular.

Comparative remarks. One of the characteristic features of the genus *Sphenomorphus*, which includes the species described above, is the absence of an undivided transparent disc in the scaly lower eyelid, a feature characteristic in particular of the representatives of the closely related genus *Leiolopisma*. It is assumed that lygosome skinks possessing such a disc originated phylogenetically from forms with nontransparent scaly eyelids. According to Smith (M.A. Smith, 1937), the tendency toward the formation of a transparent disc is found in several typical *Sphenomorphus*, for example in the New Zealand *S. ornatum*. In the south Asiatic *Leiolopisma reevesi*, however, the ocular disc is sometimes replaced by several transparent scales. A similar phenomenon is found in *Sphenomorphus mertensi* mihi. As seen in Figure 2, the scales covering the lower eyelid of the three known specimens of the new species are markedly different in size and form, with a well-formed semi-transparent disc found in one case. Thus, according to this character the described form occupies an intermediate position between the closely related genera *Sphenomorphus* and *Leiolopisma*, and is quite different in ~~this~~ relation from all other Indonesian representatives of the genus. According to the other characters, *S. mertensi* is close to the group of short-legged Lygosoma, which were once considered a separate section, and later an independent genus Homolepida (Boulenger,1887; de Rooij, 1915).

Among the Indonesian species of this group the new species resembles the New Guinean Sphenomorphus unilineatus de Rooij in its general habitus and in some plastic characters.

Range. The Island of Padar between the islands of Komodo and Rintja in the Lesser Sunda Archipelago. Known only from the terra typica. The three known specimens were obtained from the depth of a forested canyon on the western shore of the island. The lizards inhabited forest cover of fallen leaves under trees.

SPHENOMORPHUS OXYCEPHALUS sp. n. (Figure 3)

Diagnosis. Small short-legged lygosome skinks with wide ear opening, 5 supraocular scutes, 24 rows of smooth scales around midbody, 9 lamellae under fourth digit of hindlimb, slightly enlarged preanals and distinct nuchal scutes.

Holotype. Zoological Institute of the Academy of Sciences of the USSR (Leningrad), No. 17598, Island of Rintja in the Lesser Sunda Archipelago, 13 August 1962, I.S. Darevskii.

Description. Head conical. Lower eyelid covered with scales. Ear opening large, round, shorter than eye in diameter, without scaly lobules. Nostril in nasal scute, supranasal absent, frontonasal wider than long, in contact with rostral anteriorly. Prefrontals in contact with each other anterior to frontal, latter not longer than frontoparietals and interparietal together. Five supraoculars, third largest and first very small; first three suboculars in contact with frontal. Five supraciliaries. Parietals in contact with each other posterior to interparietal. Several pairs of enlarged nuchals. Five supralabials, last 3 situated underneath the eye. Orbit separated from supralabials by longitudinal rows of scutes. Twenty-four rows of smooth scales around midbody, the two rows passing along spine markedly widened, especially in the area between head and forelimbs. Preanals slightly enlarged. Limbs very short, do not meet when appressed to sides of body, leaving a distance somewhat longer than head. Hindlimbs much shorter than distance between tip of snout and base of forelimbs. Distance between fore- and hindlimbs 1.7 times the distance between tip of snout and base of forelimbs. Fourth digit of hindlimb longer than third, with 9 subdigital lamellae.

Brownish-grey color above with bronze tinge. Two light stripes pass along sides of spine, starting from posterior supraocular scute and disappearing at the base of tail. They distinctly border from above the dark-brown color of sides, which gradually becomes lighter towards the greyish abdomen. Two dark wavy lines with uneven edges on sides of tail, forming characteristic pattern (Figure 3).

Length of body with head 27 mm. Length of unautotomized tail 36 mm.

Comparative remarks. The species described belongs to the group of small short-legged lygosome skinks, previously separated into the genus Homolepida. According to many plastic characters and body proportions it is closer to the New Guinean S. crassicauda and S. forbesi. Judging from the description of the only known specimen of S. schlegeli (Dunn, 1927), which inhabits neighboring Komodo Island, this species differs from it by the pointed shape of the head, larger ear opening and the presence of nuchal scutes, a somewhat different arrangement of head scutes, the larger number of scales around midbody, and different proportions and patterns of coloration. It is also fairly well distinguished from the related West Indonesian species S. temminckii and S. vanheurni (Brongersma, 1942).

Range. The island of Rintja in Lesser Sunda Archipelago. Single specimen found in the dense wet jungles on the summit of the island (approximately 700 m above sea level). A second specimen was seen at the same locality but was not caught. The lizards hide in the thick wet cover of fallen leaves and moss.

LEIOLOPISMA KADARSANI sp. n. (Figures 4 and 5a, b)

Diagnosis. Short-legged Leiolopisma with undivided frontoparietal and no interparietal scute. Twenty-four to 26 smooth scales around midbody, fourth digit of hindlimb with 20 to 23 subdigital lamellae.

Holotype. Bogor Zoological Museum (Indonesia), No. 976, 1 female, adult, Island of Komodo in Lesser Sunda Archipelago, 2 August 1962, I.S. Darevskii.

Paratypes. Zoological Institute of the Academy of Sciences of the USSR (Leningrad), No. 17599, series of 14 specimens, same locality.

Description. Head short, obtuse anteriorly. Lower eyelid with undivided transparent disc. Ear opening round, smaller in diameter than ocular disc, without any distinct scaly lobules. Nostril between nasal, first supralabial and postnasal scutes. Supranasal scute absent. Frontonasal wider than long, bordering rostral anteriorly and frontal posteriorly. Latter shorter than single frontoparietal and in contact with two of the four supraoculars on each side. Five supraciliaries (6 in each of the three paratypes). Interparietal absent, one large nuchal and temporal posterior to parietals. Four supralabials anterior to subocular. Twenty-five longitudinal rows of smooth scales around midbody (26 in 11 paratypes and 24 in 3). Dorsal scales somewhat larger than ventral. Preanals slightly enlarged. Limbs slightly developed, do not meet when appressed against the body (in young specimens they overlap markedly in a similar position). Hindlimbs somewhat shorter than distance between tip of snout and base of forelimbs. Distance between fore- and hindlimbs 1.7 times the distance between tip of snout and base of forelimbs (in many paratypes not less than 1.5 times). Fourth digit of hindlimb longer than third and covered ventrally by 23 lamellae (19 to 23 subdigital lamellae in the paratypes). Dark-brown color above with 5 silvery-white longitudinal stripes, each of which passes on the border of two adjacent rows of body scales. (In some paratypes these stripes are light-creamy and situated on a dark-brown, almost black background of body.) Occipital stripe passing along spine starts posterior to the head and passes onto the anterior third of tail. Both ciliary stripes start from the anterior supraciliary scutes and also disappear on the tail. Two less distinct axillary stripes on the sides of the body between the fore- and hindlimbs. Abdomen greyish-white, tail light bluish-grey above. Length of body with head 45 mm, length of nonregenerated tail 57 mm (the paratypes are smaller).

Named after the head of the Indonesian-Soviet expedition, Dr. Sampurno Kadarsan, the director of the Bogor Zoological Museum, whose energy was responsible for the successful completion of the expedition.

Comparative remarks. According to many plastic characters, closely related to Leiolopisma sembalunicum Mertens, but essentially different from it by a different type of coloration and pattern of body. In the latter character closely resembles some Lygosoma of the related genus Emoia, in particular E. cyanurum and E. lessonii, which occupy a wide range. Judging from the description, it is rather closely related to Emoia similis, described by Dunn (1927) from the Island of Komodo, but the presence of supranasal scutes in the two known specimens of the latter species does not leave any doubt as to its belonging to a genus separate from Leiolopisma. Lygosome skinks of the genus Emoia were not found by the Indonesian-Soviet expedition on the Komodo.

Range. Island of Komodo in the Lesser Sunda Archipelago. Fairly common on the plateau of the central part of the island at an altitude of 500-600 m above sea level. All 15 specimens were collected in grass on the edge of a bamboo forest.

Leiolopisma kadarsani padariensis subsp. n. (Figure 5, c)

Diagnosis. Differs from the typical form described above mainly by the peculiarities of coloration and pattern of body.

Holotype. Zoological Institute of the Academy of Sciences of the USSR, No. 17605, one male, adult, Island of Padar in the Lesser Sunda Archipelago, 8 August 1962, I.S. Darevskii.

Paratypes. The Zoological Institute of the Academy of Sciences of the USSR, No. 17606 (2 specimens), same locality.

Description. The central occipital stripe wider than in the nominal subspecies, more widened at the head, occupying here entire width of two adjacent rows of body scales, while the bordering black stripes almost disappear in this area. Dark pattern on head slightly distinct. Tail above of a greyish-cream color similar to the occipital stripe. Twenty-four rows of body scales around midbody (26 in each of the two paratypes), 21 lamellae on the lower side of the fourth digit of hindlimb (25 in one of the paratypes).

Length of body with head 41 mm, tail 76 mm.

Range. Island of Padar between the larger islands of Komodo and Rintja in the Lesser Sunda Archipelago. All three specimens were obtained in the western part of the island in the forest cover under trees.

Leiolopisma sembalunica rintjana subsp. n. (Figure 6)

Diagnosis. Relatively small Leiolopisma with one frontoparietal scute and no interparietal. Twenty-six to 28 smooth scales around midbody, 18 to 22 smooth lamellae underneath fourth digit of hindlimb.

Holotype. Bogor Zoological Museum (Indonesia), No. 977, one female, adult. Island of Rintja in the Lesser Sunda Archipelago, 10 August 1962, I.S. Darevskii.

Paratypes. Zoological Institute of the Academy of Sciences of the USSR (Leningrad), No. 17607, series of 19 specimens, same locality.

Description. Head obtuse anteriorly. Lower eyelid with undivided disc. Ear opening round, somewhat shorter in diameter than ocular disc, without scaly lobules. Nostri between nasal, postnasal and first supralabial. Supranasal absent. Frontonasal wider than long. Rostral in contact with frontonasal and frontonasal in contact with frontal. Latter shorter than frontoparietal (in the typical subspecies both are equal in length). Four supraoculars, first in contact with frontal. Five supraciliaries (6 in some paratypes). Interparietal absent. Two large nuchals and 2 temporals. Four supralabials (5 in the typical subspecies). Twenty-six longitudinal rows of smooth scales around midbody (28 only in one of the paratypes). Dorsal scales somewhat larger than ventral. Preanals slightly enlarged. Limbs weakly developed; the tips of digits of appressed limbs barely overlap (in the typical subspecies they do not touch in a similar position). Hindlimbs shorter than distance between tip of snout and base of forelimbs. Distance between limbs 1.7 times the distance between tip of snout and base of forelimbs. Twenty-one transverse lamellae on the lower side of fourth digit of hindlimb (20 in 7 out of 19 paratypes, 18 in 2 and 22 in the rest). Brownish-olive color above with characteristic bronze tinge. (Some of the paratypes are brownish.) Light ciliary stripes pass on sides of back, beginning from the supraciliary scutes on the head; they are bordered by thinner black stripes on the outside. A dark, similar, distinct dotted line passes on the inner margin of the ciliary stripes and disappears on the tail (the ciliary stripes with their dark border are more distinct in the typical subspecies, and two additional black stripes are found between them on the back). Sides are brownish-grey with longitudinal rows of small black speckles, gradually becoming lighter towards the greyish-white abdomen. Tail greyish above.

Length of body with head 39 mm, length of undamaged tail 58 mm. (In many paratypes the maximum measurement of body with head is 43 mm.)

Comparative remarks. The typical form *Leiolopisma sembalunicum* was described in 1927 from one female from Lombok Island and has not been found since. Certain damages of the nasal area in the typical specimen made the absence of supranasal scutes in it uncertain, and shed some doubt on the correctness of the inclusion of this species in the genus *Leiolopisma* (Mertens, 1930). The study of a series of 20 specimens of *L. sembalunica rintjana* obtained by us confirms the validity of the generic identification made by Mertens. The new subspecies differs from the typical form in some plastic characters mentioned above, and in the peculiar coloration. According to Mertens (1930), *L. sembalunicum* is most closely related to the species *L. nitens* and *L. subitens*, the first of which inhabits Borneo and the second New Guinea.

Range. Island of Rintja in the Lesser Sunda Archipelago. Probably an endemic form on this island, where it is fairly numerous in the western and northwestern part, inhabiting forested canyons at an altitude of 200m above sea level. The typical form was described from the Island of Lombok, not far to the west of Rintja between the island of Bali and Sumbawa.

FIGURE LEGENDS:

Fig. 1. *Sphenomorphus mertensi* sp. n. female. Holotype. a - general view; b - head, dorsal view; c - head, lateral view.

Fig. 2. *Sphenomorphus mertensi* sp. n. Structure of orbit of right eye in the three known specimens.

Fig. 3. *Sphenomorphus oxycephalus* sp. n. Holotype. a - general view; b - head; dorsal view; c - head, lateral view.

Fig. 4. *Leiolopisma kadarsani* sp. n. female. Holotype.

Fig. 5. *Leiolopisma kadarsani* sp. n. a,b - head of nominal subspecies; c - head *L. k. padariensis*.

Fig. 6. *Leiolopisma sembalunica rintjana* subsp. n. Holotype.

8

GEOGRAPHICAL VOICE VARIABILITY IN ANIMALS AS AN ECOLOGICAL AND EVOLUTIONARY PROBLEM

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The problem of geographical voice variability in animals is far from new. The great increase of interest in this field in our time can be laid to the development of complex physical, physiological and ecological investigations, which have transformed bioacoustics from an unsophisticated 19th century field of study into a modern, clearly defined science with its own problems, tasks and methods of investigation.

In regard to the practical applications of bioacoustics, the two following branches are developing rapidly: bionics and studies concerning the factors affecting the behavior of animals. In both cases the geographical aspects of bioacoustics find wide application.

Regarding bionics, bioacoustics provides material concerning the means employed by animals for coding and communicating vocal information under specific environmental conditions and concerning the dependence of vocal communication on noise and interference against the background of "sound environments," the biotope, etc. Regarding the investigation of the factors governing the behavior of animals, bioacoustics contributes valuable information on the specific aspects of the vocal signals of various territorial (interspecific and intraspecific) groupings of animals. These signals often lose their universality because of the development of "local information codes." The discovery and investigation of "local dialects," and the wide use of recorded voices to frighten off predatory animals, have directed special attention to the study of the geographical variability of the mechanisms of vocal communications.

The development of the theory of communication between animals (Sinnot, 1961; Frings, 1962; and others) is an important contribution to the above fields of study. The development of the science of ecology, especially in its geographical and evolutionary aspects, had a considerable influence on the formation of the theoretical bases of bioacoustics. Here the following kinds of investigation should be differentiated: the study of populations, landscape ecology, general ecogenesis, and ecological-geographical isomorphism.

All this has led to the following situation: the old theories and reviews - as found, for instance, in the excellent works of F. Groebbels, 1925; C. Witchell, 1896; O. Heinroth, 1924, and other workers - have become outdated. In the meantime the new data which have been accumulating remain unprocessed. The introduction of mechanical instruments for sound recording and sound analysis into the study of bioacoustics has brought present-day research to a level far above that of previous work. Present-day data arouse the interest of biologists of the widest variety: evolutionists, ecologists, and also specialists in the field of acoustic bionics. The problems of communication and mechanisms for coding and communicating vocal information under specific environmental conditions thus acquire general biological interest and significance.

From the time at which the early works of N. I. Dergunov (1925) and A. I. Promptov (1927) appeared, the problems of local dialects and geographical voice variability in birds have been intensively studied in the USSR (Promptov, 1930; Kistyakovskii, 1958; Mal'chevskii, 1958, 1959, 1963;; Dement'ev and Il'ichev, 1963; Simkin and Il'ichev, 1963; and others). In addition to these investigations, the following original works are of great interest: A. N. Promptov, 1944, 1956; A. N. Promptov and E. V. Lukina, 1945. These works deal with the mechanisms of the above phenomena.

At the end of the 19th century, the problem of geographical voice variability began to be studied with material on other animal groups; it was established that amphibians, insects and apparently mammals as well as birds are subject to the phenomenon of geographical voice variability, and can thus be utilized as models for study. Immense quantities of data have been accumulated over the last years. The following works are of special interest: W. F. Blair, 1955, 1956, 1958; H. Allard, 1957; B. Alexander and Borror, 1956; A. Faber, 1953; G. Pierce, 1948; H. Frings, 1956. The above authors have collected extensive material on different species of insects and amphibians. No less important is the contribution of ornithologists: Marler, 1956; Thorpe, 1961; Sauer, 1955; Benson, 1948; and others.

An innovation which considerably broadened the scope of bioacoustics was the recent attempt to conduct a parallel study of the voice and hearing mechanisms as a single functional system. Reviews on this subject by J. Schwartzkopff, 1962, and by G. Tembrock, 1959 - which examine the factual material precisely from this point of view - have opened new and unexpected vistas.

Among these is the recently outlined division of geographical voice variability into two basic categories: adaptive variability and nonadaptive variability. Adaptive variability embraces those cases in which the voice serves to indicate the setting apart of individuals or a group of individuals and thus the territory they occupy. This is biologically significant in that it allows animals to utilize the possibilities offered by their ecological niche and thus enables the species to flourish.

At the root of this phenomenon is the well-known individual variability of the voice, which is particularly well defined in birds. A highly developed faculty for sound analysis and excellent coordination of the complex vocal musculature combined with the perfect functioning of higher nervous activity are the most important acquisitions of this group. The physiological mechanism of the highly individual voice variability in birds also enables them to learn at an early age and to imitate the sound elements of their environment. Thus, the individual variability of the voice of a chaffinch indicates, on one hand, the delimitation of its territory, and, on the other, facilitates recognition between mates (Marler, 1956; Thorpe, 1961). In this case the information communicated is primarily intended for one's "own" mate and only to a lesser extent for another's. The individual variability of the voices of penguins and other bird species serve a similar purpose (Borror, 1959; Benson, 1948; Thieckle, 1961; Tembrock, 1959; and others).

Experiments in raising birds under conditions of sound isolation (Kaspar-Hauser isolation chamber), have shown that it is not so much the song that is inherited as a certain rhythm, or way of rendition. In ontogenesis the young bird creates its song with relation to the sound background of its environment, which differs with each individual and group of individual populating different territories. This mechanism of song formation permits the delimitation of a territory, and subsequently facilitates the recognition of a mate (Marler, 1956; Thorpe, 1961). The acquired components influence the calls to a lesser degree, but even they are influenced by differences in geography. This somewhat simplified description becomes far more complicated when one turns to experimental conditions that are as similar as possible to natural conditions. This is demonstrated by the ecological investigations of A. N. Promptov and E. V. Lukina (1945). The majority of species apparently inherit the basic ability to render a song, including the general specific character, the tempo, and sometimes even the pitch. All the other attributes and qualities are acquired (Promptov, 1944).

The establishment of a particular melody in a certain territory is abetted by the fact that the development of the young male's song is completed in the first spring of his life - that is, after his arrival in the district, to which he will return all the following years of his life by force of nesting conservatism. It has been observed that the song of the chaffinch acquires its specific traits as early as autumn; but it becomes more refined and finally stable in the first breeding season (Thorpe, 1961; Marler, 1956). This development of the song in spring lasts several weeks and undergoes no subsequent essential change. Due to this prolonged development of the of the song, the voice of every individual acquires the characteristics of the group in whose territory the young bird has established residence. Its voice becomes more "comprehensible" to surrounding pairs, even if the bird arrived as a "stranger," genetically unrelated to the group living in the territory.

In the creation of optimal territorial relations within a population, the most important role falls to the song, which is the most adaptable, changeable, and individually variable aspect of the voice (Mal'chevskii, 1958; 1959; Kistyakovskii, 1958; Smogorzhevskii, 1950). These characteristics of the song, together with its identificational functions, are at the same time an essential specific adaptation that indicates, on one hand, the delimitation of the nest territory, and, on the other, serves to attract the female and thus assumes a role in sexual selection.

The delineation of territory is of the greatest importance in groups with pronounced nesting conservatism. In this case the need arises for a permanent "fixation" [the staking of a claim], which signifies the occupation of the territory by the group. This is achieved by certain modes of behavior, and in the event of extremely well-developed hearing and voice mechanisms, sound becomes the most important means for supporting and maintaining the territorial structure of a species. Birds, which are not provided with a well-developed sense of smell, nor with glands that excrete odiferous substances, as in the case of insects and mammals, have vocal-communication systems developed to absolute perfection. The importance of sounds serving as signals increases with the distribution of the species in "closed," easily overlooked biotopes, where sound becomes practically the only certain means of communication and maintenance of contact. Sound orientation acquires an even greater importance under conditions of high population density; or, conversely, when the population is dispersed.

The role of the voice as a means of identification is particularly important in the case of birds with antiphonal song (Cisticola, Trachyphonus, Laniarius) that live in dense thickets, where the role of visual signals is reduced to a minimum. All the principal behavior patterns (recognition of the mate, nuptial display, patrol of the territory, etc.) are achieved here almost exclusively by means of the voice. Each pair of birds living under the above conditions has its own song pattern (Thorpe, 1963).

Similar conditions bring about the intensification of vocal communication in both sexes in other orders. For instance, in owls the necessity for vocal communication is apparently caused not only by the limited visibility under conditions of "closed biotopes" but is also related to their nocturnal way of life (Kistyakovskii, 1958). In the cuckoo the same phenomenon is due to its polygamous way of life. Sometimes it is not the male but the female who clearly establishes her individuality by making a loud call, which causes her to stand out against the background of surrounding sounds. The male then seeks her out by her voice (as described for painted snipes, button-quails, phalaropes, and some species of Anatidae, by Kistyakovskii, 1958).

By mastering and using the signals of other species, some of them even belonging to different classes, species which specialize in the imitation of the elements of their sound environment elaborate the isolating mechanisms of individual pairs and their groups. Yet they provide the biogenic sound background of the biotope, landscape, etc., with a highly specific character. It is well known that many wheatears incorporate the screams of gerbils, susliks and many other species into their song pattern (Varshavskii, 1959). Warblers and mockingbirds often imitate the voices of birds of prey. Consequently, the acquired, the "learned" component can be utilized and already is utilized as a finely differentiated zoogeographical criterion.

In a number of cases the "learned" component in mockingbirds may even be inherited, especially in those cases where too great a proportion of foreign sounds in the song begins to interfere with communication. Thus, according to A.B. Kistyakovskii (1958), the crackling musical phrases of the warbler have apparently become inherited by the red-spotted bluethroat, and the whistling of the redshank (Tringa totanus) by the skylark.

Group (population) variability of the voice, manifested in the above-mentioned local dialects, was described as early as the 18th century by Thomas Ward, and was re-discovered by Lucanus in 1907. The smallest groups recognizable by their local dialects sometimes occupy territories of not more than a few hectares, and sometimes even less. Described with the example of several species, especially of the Isabelline Wheatear and of the red-headed bunting (by S.N. Varshavskii, 1959) and of the thrush (by A.S. Mal'chevskii, 1959), they are apparently groups of closely related families of different taxonomic rank. It is quite possible that some of them cannot be compared in size with the basic population. Others, on the other hand, may correspond to the basic and ecological populations. The local dialects of these small groups are not stable. They have their own dynamics, they disappear and re-appear, change with the territory, etc. In other words, they are not yet fixed genetically, and are phenotypical phenomena.

More stable are the dialects of large territorial groupings; according to our own terminology - geographical populations. These "vocal races" have been discovered within the limits of one subspecies, and are not characterized by any systems. An excellent study was made by F. Marler and M. Tamura (1962) on the voices of geographical populations of Zonotrichia leucophris, the white-crowned sparrow. The first investigations of geographical differences of the chaffinch were made by N.I.Dergunov (1925). Subsequently they were considerably enlarged and supplemented by A.N. Promptov (1930), in a book which became a classic, authoritative work. Geographical differences have already been established in the singing of chaffinches in the surroundings of Moscow, in the Southern Urals, in the Alps, the Mediterranean regions and Greece (Promptov, 1930; Marler, 1956; Stresemann, 1942; Sick, 1939; Steinbacher, 1927). The rain-call of that species is also subject to geographical variability. South German, Alpine and Mediterranean blackcaps do not sing in the same manner (Sauer, 1955; Emeis, 1957). Benson (1948) found geographical variability in the voices of 33 species of passerines in Central Africa. Borror (1961) established that the Carolina Wrens (Thryothorus ludovicianus) in Florida differ in their songs from those of Ohio. The little bunting of Sweden, Norway, Schleswig-Holstein and Denmark sings differently from that of Eastern Europe (Solomonsen, 1935). Geographical voice variability has also been established for the pika, various Fringillidae, tits, nightjars, and many others (Thieckel, 1961; Stadler, 1917, 1930; Thoenen, 1962; Peterson, 1941). Instrumental sounds are also subject to geographical variability, as they actually have the same functions. According to Blum and Young (1958), the drum roll of the black woodpecker in Holland lasts 3.5 seconds, and in Germany - 1.5 seconds.

Among insects and amphibians, the voice apparently is hardly used at all as a marking signal of small intraspecific groups (Blair, 1955, 1956; Frings, 1958). This is mainly due to their morphologically imperfect vocal apparatus and a lower organization of higher nervous activity. In these groups the voice is apparently mainly used as an isolation mechanism in higher taxonomic divisions (species and subspecies).

Among insects and amphibians there is widespread nonadaptive geographical voice variability, which does not include any "marking" properties but is related to the general influence of climatic and other landscape factors on the metabolism, and, consequently, on the voice as well. In recent years there has appeared much data on the nature of the climatic conditions influencing the voice of insects (Hukusima, 1948; Harz, 1956), amphibians (Blair, 1955, 1958), and even birds (Heyder, 1954; Sick, 1939; Peitzmeier, 1955; Schwan, 1921-22). Under the influence of temperature and humidity there occur changes in the frequency characteristics, intensity, and even qualitative character of individual syllables. But in birds the changes usually affect the rhythm of the singing (Scheer, 1952; Thorpe, 1961). In this case we consider the dependence of the voice on natural conditions a particular feature of the general phenomenon of ecological-geographical isomorphism, the idea of which, in its application to animals, was elaborated by G.P. Dement'ev (1948, 1951).

Geographical voice variability in insects is a subject which has occupied many investigators. A. Faber (1953) was one of the first to establish this phenomenon. H. Jacobs (1957) observed differences in the voices of insects of the locust family in Munich and the Tyrol. Pierce (1948) described the geographical voice variability of Nemobius fasciatus. Highly interesting and informative work on amphibians as carried out by Blair (1955-1962). A good review of the cases mentioned in the literature can be found in the works of Schwartzkopff (1962).

But the geographical variability of voice not only perfects itself in the process of evolution - it also exercises an ever-increasing influence on the processes of form and species formation, acting as an isolation mechanism. In this respect the coincidence of geographical voice variability within species and subspecies is of considerable interest.

Thus three subspecies of quail: the African (*Coturnix coturnix africana*), the Japanese (*C. c. japonicus*) and the European (*C. c. coturnix*) can be easily differentiated by their voices. *Parus atricapillus salicarius* differs from *P. a. rhenanus* by its call. *Zonotrichia capensis antillarum* from San Domingo has a much louder song than other subspecies. According to Pierce (1948), the frequency of the voice of *Nemobius fasciatus fasciatus* is 7,500 cps, while in *Nemobius socivis* it is 7,740 and in *N. f. tintulus* 6,300 (1961). A good review of the interspecific variability of birds' songs was written by Borrow (1961).

The processes of sympatric and allopatric species formation, and partial or complete overlapping of distribution areas, are clearly reflected in the voice. These processes produce cases in which the voices in an area in contact with that of a closely related species or subspecies differ more strongly than voices in areas having no contact.

Thus in the group *Bufo americanus* (Blair, 1962), *Bufo woodhousei* differs more markedly from the sympatric *Bufo terrestris* from Louisiana and Georgia than from the allopatric *Bufo terrestris* from Florida. *Bufo woodhousei* also differs to a greater extent from the sympatric *Bufo americanus* from Oklahoma than from the allopatric *Bufo americanus* from Wisconsin and Michigan.

Microhyla olivacea and *Microhyla carolinensis* have different voices in contiguous areas; but in more distant parts of their areas have more similar voices (Blair, 1955). Similar cases are described, offering as examples the willow warbler, Palla's warbler, some *Hylocichla* and others (Tembrock, 1959). Of great interest are the data published by Thoenen (1962). According to his investigations, *Parus montanus montanus* is easily distinguished from *P. m. salicarius* in the Alpine zone. But the Alpine *P. montanus* resembles the American *P. atricapillus* and *P. carolinensis* in its song. There is greater resemblance between *P. m. salicarius* and *P. palustris* than between *P. m. montanus* and *P. m. salicarius*. The differences between the songs of *P. m. montanus* and *P. m. salicarius* are so great that the birds do not "understand" each other at times.

All the above-mentioned demonstrate, without a doubt, that sound mechanisms play an extremely important role in the processes of intraspecific (populational) and specific divergence, especially in the case of birds. It has become clear that at present we underestimate the importance of this role. Further development of investigations in this direction will undoubtedly produce valuable new data concerning the mechanisms of populational and specific isolation, and will serve to broaden our concepts of the mechanisms of microevolution.

Local dialects, while reflecting and preserving the complex and involved patterns of the specific population, also acquire traits of complexity and of heterogenity. Some investigators (Thorpe, 1961; Marler, 1956) make use of this fact in order to deny the functional importance of local dialects. Marler (1956), for example, considers them by-products of the imitative faculty of birds, and relates population variability exclusively to the genetically fixed song. This tendency is also clearly noticeable in the work of Marler and Tamura (1962) on the voice of Zonotrichia leucophrys. In our opinion, the absence of uniformity in the local dialects of various species and groupings is an additional argument in favor of the further development of hierarchical classification of dialects, and their comparison with the classifications of populations existing in ecology. The need for further study is already definitely felt.

Of special interest is the system worked out by N.P. Naumov, according to which genetically isolated populations regularly merge into a single system with phenotypical populations. The attempt to apply the same principles to the classification of vocal dialects appears justified to us, especially since with birds, as we have attempted to explain, the voice happens to be the most flexible and convenient mechanism for fixation (marking) of any grouping, beginning with single specimens and pairs (as is the case with antiphonal species), and up to several groups of families and populations.

The principles and methods of coding geographic information in the voice of animals present a somewhat separate problem. Valuable material has accumulated on this subject in recent years. It happens that geographical variability of the voice has a close, though rather peculiar, relation to the apparatus of sound analysis. This circumstance has become especially important after the discovery of the so-called "secondary" or "accessory" sounds in the voice of animals: sounds which, according to some authors, have no functional significance. These sounds arise together with the rendering of the basic, biologically important ones. Thus, in the voice of birds there are ultrasonic frequencies reaching 45,000 cps, while it is currently believed that the upper limit of their sound registration is only 29,000 cps (Schwartzkopff, 1962). W. Thorpe and D. Griffin (1962), who made a special investigation of this problem, have found ultra-sounds in the voice of Locustella naevia, Erithacus rubecula, Emberiza calandra, Sylvia communis, Acrocephalus scirpaceus, and others. Inasmuch as naturally registered sounds have a functional significance, it is tempting to connect the nonadaptive geographical variability of voice with secondary sounds. However, this assumption requires further investigation and development. Besides, the possibility is not excluded that many of those sounds which until now have been considered as secondary may in reality have a functional significance.

The importance of the sound analyzer* as a system limiting any functional reorganization in the voice is first of all expressed in the extreme differences in acoustic means utilized for the transmission of information by groups having different levels of hearing.

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* [According to Pavlov, an analyzer consists of the nerve endings, peripheral nerves and cerebral connection of one particular faculty; there are thus auditory, olfactory, gustatory, cutaneous and motor.]

Thus geographical variability in the voice of insects and amphibians is based on sharp fluctuations of both frequency and intensity. Nemobius fasciatus achieves the transmission of relevant information by frequency variations in a spectrum of 200 to 1,000 cps (Pierce, 1948). Sometimes the number of syllables (Jacob, 1957) or temporary peculiarities of each syllable (Faber, 1953; Allard, 1957) indicates special meanings. In the voice of amphibians frequency variations play an important role (Blair, 1955-58). Geographical information in the voice of birds can be coded according to the same principles, though more often than not it is coded by finer variations in the singing.

Thus, the races of Parus atricapillus are distinguished by their loud call, those of Zonotria capensis by the rapidity of their rendition of certain elements of their song, and those of Emberzia or Coturnix by the presence or absence of an introduction (Salomonsen, 1935; Chapman, 1940; Borror, 1956).

Quite often information is conveyed not by a special song but by a particular aspect of its rendition. Thus Finnish and English nightjars (Caprimulgus) sing at different times of day and night (Tembrock, 1959).

The high level of development of the analyzer and of the higher nervous activity in birds produces the following phenomenon: geographical voice variability in birds is as a rule related to the separate parts of the spectrum. On the other hand the stridulation of insects and the rather monotonous voices of amphibians vary throughout their entire spectrum. All this has a definite biological significance.

The functions of insect and amphibian voices, as compared to the voices of birds, are considerably more restricted. In birds the voice plays a part in all the principal phases of life: pairing, migration, rearing of the young, defense against predators, etc., which explains the rich range of possibilities in birds' voices. Cariama cristata alone possesses over 200 notes; Passeriformes, of course, have many more notes at their disposal. Yet, although each of these notes can be utilized for conveying several different signals, the possibilities of coding them in that direction are not infinite. (A single note produced by passerines can have up to 15 connotations, depending on its variations.)

In certain cases there arises the need for preserving the stability of the "meaning" of a signal and of restricting its functional load. In other cases the opposite is true, and a greater polyfunctionality is required.

Thus, for example, single phrases in the song of the chaffinch may serve many purposes: delimitation of territory, identification of a mate or a pair, danger signals, mating calls, nuptial display, flocking signals and so on. (Marler, 1956). The element of geographical variability has very little effect on these functions, but can also be included in these phrases. On the other hand the screams of the young birds (nestlings), which indicate only one thing - hunger - are narrowly specialized, stable, and do not carry any additional connotations, such as geographical information. Besides, there is no biological justification for the latter. Thus, the coincidence of geographical (populational) variability with certain elements in the voice of birds has an adaptive character and is the result of an important evolutionary acquisition - the narrow specialization of separate elements.

Until recently the problems of the acoustics of associations did not arouse any particular interest. In our opinion they are of considerable interest, since each of the mechanisms of vocal communication is formed not only under the influence of one's own species and physical environmental conditions but is also influenced by the general biogenous sound background, which is characteristic of the habitat in which the species evolves.

The physical foundations of the acoustics of natural zones and landscapes have also been insufficiently investigated, and our information is scant. The greatest differences are noticeable in the case of "closed" and "open" habitats. Thus, for instance, in the tundra the distance a voice carries is limited by air humidity, but the weak absorption of sound by the extremely humid soil is a compensatory factor. In the forest the distance a voice carries is greatly reduced owing to the strong absorption and multiple reverberation of sound by tree trunks, branches and leaves. In steppes the development of the grass cover creates the conditions of a "closed" landscape for many animals. In the desert, the sound-absorbing properties of sandy soils are unfavorable to the propagation of sound. Another phenomenon with a similar effect is the particularly active air movement produced by constant winds, convection of heated layers, etc. Similar conditions influencing the propagation of sound also exist in the various biotopes.

It is therefore natural that such marked differences in conditions exert a considerable influence on the mechanisms of vocal communication. Species which have become adapted to life in open spaces tend toward a generally limited reliance on sound signals, and utilize visual cues to a greater extent. This can be easily observed in Ratitae, Otididae, Cicoriformes, sandpipers, cranes, etc.

Observations have shown that the nature of vocal communication may serve as an indication of the place of origin, development and further expansion of a group. It can also indicate the antiquity of its link with a particular landscape and type of association.

The influence of the biogenous background on sound signalization is also subject to the laws of geographical variation. It is closely related to the structure and stratigraphy of associations. The following changes in the role of the biogenous background in the formation of sound signalization can be observed from north to south, from the tundras towards zones of optimal life conditions.

Under tundra conditions the degree of sound saturation of the environment is rather limited, and its formative influence therefore insignificant. The ability to see great distances in the surroundings, together with a weakly developed sound background, results in a simple song pattern in autochthonous tundra birds. With other morphological indices as well, differentiation between single individuals and pairs depends on the distance at which communication can be continuously maintained by vocal contact.

Proceeding southward one finds that, together with the increasing complexity of the environment, the structure and stratigraphy of associations also become more complicated. Interspecific relations acquire greater importance, as does, in particular, the natural sound background, which plays an increased role in the formation of mechanisms of vocal contact. The biogenous sound background reaches its highest degree of saturation in the so-called "bird markets," i.e., in mixed forests consisting of coniferous and broadleaved trees, and in broadleaved and tropical forests. When speaking of associations inhabiting these types of forests, it is possible to speak of the objective existence of an involved acoustic structure. There arises here a definite need for the strictest form of animal adaptation, since sound signals have to be easily recognized and differentiated by their frequency, intensity, pitch, modulation and general pattern, over and above the general choral background. Should this fail to be achieved, the birds are in danger of having their means of orientation and communication greatly reduced. The problem is to find a "free area" in the acoustic field, that is, one not filled with signals of the same parameters. In addition, the importance of other means of orientation in the forest, such as visual perception, becomes greatly reduced. With a weakly developed sense of smell, sound communication becomes the only really certain means for maintenance of contacts. All this makes it difficult to find such a "free area," which we suggest calling an "acoustic niche."

Data obtained from recording and analyzing voices already indicate the existence of such niches. The peculiarities of sound signalization in the Turdidae family are sufficient to give an idea of how originally and rationally vocal communications are organized among these birds.

In our opinion, comparisons of the biogenous sound backgrounds of various faunistic complexes of high tasonomic rank are of special interest. They will undoubtedly show correlations and parallelisms of which we as yet have only the vaguest idea. Investigations in that direction will be of great help not only for discovering the laws of formation and evolution of the mechanisms of vocal communications, but also will perhaps help in defining certain aspects of the general character of evolution with greater precision.

However, data on the bioacoustics of associations have not only an exclusively scientific interest. During recent years their great practical importance has been demonstrated. This is clearly illustrated by the practical application of such knowledge to associations in oceans and seas, where the study of the biogenous sound background has opened new practical vistas for perfecting methods of underwater navigation. Such investigations, carried out in France and other countries, have led to the idea of drawing up "acoustic underwater sea maps."

Thus, one can see that the present successes of the science of bioacoustics, especially in its geographical aspects, have found increasing application in related biological fields, touching, as it does, upon many major problems, among which one can primarily number bionics, the laws governing animal behavior, ecology, geography, the evolution of populations and associations, and, in addition, problems concerning the formation of forms and species, structure, formation and dynamics of fauna, etc. Further development in the study of bioacoustics promises data of the greatest interest in all the above fields.

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THE SYSTEMATIC POSITION OF THE POISONOUS SNAKE <u>Ancistrodon rhodostoma</u> (BOIE) (SERPENTES, CROTALIDAE) BASED ON ITS CRANIAL OSTEOLOGY

by S. A. Chernov

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Following the world famous "Catalogue of Snakes of the British Museum of Natural History," by Boulenger (1896), all modern herpetologists regard the species of poisonous snakes described from Southeast Asia by Boie (1827) under the name Trigonocephalus rhodostoma [as belonging] to the genus Ancistrodon Beauv. Actually, according to its external characteristics, this species in general answers the diagnosis (strictly speaking, based only on external morphology) of the genus Ancistrodon. However, in contrast to the latter, the scales of this species are absolutely smooth, without keels. In 1853 Duméril gave attention to this detail, which warranted placing this species in the monotypic genus Leiolepis (from the Greek words meaning "smooth" and "scales"). Earlier, however, Cuvier (1829) had described a genus of lizards of the family Agamidae under the very same generic name, which is still used today. No other external morphological differences from Ancistrodon are found in this snake. As a consequence, Boulenger placed the generic name of this species of pit viper in synonymy with the genus Ancistrodon. On the other hand, one must note its significant biological peculiarities, which, so far as I know, do not occur in all the other species of this genus. Thus, A. rhodostoma exhibits oviparity, not viviparity, depositing 13-30 eggs, which the female protects during the entire period of incubation, lasting 42-47 days.

In connection with the treatment for "The Fauna of the U.S.S.R." of the genus Ancistrodon, specimens of which occur in the Soviet Union, I prepared and made a careful study of the skulls of a number of species of this genus, including A. rhodostoma. As the comparison of skulls of Nearctic species [A. piscivorus (Lacép.) and A. mocasen (Beauv.)] with skulls of three Palearctic species [A. halys (Pall.), A. blomhoffi (Boie) and A. strauchi Bedr.] showed, there are few significant differences among them. [p. 791] The skulls are very similar to each other and differ mainly in some details of structure of the palatine bone, in particular its shape, the number of fixed teeth, and by the insertion of the caudal end of the transverse [ectopterygoid] bone into the pterygoid. In other words, the Palearctic and Nearctic species undoubtedly exhibit close relationships to one another within the genus Ancistrodon.

A completely different situation exists in the skull of A. rhodostoma -- the species which is rather common in the southeastern part of outer Palearctic Asia, is widespread on the peninsulas of Indo-China and Malacca and is also on the Greater Sunda Islands. Even with a superficial glance at the skull of this species, it is easy to observe the very broad intraorbital space, formed by the frontal bones; also, there is a significantly greater breadth of skull in the parietal region, that makes the general appearance of the skull from above similar to that of some other genera of rattlesnakes, for example Crotalus and Sistrurus.

One of the peculiarities of the skull of this species, sharply differentiating it from other skulls at my disposal, is the presence of a high nail-like crest, passing along the suture between the para- and basisphenoids. The greatest height of this crest is equal to the width of the parasphenoid. The strong development of such a bony crest on the lower surface of the para- and basisphenoids indicates significant development of muscle, passing along both its sides.

Even the palatine bone, which by its form has little in common with the same bone of other species of Ancistrodon, deserves to be noted. It has not yet been mentioned that it carries no more than one tooth (the skulls of other species examined by me have no less than three -- figure a). The bone has a very distinctive form owing to the presence on it of a long, gradually tapering bony appendage, directed upward and forward (figure b). This structure on the palatine bone of this species was first noted by Peters (1862), who put rhodostoma into the genus Tisiphone, which had been established by Fitzinger (1826) for a single species of American snake. Peters included a number of other generic synonyms. Among other craniological characters, which prevent placing this species in the genus Ancistrodon, there should be pointed out the structure of the transverse bone, the expanding caudal end of which is almost perpendicular to its anterior, elongated lever-like end, resting against the upper maxillary bone. Furthermore, it is necessary to note the absence on the lower surface of the prefrontal bone of any noticeable opening, through which might pass blood vessels and nerves, and larger or smaller slit-like openings for the passage of an optic nerve. I might cite here other characteristics, less important, which I consider testify to the fact [p. 792] that this species is included in the genus Ancistrodon completely artificially; according to the structure of its skull, it is very remote from the genus Ancistrodon, and so it must be put into another genus. According to the rules of international zoological nomenclature, it must be called Calloselasma, since in the year 1860 Cope proposed this name in place of the name Leiolepis, already used for the genus of lizards. I will mention that Cope considered Calloselasma as a subgenus of the genus Trigonocephalus, since it was based only on the absence of keels on the scales in this species.

The possibility is not excluded that other southern Asian species, now in the genus Ancistrodon, will also be excluded from it after examination of their cranial osteology, and will prove to be related to Calloselasma.

10

ON THE ADAPTATION OF CERTAIN OF OUR SNAKE SPECIES FOR EATING BIRDS' EGGS

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I set forth my observations in 1940 on a large specimen of an Amurian runner (Elaphe schrencki Str.), taken from the Soviet Far East. In captivity it readily and repeatedly swallowed chicken eggs, even very large ones.

As a rule, the runner began to swallow the egg from its blunt end. Depending upon the size of the egg the whole process of swallowing - from the moment of its seizure to dropping into the esophagus - lasted 10 - 20 minutes. It is interesting that the shell of the egg was not damaged and bore no visible marks from the snake's teeth. After the egg entered the esophagus, the runner pressed head and fore part of the body to the floor of the terrarium and bent almost vertically the part of its body which was situated behind the egg in the esophagus. Then followed a movement of the elevated section of the body forward and downward. The noise of the shell breaking was heard, and the part of the body which was stretched by the swallowed egg, immediately very much diminished in diameter. It is very certain that the egg was crushed in the esophagus, and by no means in the intestines, as described by A. A. Emelyanov, and the contents of the egg dealt with in the stomach. In contrast to the egg snake, which apparently eats birds' eggs exclusively and regurgitates the shell immediately after it has been crushed in the esophagus, the Amurian runner passes the shell through the entire alimentary canal and it appears with the excrement. In the runner which I observed pieces of the broken shell appeared with the excrement 5 - 8 days after the egg was swallowed.

Having repeatedly observed this process in the Amurian runner living in a terrarium, I have concluded that in crushing the shell, part of the hypapophyses of the fore section of the spinal column must have participated. An investigation of the spinal column of three specimens of the Amurian runner, of which one was young, verified this assumption (Chernov 1945).

As in many other species of the family Colubridae, in the Amurian runner there are hypapophyses only in the anterior vertebrae of the spinal column. The hypapophyses of the first 10 - 11 vertebrae are turned backward and in this respect are not different from those of most other species of the family. However, beginning with the 11 - 12th vertebrae, they take a vertical position, and from the 15 - 16th curve forward and become somewhat thicker. In all vertebrae, from the 15 - 16 to the 39 - 40, the hypapophyses are directed forward and downward (fig. 2). In the following 2 - 3 vertebrae the hypapophyses again take a vertical position and later, becoming sharply diminished, again are directed backwards. Beginning with the 44 - 45th vertebrae the hypapophyses are missing (fig. 1).

The fact that in the African egg snake - Dasypeltis scabra (L.) - the lower aristate hypapophyses of the anterior vertebrae penetrate the wall of the esophagus and serve for crushing in the center of the shells of eggs, which comprise the basic, and often the only food of this snake, has been known widely and early. It was worked on and demonstrated in great detail at the end of the last century by L. Katheriner, 1898 and recently by C. Gans, 1952.

An analogous function of the hypapophyses is also assumed in the furrow-backed snake Elachistodon westermanni Reinhardt which is known only from a few specimens from N. Bengal (India and East Pakistan). The ecology of this very rare species is entirely unknown. The conclusion that it is an egg-eating snake was based on the similarity of its hypapophyses with those of the egg snake and on finding an egg yoke in the stomach of one. However, undoubtedly, this snake must eat other food also, consisting primarily of various small vertebrates. I note that Gans and Williams (1954), having re-examined specimens kept in the British Museum of Natural History, and parts of its skeleton, are agreed that the hypapophyses perforate the wall of the esophagus.

In these species of snake there are few teeth (in the egg snake, for example, there are 5 - 9 on the maxilla, 4 - 5 on the dentary, where they are situated only in its hind section, 4 - 8 on the palatine, and none at all on the pterygoid, and they are so small that they do not protrude from the mucous membrane. The reduction in the number and size of the teeth, just as in a number of other peculiarities of skeletal structure, is considered an adaptation for swallowing eggs, which have a firm shell, and, particularly, for regurgitating the latter from the mouth in a crushed state.

Some authors (Boulenger, 1894, etc.), considering the structural peculiarities of the anterior hypapophyses, separate the monotypic genera Dasypeltis and Elachistodon into special subfamilies of the family Colubridae: the first into the Dasypeltinae, and the latter, in which there are 1 - 2 grooved teeth in the hind section of the upper jaw, into the Elachistodontinae.

Along with these species of snakes, there exist also a number of those which eat birds' eggs as well as small mammals, lizards and other animals. However, in the past 40 years the adaptations for and mechanics of crushing the firm lime shell of eggs have not been studied. I know only of A. A. Emelyanov's indication (1929) of the fact that the Amurian runner, climbing to a chicken-coop, eats chicken eggs, and, "having swallowed the egg, it [the runner -- S. Ch.] bends it and breaks it in its intestine." However, the latter, as can be expected, has not been confirmed in observations of the swallowing of eggs by this runner.

The hypapophyses of the vertebrae along the esophagus jut into its dorsal wall, adhering rather solidly to the vertical surface of the muscle by means of a connecting tissue. However, the hypophyses in the Amurian runner do not perforate the wall of the esophagus and do not enter its cavity, as in the egg snake. Also, the lower surfaces of the hypapophyses in this runner are approximately of identical form, whereas in the egg snake the hypapophyses of the 22 - 26th vertebrae are sharply different from all the others in their more or less spherical form.

The observation of the swallowing and crushing of large eggs by the Amurian runner combined with the structure of the fore section of its spinal column leads me to the conclusion that the latter is an adaptation for crushing egg shells in the esophagus. The mechanism of this adaptation consists of the fact that having swallowed the egg the runner squeezes it between the tips of the foreward-directed hypapophyses, which are wedged in the wall of the esophagus, and shortening the muscles, presses the shell and breaks it.

I have observed a similar adaptation in the spinal column in a number of other snake species which eat eggs of various birds along with other types of food. Similar structure of the hypapophyses occur on the vertebrae lying along the esophagus in the figured runner (E. dione), 4-striped runner (E. quatourlineata) and insular runner (E. climacophora), and also in the American E. obsoleta. Thus, in the figured runner the hypapophyses of the 5 - 6th anterior vertebrae are directed, as in the other species, backward and downward, the two following stand almost vertically, then their direction changes and beginning with the 8 - 9th vertebrae, they are turned forward and downward (fig. 3). The last vertebrae bearing hypapophyses are the 34 - 35th (in 3 specimens).

Gans and Oshima (1952), not knowing of my data on the adaptation of snakes to eating birds' eggs (Chernov 1945), in 1952 published an article on the same subject. The species on which their observations were based was the insular runner (E. climacophora). Their publication confirm my data[1] and -- with the addition of E. guttata, E. taeniura and E. carinata -- increase the number of species, in the structure of the spinal column of which the authors were able to observe analogous characteristics. It is interesting to add that, according to those authors, in E. carinata several hypapophyses perforate the wall of the esophagus, which is not found in other species of the genus Elaphe. It must be said that in my other investigations of species of the genera Elaphe (E. rufodorsata, E. longissima, E. hohenackeri) and Coluber all the hypapophyses are directed backward and below (fig. 4).

((

[1] In their material the last hypapophysis bearing vertebra in the "spotted?" (   ) runner is the 39th, which testifies to the possibility of some variations in the number of vertebra present in one and the same species.))

So far as is known, these runners do not eat birds' eggs; in any case, in their stomach-intestinal tract remains of egg shells have not been found. I note that in its external morphology the red-backed runner in general differs comparatively little from the patterned one, but in contrast to the latter, leads a semi-aquatic life, eating small fish and amphibians, and are oviviparous snakes.

This whole discussion about the structure of the spinal column in snakes in the food of which hard-lime-shelled eggs are known to occur, has led me to the conclusion that Dasypeltis and Elachistodon cannot be separated as special -- or a special -- subfamilies, as is presently done.

11

ATTEMPT AT APPLICATION OF ANALYSIS OF VARIATION TO THE QUALITATIVE RICHNESS OF THE FAUNA OF TERRESTRIAL VERTEBRATES OF THE U. S. S. R.

by P. V. Terent'ev

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The Problem

The term "richness of fauna" may be understood in two ways: first, as a great number of species found in any one place, and second, as a large number of individual animals. For the first case, it is better to use the term "qualitative richness of fauna" and for the second, "quantitative".

The significance of topographic variation on qualitative richness of fauna is generally known. The majority of zoogeographers explain diversity by historical causes, although no one denies the influence of present-day ecological conditions. The relative importance of these two groups of factors is still uncertain.

Introduced to science by Fisher (Fisher, 1925, 1928) and rapidly developing now (Sheffe', 1959; Plokhinski, 1960), the method of "dispersion analysis" or otherwise called "analysis of variance" affords the opportunity to determine the relative significance of the influence of separate factors on the total variability of a phenomenon. Statistically eliminating contemporary ecological factors (in the first place, abiotic), it is possible to approach the determination of the magnitude of influence of historical factors. Will this be the same for different groups of organisms?

Methods

Inventories of the terrestrial vertebrates of the USSR have reached a stage which permits the application of quantitative methods. The icthyofauna has also been well studied, but the complex of basic ecological factors on land and in the water is so varied (Hesse, Allee, Schmidt, 1951) that it would be more reasonable to devote a special paper to the analysis of the icthyofauna.

The entire surface of our country was divided into 66 equal-sized quadrats, of 10° longitude (about 700 miles on a side). Then the number of species found in each quadrat was determined by the superposition of areas on this grid. The raw data for these compilations was obtained from the most complete summaries of the distribution of terrestrial vertebrates of our country (Bobrinski, Kyznetsov, and Kyziakin, 1944; Denent'ev and Glavkov, 1951-1954; and Terent'ev and Chernov, 1949). In some individual cases from the data taken out of the aforementioned summaries, changes and additions were made according to more recent information. The entire labor-consuming task of the transposition of range maps into quadrats was completed by S. V. Kanep and D. N. Fugenov. Climatic and other indices of abiotic (physical) conditions for the separate quadrats were calculated on the basis of maps from the Bol'shoi Sovietskoi Encyclopedia (1957), the Bolshovo Sovietskoi atlas of the world (1937), and the book by A. A. Borisov (1948).

For the sake of standardization and generalization of present statistical treatment, the systematized scheme and designations of the book of N. A. Plakhensk (1961) were used, with the exception of the term "deviation" for which the more common term "variance" was substituted. Variance for each quadrat is the square of the deviation of that quadrat's value from the mean value for all quadrats; r-1 is the number of degrees of freedom of non-random factors; n-r is the number of degrees of random factors; λ^2 is the correlation ratio for non-random factors; σ_x^2 is the factor's variance; σ_z^2 is the error's variance; F is the variance ratio (the confidence level of 95% is used). For condensation in the tables, the following abbreviations are made: M = mammals, A = birds, R = reptiles, and Am = amphibians.

Formal Indices

It stands to reason that latitude and longitude, taken by themselves, do not take into consideration "ecological factors", but when these are taken in combination with several real causal factors it is possible to consider several excellent summarizing indices. Rekliv (1901) noted that "animal and vegetable species become more numerous as one preceeds from the poles to the equator", and this is now known to be generally true with respect to latitude. Analogous views are contained in many other reports (Eccart, 1913; Jacobi, 1919; Dahl, 1921; Hesse, 1924). Romer devoted an entire speech on the 1st of December 1906 to the Zen Kenderyskon Society of Naturalists especially to the question of the dimunution of the numbers of animal species with the increase in geographic latitude (Romer, 1907). In the following years, work was devoted to the quantitative expression of the stated dependence for different animal groups (Terent'ev, 1946; Kusenov, 1957; and others). By a priori considerations one is forced to conjecture that the changes in dependence on longitude will be in great measure determined by historical, but not ecological, principles.

Table 1. Analysis of the degree of influence of latitude on the number of species.

	M	A	R	Am
r-1	5	5	3	3
n-r	60	60	42	42
η^2	0.74	0.84	0.68	0.25
σ_x^2	10028	77544	3035	67
σ_z^2	288	1382	104	14
F	35	56	29	4.8

Table 2. The mean number of species found at the various latitudes.

Latitude	M	A	R	Am
30-40°	87.0	229.5	47.5	4.5
40-50°	80.7	213.0	27.3	8.1
50-60°	67.3	207.1	7.9	6.7
60-70°	39.9	153.4	2.4	3.0
70-80°	16.4	42.0	0	0
80-90°	1.8	12.3	0	0

Four separate analyses of variance were made, one for each taxon and its dependence on latitude, and the parameters calculated are given in Table 1. The decreasing number of degrees of freedom for Reptiles and Amphibians are explained as follows: representatives of these taxa at latitudes above 70° are found only as exceptions. From the preceding table, it is obvious that latitude imparts its maximum influence on the richness of fauna of the birds, while the poikilotherms, apparently, are more influenced by other factors. The empirical significances of the regression of the number of species with latitude are given in Table 2. Attention is drawn to the fact that the number of species diminishes with increase in latitude in all cases except amphibians. The alien value for poikilotherms makes it foolish to search for interpreting formulas, whereas for homeotherms, the values are all alike (Figures 1 and 2).

Mammals: $y = 102.1050 + 0.2670x - 0.0178\,x^2$
Birds: $y = -24.4275 + 11.9590x - 0.1401\,x^2$

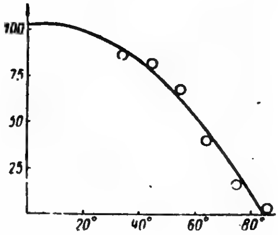

Figure 1. Regression of number of species of mammals on geographic latitude. The abscissa is graduated in degrees latitude, the ordinate in number of species.

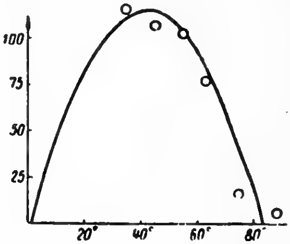

Figure 2. Regression of number of species of birds on geographic latitude (abscissa and ordinate are the same as in Figure 1).

The analyses of variance based on longitude give the figures presented in Table 3. The homeotherms show no correlation with longitude, but there is a weak correlation with longitude for the poikilotherms. Therefore, the detailed analysis of regression (Table 4) does not have meaning, although it does demonstrate the presence of two patterns: the number of species of homeotherms generally decreases from West to East (an artifact of the study?), whereas the

Table 3. Analysis of degree of influence of longitude on the number of species.

	M	A	R	Am
n-1	8	8	7	7
n-r	57	57	56	56
η^2	0.14	0.15	0.26	0.56
σ_x^2	1182	9026	541	95
σ_z^2	1017	6990	245	9.3
F	1.2	1.3	2.5	10.2

Table 4. The mean numbers of species ocurring at various longitudes.

Longitude	M	A	R	Am
20-40°	60.0	193.4	9.7	9.7
40-60°	57.9	162.9	22.1	6.1
60-80°	53.3	154.8	16.7	2.9
80-100°	51.9	141.5	5.5	2.8
100-120°	39.5	147.3	3.0	2.5
120-140°	47.4	149.4	4.4	3.6
140-160°	29.4	94.0	2.1	2.0
160-180°	18.4	79.6	0.2	0.6
180-200°	12.0	47.5	0	0

number of species of poikilotherms shows an East-West maximum (at roughly the Carpathians and the Caucasus on one side, and the Far East on the other side). These observations may be considered to be evidence that longitudinal distribution is dependent in Eurasia first and foremost upon historical factors (the glacial impoverishment of the Siberian fauna).

The Influence of Climatological Factors

The primary role of temperature and humidity amongst the physical factors is generally accepted. Unfortunately, it is difficult at this time to obtain satisfactory information on many parameters. Therefore, as a first approximation, three mean long-term quantities were used: air temperature in January (t_1), air temperature in July (t_7), and the sum of yearly precipitation in centimeters (S).

Analyses of variance using January temperatures gave the values presented in Table 5. A weak correlation is demonstrated for all four taxa, but comparisons of the taxa do not lead to clear-cut conclusions. The insignificance of the observed correlations makes it useless to calculate empirical lines of regression (Table 6), but it should be noted that in all cases the richness of fauna increases with increasing temperature. It is interesting also that the number of species of reptiles and amphibians is almost exactly equal at low temperatures, but that, at higher temperatures, the number of species of reptiles rapidly exceeds the number of species of amphibians.

Table 5. Analysis of degree of influence of the January temperature on numbers of species.

	M	A	R	Am
r-1	4	4	4	4
n-r	61	61	61	61
η^2	0.42	0.37	0.62	0.42
σ_x^2	7006	43600	2466	127
σ_z^2	646	4850	101	11
F	11	9	24	12

Table 6. The mean number of species found in areas with different mean January temperatures

t_1 in °C	M	A	R	Am
-50- -30	30.0	98.7	1.2	1.3
-30- -20	27.5	93.8	1.9	1.9
-20- -10	62.1	189.3	11.6	4.8
-10- 0	72.9	206.8	21.4	9.6
0- 10	90.0	227.3	55.0	5.3

An entirely different picture is obtained from the analyses of variance using mean July temperatures (Table 7): a very strong dependence is obtained for all taxa except amphibians, exceeding everything hitherto reported in this paper. Empirical lines of regression are given in Table 8. The dependence for mammals, birds and reptiles may be described with the following curvilinear equations:

Table 7. Same as Table 5, except for July temperatures.

	M	A	R	Am
r-1	6	6	5	5
n-r	60	60	45	45
^{2}	0.89	0.89	0.90	0.46
^{2}	11923	84066	3175	104
^{2}	127	836	32	11
F	94	101	100	9

Table 8. Same as for Table 6, except that the data is for July temperatures.

t_7 in °C	M	A	R	Am
0- 5°	8.4	28.3	0	0
5- 10°	27.6	85.6	0.2	0.7
10- 15°	41.4	159.1	3.2	3.4
15- 20°	70.7	215.5	8.8	7.5
20- 25°	97.0	253.8	29.3	9.3
25- 30°	88.0	212.0	52.8	5.0

Mammals: $$y = \frac{x}{0.2052 + 0.027276x - 0.002612x^2 + 0.000064x^3}$$

Birds: $$y = \frac{x}{0.1094 - 0.0048x + 0.000185x^2}$$

Reptiles: $$y = \frac{x}{13.0256 - 0.9828x + 0.0192x^2}$$

The graphs (Figures 3, 4, 5) indicates satisfactory correspondence between these curves and the empirical data. The question of the amphibians will be considered below.

Analyses of variance using the sum of the yearly precipitation gave the results presented in Table 9. It is seen that the total precipitation plays, even as was expected, a more significant

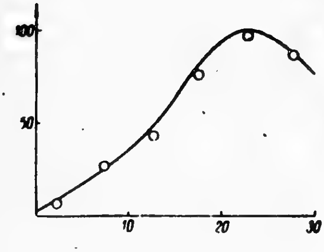

Figure 3. Regression of the number of mammal species on July temperature. The abscissa is graduated in °C, the ordinate in numbers of species.

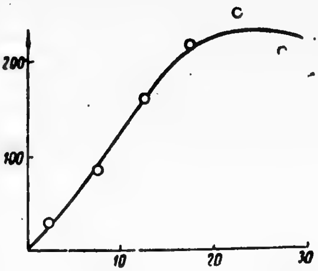

Figure 4. Regression of the number of bird species on July temperature (abscissa and ordinate same as in Fig. 3).

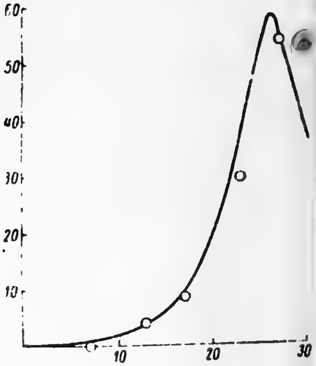

Figure 5. Regression of the number of reptile species on July temperature (abscissa and ordinate same as in Figure 3.

role only for the amphibians, but that even this is not great. Thus, the problem is not to look for an equation for the corresponding regressions, but to give these empirical meaning.

Table 9. Analysis of the degree of influence of total precipitation on the number of species.

	M	A	R	Am
r-1	6	6	6	6
n-r	60	60	60	60
η^2	0.20	0.28	0.18	0.42
σ_x^2	2658	26305	575	103
σ_z^2	902	5652	219	12
F	3.0	4.6	2.6	8.6

Discussion

The previous evidence shows without doubt that the number of species of the fauna is primarily a function of the presently operating factors (ecological), whereas the historical factors are responsible for the basic form of the specific composition of species. In other words, history determines how much of the potential size of the fauna is filled (saturated), which itself is determined by contemporary ecological conditions; i.e., in itself, the quantitative richness of the fauna (species diversity) is 80-90% a product of the present day conditions. By these means, the old zoogeographers-ecologists (Schmarde, 1853) have been shown to be correct, as are the contemporary zoogeographers, in giving attention to basic historical principles. The above is reasonable and correct only for faunas of a more or less substantial area; for, if we consider areas of small size, in the first place, stationary features and local perturbations arise. It is difficult to determine that minimum area, above which zoogeographical conformity prevails over local patterns (of diversity). It is reasonable to assume that the above findings hold for quadrats of the order of $n \times 10^4$ or $n \times 10^5$ kilometers^2. Amphibians, and very likely many groups of invertebrates, present exceptions: the numbers of these animal species depends, in general, rather strongly upon the general local situation, on microclimate rather than upon the macro-climate. Obviously, the minimal area necessary for zoogeographical regularity for mammals must be considerably larger--of the order of $n \times 10^6$ kilometers^2. Further investigation will be required to verify these suppositions and tentative findings.

As far as the correlation between latitude and temperature, localities (in soviet Russia) show a strong correlation - of the order $\eta = .84 \pm .01$ (Terent'ev, 1946); considering the shortage of information concerning local climates, it is possible to infer these from latitude. As mentioned earlier (p. 1), Rekliv was the first to note the latitudinal increase in total number of species. Thus, we may call this phenomenon "Rekliv's Rule". Furthermore, the increasing numbers of species associated with increases in temperature may be called "Schmarda's Rule", inasmuch as this author clearly noted the decrease in number of species with decreased annual temperatures.

Mere recognition of a positive or negative correlation does not definitely determine its form. Examination of the graphs of the present paper shows that some (Figures 3 and 4) appear to have two slopes: after the achievement of some optimum, the curve begins to descend. (Translator's note: here Terent'ev is referring to his mean values for the numbers of species--the data points.) One may examine other plots (Figures 1, 2, and 5) as parts of two-sloped curves. Given such a form, it is possible to make a more exact "Schmarda's Rule", taking the peak as the "optimum value". In the territory of the USSR, the greatest numbers of mammal, bird, and reptile species are found in quadrats with long-term mean July temperatures around 20-26°C. It is interesting to note that there is no difference in the optimum for amphibians, either.

Is it possible to express the mathematical dependence of the qualitative richness of fauna on temperature with such equations? An extension of this method gives the parabolic interpretations: $y = a + bx + cx^2 \dots$ Theoretically, with such equations it is possible to express the course of any curve, if one includes a sufficient number of terms. Such a flexible function is adequate for a first approximation but is not devoid of basic shortcomings. The parabolas, in smoothing the mean of the curves, can give negative ordinates and may descend to approach zero. A negative quantity of species appears senseless, but the character of the region empirically analyzed has the meaning of a different function. Therefore, making use of the parabola, it fits the system to specify the limits of significance of the argument within which it is justified. For example, the parabolas of Figures 1 and 2 take on the meaning of an independent variable between 26° and 80° latitude. Presently there is no determining the ideal formula for the expression of the rule of the optimum ("Schmarda's Rule"). The important conditions which such a theoretical curve must possess are (1) that it must not allow the dependent variable to take on any negative values, and (2) that the asymptotes must approach the observed (empirical) values at each end of the curve. The necessary equations must take the following general form:

$$y = \frac{1}{a + bx + cx^2 + \dots} \qquad \text{and} \qquad y = \frac{x}{a + bx + cx^2 \dots}$$

The second formula is the preferred one, which even with only a second degree term in the denominator of the parabola, still shows the asymmetry so peculiar to the curved reaction in ecological factors. In practice, it is recommended to compute the ratios $\frac{x_1}{y_1}, \frac{x_2}{y_2}, \frac{x_3}{y_3}, \dots$ from the empirical data, and then to smooth these with a parabola of suitable degree (first, second, third, etc. . . .).

What do we obtain, in any given case, from such equations of regression? First of all, they make our theoretical ideas more precise, and secondly, they allow us to predict the value of data concerning the number of species, found in any given place. In making use of such standards, it is taken for granted that inevitably there will be scatter of empirical points about the predicted line of regression. It makes sense to look for causes only for those factors which show significant correlations. For example, the long-term mean air temperature in Leningrad is about 17.5°C (Syelyaninov, 1937). From this, it follows that we should expect about 211 species of birds in the Leningrad region. V. Bianki (1907) counted 237 bird species in this region, but noted that of these 237 species, 16 were rare, and another 24 were rather uncommon. This is very good agreement between the number of species predicted and the actual number occurring in the Leningrad region. On the other hand, if we try our prediction in the Crimea, we estimate that there will be from 39 to 46 species of reptiles. In fact, there are, according to old data, 15 species (Nikolski, 1905), and according to the latest investigations of N. N. Scherbak, only 14 reptile species in this region. Clearly, this particular fauna appears to be impoverished, which is precisely what N. N. Scherbok considers to be the case for the Crimea.

The amount of impoverishment carries with it a guiding character. On such areas it is desirable to check and to make our estimates more precise, with more detailed investigations in the separate regions of the USSR; and on the other hand, it is desirable to make further, more vast studies, taking in even other countries.

Summary

A number of species may be named "Qualitative Richness of Fauna", in opposition to the number of individuals, termed the "Quantitative Richness of Fauna".

The USSR territory was divided into 66 rectangles (10° latitude by 10° longitude). For each rectangle separately the number of Mammal species (M) was determined, the same for Birds (A), for Reptiles (R), and for Batrachians (Am). Deviances, estimates, variance-ratios (Tables 1, 3, 5, 7, 9) and regressions (Tables 2, 4, 6, 8) were calculated. Equations are given for the dependence of mammal and bird species numbers on geographical latitude, and for the dependence of mammal, bird, and reptile species numbers on the local mean July temperature. Dependence on geographical longitude and mean rainfall is insignificant. The number of species of amphibians is determined more strongly by micro-, rather than macroclimatic conditions.

Conclusions

(1) The number of species in a fauna is primarily determined by the mean temperature of the warmest month of the year (July).

(2) The greatest number of species of mammals, birds and reptiles in the territory of the USSR are found in areas with a July temperature on the order of 20-26°C.

(3) The quantity of species of amphibians is determined chiefly by microclimatic factors.

(4) An expression for the approximation of the "rule of the optimum" for species diversity is the following equation: $y = \frac{x}{a + bx + cx^2 + \ldots}$

ON THE MONO- OR POLYPHYLETIC ORIGIN OF TETRAPODS

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The problem of the origin of terrestrial tetrapods is one of the controversial questions of biology. Many investigations have been devoted to it in the field of paleontology, comparative anatomy and embryology. In the past decade, interest in this problem has increased especially in connection with new discoveries of fossil forms which are more or less close to the ancestors of the tetrapods.

As long as the links which connect fishes with tetrapods are not conclusively established, there is room for hypotheses and propositions about the peculiarities of the structure, taxonomic position, singleness and multiplicity of initial forms, the time and places of the appearance of the first tetrapods and the causes for their appearance.

At the end of the 19th century, terrestrial amphibians were linked with dipnoan fishes. Paleontology rejected this proposition, based on the great specialization in the Dipnoi and the impossibility of the homology of their bones with the bones of tetrapods. In the 20th century, only a few investigators consider that the origin of some tetrapods, namely tailed amphibians (Urodela), is possible from the Dipnoi (Wintrebert, 1910; Holmgren, 1933; Save-Soderbergh, 1934; Lehman, 1956). At the present time, one can consider it generally accepted that tetrapods derived from lung fishes of the order[1] Rhipidistia which unites two suborders, i.e., Holoptychioidei and Osteolepidoidei, which correspond to the groups Porolepiformes and Osteolepiformes of Jarvik (E. Jarvik, 1942).

The opinion of investigators is divided as to the actual representatives of the Rhipidistia which served as starting points for the tetrapods. The most widespread hypothesis is that of polyphyletic derivation. Its basic source was the detailed survey of the anatomy of the ethmoid region of the skull of lower Gnathostomata by Jarvik (1942). As a result of the comparison of the structure of the snout of *Eusthenopteron* (Osteolepiformes) and *Porolepis* (Porolepiformes) and their comparison with the skull structure of amphibians, primarily *Rana* (Anura) and *Salamandra* (Urodela), Jarvik came to the following conclusions: 1) The Rhipidistia represent two separate groupings, i.e., Porolepiformes and Osteolepiformes; 2) modern tailless and tailed amphibians are sharply distinguished from one another by the structure of the ethmoid, which indicates their derivation from various fishlike ancestors; 3) the distinctions between Anura and Urodela correspond to the differences in the structure of the snout of Rhipidistia and in connection with this the former should be considered to issue from Osteolepiformes and the latter from Porolepiformes. Osteolepiformes served as the beginning for all remaining tetrapods (Eutetrapoda). Lepospondylous amphibians (Lepospondyli) which are brought into question with Urodela just as are Apoda are not examined by Jarvik (fig. 1).

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In recent years, Jarvik has published a series of works devoted to the questions of the origin of the tetrapods, with an analysis of the structure of separate components of the skeleton and especially of the skull. The hypotheses of diphyly in his later works has developed into full polyphyly (Jarvik, 1955). Thus, one of his graphs (Jarvik, 1960, figs. 18n and 30) shows that not only Anura and Urodela but also Labyrinthodontia, Sauromorpha and Theromorpha arise independently from Osteolepiformes. The time of the appearance of tetrapods moves to the lower Silurian or even Ordovician (Jarvik, 1964).

--fig. 1--

The investigations of Jarvik created lively discussion among biologists. They present a pattern of detailed study of the skeleton of fossil vertebrates. However, a whole group of scholars are not in agreement with the conclusions of these studies. Many zoologists (Shmal'gauzen, 1959, 1964; Eaton, 1959; Szarski, 1962; Parsons and Williams, 1962, 1963) consider this contrasting of Anura and Urodela untenable and reject the hypotheses of their diphyletic derivation. The studies of I. I. Shmal'gauzen in this regard deserve special attention. He has dealt for many years with questions of the origin of terrestrial vertebrates. A series of experimental investigations was conducted under his direction on the development of amphibians with the aim of clarifying the succession in evolution of the structure of fishes and tetrapods and the degree of similarity and difference in their beginnings in Anura and Urodela. The investigations, which dealt with the development of many elements of the skeleton and sensory organs in amphibians, in no way support their polyphyletic origin. On the other hand, data from embryology indicating the homology of many organs of Anura and Urodela along with their possession of a complex of tetrapod characteristics which hardly could have appeared in a parallel way in various evolutionary lines and along with the

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[1] The taxonomy of lungfishes (superorder Crossopterygii) is according to "Osnovy paleontologii" (1964).

presence of traits characteristic only of amphibians, rather bear witness in favor of a monophylatic origin of modern amphibians (Shmal'gauzen, 1959). Special interest is created by the ascertainment of the homology of "doubtful structures", i.e., structures casting doubt on the generality of their origin among various forms of amphibians. Their number includes, in part, the lepospondylous type of vertebrae and the structure of the limbs of Urodela. The wholly cylindrical vertebrae of Lepospondyli are similar to the vertebrae of Urodela. As the studies of I. I. Shmal'gauzen (1959, 1964) have shown, in the latter, the vertebrae are formed by the same elements as in other amphibians. They could easily have

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issued from a rachitomous type basic for all tetrapods, i.e., the representation of the isolated situation of Lepospondyli is without foundation.

The difference in the embryonic development of the limbs of the modern Urodela and Anura served as one of the bases for their diphyleticism. At one time Holmgren (1933) presented a diagram of the limbs of the Urodela and Anura on the basis of embryological investigations and generalizations. The first diagram was notable for the presence of the jointed skeletal axis testifying, as it were, to the origin of the limbs of Urodela from biserial archipterygium of lungfishes or the Dipnoi. The basis for the formation of such an axis was the presence of a skin formation between the first two digits in the larvae of Hynobius at early stages of development. This formation in the opinion of I. I. Shmal'gauzen (1959) is coenogenetic. This diagram does not correspond to the formation of the limbs of a single representative of tetrapods including mature Urodela. The composition of the limbs of the latter is very similar to that of the remaining tetrapods especially the labyrinthodonts, e.g., Eryops and Trematops (Shmal'gauzen, 1915). The diagram given by Holmgren for Anura reflects the general structure of a pentadactyl limb with the exception of mature Anura whose limbs are highly specialized.

The difference in the embryonic development of the limbs of Urodela and Anura were examined even before Holmgren by A. N. Sewertzoff (Sewertzoff, 1908) as has been noted by Jarvik (1964). The latter, citing these differences as one of the arguments for the diphyleticism of amphibians, used a partial quotation from the work of A. N. Sewertzoff, "Must we therefore accept that the limbs of the reptiles Anura, on the one hand, and Urodela on the other developed phylogenetically in complete independence from one another?" However, A. N. Sewertzoff strongly upheld the idea of the monophyletic origin of terrestrial amphibians as the continuation of this quotation omitted by Jarvik indicates: "But in what way should we explain in this case the unquestionable similarity in the position of skeletal elements of the limbs in these forms? I will not develop these conclusions further. They lead to such improbable results, that it is clear to anyone who does not have a preconceived opinion, that they derived from an incorrect precondition, i.e., that the heterochromy in the development of the digits is an expression of the primary line of development of the limbs of the ancestors of terrestrial vertebrates. We see, however, that for this phenomenon there is another, more probable explanation, and we have come to the conclusion that the phenomenon of heterochromy in the development of elements of autopodium does not provide a basis for the proposition that the limbs of Urodela developed from a form with a small radius" (Sewertzoff, 1950, p. 214).

The conclusions of Jarvik produced critical response even from some paleoichthyologists. (Vorob'eva, 1962; Kulczycki, 1960; Romer, 1962; Thomson, 1962, 1964; Gross, 1964). As was shown by the study of a series of lungfishes (Porolepis, Panderichthys, Platycephalichthys, Ectosteorhachis), the characteristic types of snout in Porolepiformes and Osteolepiformes presented by Jarvik as a basic argument for polyphyleticism did not find confirmation in many points. It became clear that these types of snout embraced far from all Rhipidistia. According to a series of traits, the two types overlap because of the presence of intermediate forms. In addition doubts were expressed about the viability of the interpretation of separate structures, and also of the possibility of their being homologous with the structures of the ethmoid of modern amphibians.

Jarvik considers (Jarvik, 1942)[2] the character of the internasal wall one of the basic differences of the osteolepiform and porolepiform types of snout. In Eusthenopteron (fig. 2, 1) the nasal cavities are close together and separated

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by a fine, continuous partition (septum nasi). In Porolepis (fig. 2, 2) on the other hand, they are widely separated, and between them is situated the ethmoidal section of the cranial cavity in front of which lies the paired internasal pit (cavum internasals), which, according to Jarvik, contains the

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[2] For the subsequent survey of the peculiarities of of formation of osteolepiform and porolepiform types of snout we have in mind this particular work of Jarvik and therefore no citations to it will be given.

paired intermaxillary gland, which is homologous to that of amphibians and opens ventrally into the oral cavity. A similar gland also was in Eusthenopteron according to Jarvik but was significantly smaller and was located in a small depression (fossa apicalis, see fig. 5) which occupied the extreme anterior part of the ventral surface of the ethmoid and opened into the posterior part of the oral cavity by a canal crossing the vertical toothed plate of the vomers (iv. p). Jarvik granted great phylogenetic significance to the latter canal in comparing it with the canals of labyrinthodonts and Anura. Starting from the presence of the ethmoidal section of the cranial cavity in Porolepis, the conclusion was made that the structure of the ethmoidal part of the brain differs in Porolepiformes and Osteolepiformes.

--fig. 2--

Recent investigations have shown that a broad internasal wall is characteristic even of some Osteolepiformes: Platycephalichthys (Vorob'eva, 1959), Panderichthys (Vorob'eva, 1960, 1962), Ectosteorhachis (Thomson, 1964), and apparently Glyptopomus (Jarvik, 1950). For the first two genera, the presence of the ethmoidal cranial cavity has also been established (fig. 3, 2). Its existence in Porolepis, on the other hand, is doubted by Kulczycki (1960) who assumes that the cranial cavity in this fish begins behind the level of the anterior walls of the eye sockets (fig. 4, 3, 4). The functional significance of the ethmoidal cavity of lungfishes is still unclear. However, Jarvik's assumption that the anterior portion of the brain (fig. 4, 3, hem) is located in it is not justified. Judging by the narrow aperture of the cranial cavity in the posterior section of the sphenethmoid of Panderichthys and Platycephalichthys, only olfactory canals could pass in the interorbital area of these fishes, i.e., the ethmoidal cavity could not include the hemispheres of the brain. It is possible that the ethmoidal cavity is analogous to the rostral cavity of Latimeria and served as an organ of balance supplementing the canals of the lateral line (Vorob'eva, 1962, p. 20).

As far as the cavum internasale and fossa apicalis are concerned, Kulczycki and Thomson are inclined to consider them homologous and the only receptacle of the large front teeth of the lower jaw. This possibly does not diminish the significance of these pits since the teeth or toothed spiral is not developed at the anterior end of the lower jaw in all Rhipidistia.

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The structure of the nasal cavities also is suggested as a means of distinguishing two types of snout in Rhipidistia: the character of the walls, the presence or absence of branches and projections subdividing them, the number and position of openings of blood and neural canals, the position and size of notches and openings joining the nasal cavities with the external environment, with the eye socket and with the oral cavity and in particular the position of the nares and the size of the choanal notches. This presentation of the great phylogenetic significance of the details of the structure of the nasal cavity into sections can distinguish even close forms: Panderichthys, Eustenopteron, Platycephalichthys (Vorob'eva, 1962) and, conversely, can coincide in representatives of both groups (Porolepis, Panderichthys). Thomson considers it generally impossible on the basis of paleontological evidence to compare the sections of the nasal capsule with the divisions of the nasal sac. Therefore, although a ventro-lateral depression for example is found even in Eusthenopteron and Ectosteorhachis, it is impossible to decide whether it corresponds to the outgrowth of the olfactory sac and whether this outgrowth contains Jacobson's organ.

--fig. 3--

The position of crests and processes in the nasal cavity can also coincide in representatives of both groups. In particular, the processus intermedius or its homolog is as much pronounced in Porolepis (Kulczycki, 1960) as in Eusthenopteron (fig. 2, 1, pr. im), is somewhat altered in Ectosteorhachis (Thomson, 1964) and is lacking in Panderichthys (Vorob'eva, 1962). Therefore, the assumption by Jarvik that the rostrale laterale in Osteolepiformes always has this process in distinction from Porolepiformes is without confirmation. At the same time, in Panderichthys there is a similarity of the rostro-caudal crest characteristic of Porolepis (fig. 2, 2, ri. w. al) and a small lateral depression re. 1, corresponding in position to recessus lateralis.

The interpretation of the processes of the nasal cavity and the homologizing of them with processes in amphibians has been the object of doubt. Kulczycki opposes the homology of the rostrocaudal process of Porolepis (crista subnarina according to Kulczycki) with the processus rostrocaudalis of Urodela and considers that its appearance is connected with the passage of the suborbital sensory and postnasal canals. He does not agree with the presence in Porolepis of Seydel's process (fig. 2, 2, pr. S) and points to the fact that if the crista subnarina is homologous to the processus rostrocaudalis, then the small choanal process, appearing as its continuation, occupies a different position from that

--p. 1360--

of Seydel's process in Urodela. According to Kulczycki, there is also no recessus lateralis for Jacobson's organ in Porolepis.

There is no doubt about the homology of the upper internal postnasal opening (fig. 3, 1. f.e. enp.) with the external posterior naris (fig. 2, 2, fe. exp.) and also about Jarvik's assumption that the lacrimonasal canal (ductus nasolacrimalis) passed through this opening parallel with a branch of the upper maxillary nerve (ramus maxillaris). This homology makes the absence of a similar opening in some Rhipidistia which do not have an external posterior naris (Platycephalichthys, Vorob'eva, 1962) completely inexplicable. As investigations in the area of the embryology of tailed amphibians have shown (Medvedeva, 1960), the lacrimonasal canal is developed in them primarily at the expense of a section of the suborbital sensory canal of fishes which section is connected with the bones of the infraorbitale anterior and rostrale laterale and partly of the olfactory sac. According to I. I. Shmal'gauzen (1964), the external part of the posterior naris plays a part in the formation of the canal. Thomson (1964) considers that most probably blood vessels and nerves passed across the interior postnasal opening into the nasal cavity. The existence of an external posterior naris in Rhipidistia is somewhat doubtful. This doubt is produced by a new discovery of the skull of Panderichthys. Although, the posterior external naris was noted in this genus (Vorob'eva, 1962), it is none the less possible that because of inadequate preservation of the described skull after its excavation (fig. 3, 2, fe. exp. ?) a piece of the suborbital sensory canal was admitted in the rear corner of the ethmoid. Judging by the position of the posterior naris in Porolepis (Jarvik, 1942, pl. 4, fig. 2) which is very similar to that in Panderichthys, doubt arises as to its existence even in the first genus.

The size of the anterior naris and the choanal notches apparently does not have great taxonomic significance. Small choanal notches as in Porolepis are known for several Osteolepiformes (Panderichthys, Platycephalichthys). It is possible that small internal nares are a mark of primitiveness (Kulczycki, 1960). The internal nares of Rhipidistia and terrestrial vertebrates represent [in agreement with Jarvik] an independent formation having nothing in common with the external posterior naris, in contrast to the "false" nares of the Dipnoi which were formed by it. A contrasting opinion was expressed by A. N. Sewertzoff (Sewertzoff, 1926) who considered the internal nares of tetrapods a derivative of one of the external nares of bony fishes, which moved into the oral cavity. Later, I. I. Shmal'gauzen (1958) came to the conclusion that the internal nares of terrestrial vertebrates were homologous with the medial part of the posterior naris of fishes. He observed preserved traces of the movement of the naris in the oral cavity in the embryos of tailless amphibians. The detailed investigations of I. I. Medvedeva (1960a, 1961, 1965) on the development of internasal nares in the embryos of Anura and Urodela which affirm their complete homology with the internal nares of the other vertebrates showed that at the very early stages of development of tailed amphibians the beginnings of the naris and of its canal is situated next to the beginnings of the choanal canal or is even common with it. This can serve to some degree as a proof of the derivation of the choanal canal from the canal of the posterior naris of bony fishes.

As was noted above, the interpretation of some canals (blood vessels and neural branches) in the nasal cavity of Rhipidistia is debated. Jarvik considers that the nasobasal canal giving off the branch n. profundus across the anterior nasal wall of fossa apicalis (fig. 4, 1, c. hb) is characteristic of the Osteolepiformes group only. However, this canal was also found by Kulcycki in Porolepis. On the other hand, the orbital-rostral passage is not surrounded by it which, according to Jarvik, is characteristic of Porolepis. The canal conducting the lateral branch n. profundus (fig. 4, 4, r. prl) across the lateral part of the postnasal wall of Porolepis would, according to Thomson, more likely conduct blood vessels into the nasal cavity.

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Jarvik also considers that in Osteolepiformes there is a single neural canal leading from the nasal cavity upward to the dorsal surface of the ethmoid, but in Porolepis a multitude of such canals penetrate the dorsal part of the medial wall, the neighboring parts of the prenasal wall and the medial part of the testum nasi. In addition, the nervus profundus which is weakly developed in Eusthenopteron is well developed in Porolepis (fig. 4: 1, 3, n. pr). In Porolepis the medial nasal branch (fig. 4: 3, r. prm) in the nasal cavity divides into many

--fig. 4--

dorsal branches. At the same time, Thomson finds that n. profundus is developed approximately identically in Porolepis, Eusthenopteron and Ectosteorhachis (fig. 4: 2). However, the canal transversing the dorsal wall of the nasal capsule of Porolepis relates more closely to the nervus opthalmicus superfacialis VII than to the nervus profundus V.

In regard to quantity of apertures on the posterior nasal wall for n. profundus, there can be several variants. In particular, in Osteolepiformes there is one large (Platycephalichthys) or relatively narrow (Eusthenopteron, Eusthenodon) aperture (fig. 3: 1, c. pr), but it can also be lacking (Panderichthys). In the latter case, n. profundus possibly entered the nasal cavity together with n. olfactorius, as Kulczycki noted for one of the forms of Porolepis.

Kulczycki considers that Porolepis and Eusthenopteron have an identical arrangement of the following nerves: n. opthalmicus profundus, n. maxillaris, r. palatinus VII, r. buccalis VII (fig. 4) and accompanying blood vessels. Thomson partly supports him in this. Thus, according to Jarvik, the lateral parts of the snout in Osteolepiformes are supplied chiefly

--p. 1362--

by r. maxillaris V, but in Porolepis by n. profundus, which causes doubt on the part of Thomson. The latter considers that Jarvik was influenced here only by modern Urodela in which r. maxillaris V terminates in an orbit. Meanwhile, in some aquatic, tailed amphibians, where a system of a lateral line and corresponding buccalis lateralis VII was retained, the latter passes into an orbital-rostral passage (truncus infraorbitales) together with r. maxillaris V and this mixed trunk stretches ahead farther than in terrestrial amphibians. And as far as traces can be found of buccalis lateris VII in Porolepis, the possibility of the presence in them even of r. maxillaris V (fig. 4: 4, max plus buc) cannot be excluded. Further, in agreement with Jarvik, in Eusthenopteron r. buccalis lateris passes forward to the top of the snout laterally to the internal nares giving off small branches to the anterior parts of the infra-orbital sensory canal. In Porolepis, on the other hand, it is divided into several branches in the orbit and only one of them goes forward across the orbital-rostral passage medially from the internal nares supplying the forward part of the infra-orbital canal (fig. 4: 3, r. buc). According to Thomson, in Ectosteorhachis the nerves passed across the dermal bones rather than between these bones and the nasal capsule as in Eusthenopteron. Information about the arrangement of r. buccalis lateralis in Rhipidistia is insufficient in his opinion.

R. palatinus VII in Eusthenopteron passes across the antero-lateral part of the vomer and passing it divides into three branches. In Porolepis the nerve passes across the medial part of the vomer and does not divide at this juncture. Thomson observed an analogous picture in Ectosteorhachis.

Jarvik affirms that traces of fusion of a palato-quadrate complex and ethmoid are present in Eusthenopteron and absent in Porolepis. A contradictory opinion is held by Kulczycki who points to the traces of a synchondralic articulation between processus apicalis palato-quadratum and the olfactory tract of the sphenethmoid in Porolepis. It is possible that the merging of the palato-quadrate complex with the ethmoid was characteristic of all Rhipidistia. In any case, the groove for the palato-quadratum, which is not covered by the periosteal bone, is present also on the ethmoid of Ectosteorhachis, Panderichthys and Platecephalichthys. In connection with this, the observations on the development of the endocranium of tailed amphibians (Hynobiidae) put forth by N. S. Lebedkina (1963) are interesting. They showed that in the larvae there is a close connection of the palatal arch with the ethmoid.

It is considered that one of the differences between Osteolepiformes and the Porolepiformes is the formation of the parasphenoid and the vomers. In Eustenopteron (fig. 5) the parasphenoid is narrow and stretches under the ethmoidal tract to the prenasal area of the endocranium; the vomers with a vertical toothed plate and a long, posterior branch are met ahead along the suture on which are located a pit and the openings of the inter-vomerine canal (inter-vomerine pit, Iv. p) which connects the tracta fossa apicalis with the posterior part of the oral cavity. In Porolepis the parasphenoid is wide and barely reaches to the ethmoidal tract; the vomers without posterior branches are widely separated and lack a vertical plate of the inter-vomerine canal. In agreement with the description of Ectosteorhachis (Romer, 1937), the parasphenoid of Rhipidistia can be of a dual formation, consisting of a base and a shagreen plate resting on it. The parasphenoid in Eusthenopteron and Eusthenodon also has a similar formation (Jarvik, 1937). In connection with this, observing the formation of the parasphenoid should obviously lead to examining the level of development of both its parts. The width of the interorbital septum, which has possibly vital significance in the taxonomy of Rhipidistia in particular as a distinguishing characteristic of suborders of Osteolepidoidei and Holoptychioidei (Vorob'eva, 1962). The length of it is apparently connected with the length of the

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anterior palatal recess (fossa apicalis, cavum internasale). The length of the shagreen plate indicates various stages of evolutionary development, according to the opinion of Thomson. In particular, the gradual transition from the stage of Eusthenopteron to that of Porolepis can be seen among osteolepids in the series Osteolepis, Megalichthys, Ectosteorhachis, in which the toothed medial plate is progressively shortened. As far as

--fig. 5--

the degree of dissociation of the vomers is concerned, there is apparently a correlation with the length of the parasphenoid. The degree of development of the posterior branch, like the presence of a vertical toothed plate, is apparently a characteristic of genera or families. The majority of osteolepids (Ectosteorhachis, Osteolepis, Glyptomus, Megalichthys, Thursius) have a short posterior branch which, on the other hand, is well developed in Platycephalichthys, Panderichthys, Eusthenopteron, Eusthenodon. The vertical plate is lacking in Megalichthys. According to the theory of Kulczycki, the latter characteristic in conjunction with the short posterior branch of the vomers testifies to the primitiveness of the form.

Since in Ectosteorhachis as well as in Porolepis the vomers are not encountered along the medial suture, it is difficult to judge if they had an intervomerine canal which was able to pass even in soft tissues. (Thomson, 1964)

As is evident from the analysis presented of data on the formation of the snout of Rhipidistia, there still remain many unclear and debatable points about this problem. Apparently, however, the series of peculiarities in the formation of the ethmoid taken by Jarvik as a basis for the division of two phylogenetic trunks of Rhipidistia is not justified. They have obviously much less significance in taxonomy being characteristic of genera or at best, families.

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Comparative anatomy of the snout of Rhipidistia thus still does not present proof for the resolution of the question about the origin of amphibians from one or from several groups of lungfishes. Also, available data indicate that the Rhipidistia are much more diverse than was assumed earlier, and it is completely possible that further study of this group will lead to significant alterations in its taxonomy. However, all known Rhipidistia reveal an obvious similarity in the chief features of the formation of the ethmoid (in nervous and circulatory systems, in the internasal wall, in the nasal cavities) which testifies to the utility of considering them one.

There remain (besides questionable facts) only a few peculiarities of the formation of the snout of Rhipidistia which support the hypotheses of Jarvik, in particular, the differences in the position of the canals of some blood vessels and the quantity of neural branches and their passages (the different position of ramus opthalmicus superficialis VII, vena cerebralis anterior). To these small differences one should add also the later data of Jarvik about the structure of the branchial apparatus of Eusthenopteron and Glyptolepis and the formation of the tongue of amphibians (Jarvik, 1964). Unfortunately, however, the branchial apparatus is unknown for other Rhipidistia, and therefore making any such broad generalizations is clearly premature. Besides, Jarvik (1964) affirms that the confirmation of his hypothesis lies in the differences in the microstructure of the scales of Osteolepiformes and Porolepiformes presented by Orvig (T. Orvig, 1957). Such an assertion is without foundation since in most primitive representatives of this group (Porolepis and Osteolepis) the scales have an almost identical formation (Orvig, 1957, table to page 406). The difference between them basically comes down to the methods of formation (cyclomorial or synchronomorial) of the later layers of dentin. These methods obviously bear witness to different evolutionary stages of development. As Orvig himself affirms, in the ancestral forms of Porolepiformes and Osteolepiformes the scales were apparently covered by cyclomorial layers of dentin (Orvig, 1957, pg. 420), i.e., they had a single means of formation. In addition, Porolepis and Osteolepis had a very similar construction of the teeth differing in the simple plication of the walls and in the presence of a broad pulp cavity. This also brings these forms together.

In our view, the microstructure of the integumentary bones, scales and teeth of Rhipidistia provides the possibility not only more clearly to present the stages of their evolutionary development and the phylogenetic links between separate groups but also in some degree to clarify the closeness of one or another representatives to the ancestral forms of tetrapods. Data on the microstructure of integumentary bones and teeth of ancient tetrapods, e.g., Stegecephalia, testify in particular to the greatest closeness to them of one of the representatives of Osteolepiformes, i.e., Panderichthys (Vorob'eva, 1960, 1962).

The methods of Jarvik which served as the foundation for the hypothesis of the polyphyletic origin of terrestrial vertebrates have been justly criticized by several paleontologists (Thomson, 1962; Gross, 1964). The basic defects are the limitation of the scope of investigation (e.g., the snout of Rhipidistia) and the small number of forms analyzed. At the outset, the fact that primarily two representatives of lungfishes (Porolepis and Eusthenopteron) are considered as initial forms for amphibians which are also distant in taxonomic position and geological age, predetermines the presentation of tetrapods as diphyletic. The comparison of details of the formation of the ethmoid of these Rhipidistia is made basically with presently existing amphibians including very specialized ones (for example, the frog) which creates great discrepancies in the interpretation of these details. At the same time, Jarvik's statements on the polyphyletic origin of tetrapods, which in a series of cases are based on questionable facts are too categorical.

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While there are no indisputable proofs in paleontology of the monophyletic origin of amphibians, a group of facts does support it: 1. As indirect proofs one should include the great similarity in basic features of the formation of the ethmoid of Rhipidistia in spite of the seeming differences in individual representatives. 2. Among Rhipidistia only Osteolepiformes (Eusthopteron, Sauripterus?)

--fig. 6--

have the formation of fins similar to the formation of a pentadactyl limb (fig. 6). Fins with a biserial archipterygium (judging from the long-lobed fins of Holoptychus and Glyptolepis) could hardly have been transformed into such a highly differentiated organ. In addition, the limbs of mature Urodela and Eusthenopteron have an almost identical formation; this similarity extends even to separate bones of the hand and foot. 3. Some support in favor of monophyleticism can also be given by the absence among known Rhipidistia of groups which could be recognized as standing closely to the ancestors of the tetrapods. The closest to the latter, apparently only Osteolepiformes of the type Eusthenopteron and especially Panderichthys (Vorob'eva, 1962) unfortunately have been little studied. 4. At the same time, known finds of fossil amphibians testify in favor rather of a dichotomous than a parallel development of separate branches. In particular, Urodela, which according to Jarvik appear to the side of the main line of evolution of terrestrial vertebrates and have an origin independent from fish-like ancestors of the Silurian period, are unknown until the lower Cretaceous or Jurassic period (fig. 7). In addition, they are apparently very close to Lepospondyli which already flourished in the Carboniferous period. It is more logical to suppose that Urodela branched off precisely from them. The Lepospondyli in turn apparently derived from the same branch as labyrinthodents. On the basis of ancient finds, the origin of Anura is well known, and they are encountered beginning from the Triassic period. From the comparison of Anura with labyrinthodents one can come to a conclusion about their origin from the latter. Apoda are not known in a fossil condition. The appearance of the first tetrapods has been indicated as seemingly by the end of the middle (Vorob'eva, 1962) or upper (Gross, 1964) Devonian Period since in the Silurian Period bony fish are still unknown and in the early Devonian Period only one genus of lungfishes has been found, i.e., Porolepis, but at the end of the upper Devonian Period the first Stegocephalia are encountered, i.e., the ichthyostegids.

The ideal condition for the solution of the problem of the origin of tetrapods would be discoveries of intermediate forms between different groups of vertebrates. The ecological divergence which has existed since the very beginning of the emergence of tetrapods and which has been accompanied by significant morphological differences greatly hampers the clarification of phylogenetic

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links. For an understanding of the peculiarities and paths of the formation of the structures of tetrapods much could be gained through a study of lungfishes and especially of ancient Rhipidistia. However, since using paleontological discoveries as a base rarely permits a complete restoration of the history of the origin of a group, one must consider the data

--fig. 7--

of related disciplines. In particular, the study of contemporary amphibians and especially embryological investigations of the most primitive Urodela can be of considerable use for the solution of this problem.

A correct solution of the problem of the origin of terrestrial vertebrates is of great importance for their taxonomy. The problem concerns not only by what kind of roots lungfishes are connected with tetrapods, but also whether the existing system reflects phylogenetic links between groups or whether it is based on the principles of similarity. The attempt to introduce the concept of polyphyly into the existing system inevitably leads to the destruction of the boundaries between taxonomic categories. In particular, if discussion concerns the polyphyletic origin of amphibians, the continued existence of their independent phyletic branches destroys the boundary between classes of fishes and amphibians. The diagnostics of the old classes loses its value, and the dialectical representation of them as a new quality representing a complicated complex

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of characteristics is rejected. Instead of such classes, degrees and stages of development of separate, parallel characteristics are offered. A passion for separate characteristics leads investigators to polyphyly. At the same time, if separate traits of structure can indeed develop in parallel fashion in various groups, then the parallel development of very complex combinations of characteristics like those of families, orders and classes is very doubtful. According to the opinion of Gross (1964), which the author shares, if polyphyly of species and genera can be considered fully plausible, polyphyly of larger categories raises doubts, since it has no factual verification. Thus, as long as there are no discoveries proving transfer from class to class and, in particular, from fishes to amphibians in several independent branches, it is apparent that the polyphyletic origin of tetrapods must be rejected.

LEGENDS FOR FIGURES

Figure 1. Diagram of the polyphyletic origin of tetrapods according to Jarvik (E. Jarvik, 1964, fig. 28)

Figure 2. Restoration of the anterior part of the ethmoid, rear view.

1 - Eusthenopteron, 2 - Porolepis; magnification: 2X (Jarvik, 1942, fig. 52 A, 46 A); Vo - vomer; cav. in - internasal cavity (cavum internasale), c. ext - canal for ramus externus narium n. profundus, c. nb - nasobasal canal, fe. ch - choanal notch, fe. ona, fe. exp - notches for anterior and posterior nares; pr. im - processus intermedius, pr. S - palatal process (processus Seydol's), re. l - lateral depression of nasal cavity (recessus lateralis), ri. in - internal crest, ri. w. al. - rostro-caudal crest (crista rostrocaudalis), sn - internasal septum (septum nasi).

Figure 3. Rear view of ethmoid.

1 - Eusthenodon, magnification: X 3/2 (Jarvik, 1937, fig. 13), 2 - Panderichthys, magnification: X 1 (Vorob'eva, 1962, drawing - 3; Psph - parasphenoid, Vo - vomer, art. aup - medial surface for articulation of palatoquadrate complex, c. olf - olfactory canal, c. pr - aperture of canal for nervus profundus, etch. cr. - ethmoid skull cavity, fe. ch. - notch internal nares, fe. enp and fe. n.p.c. - innter postnasal aperture, fe. exp.? - notch of external posterior naris.

Figure 4. Top view of ethmoid.

1 - Eusthenopteron (Jarvik, 1964, fig. 20), 2 - Ectosteorhachis (Thomson, 1964, fig. 1 and fig. 6 combined, 3 - Porolepis (Jarvik, 1964, fig. 20c), 4 - Porolepis (Kulczycki, 1960, fig. 5); a. ci - artery carotis interna, an - anterior external naris, a. pn - artery palato-nasalis, b. olf - bulbus olfactorius, cav. in - internasal cavity (cavum internasale), c. nb - nasobasal canal, c. pr. - canal for nervus profundus, c. prm. - canal for ramus terminalis n. profundus, dnl - lacrimonasal duct (ductus naso-lacrimalis), hem - hemisphere of anterior brain: max plus buc - n. maxillaris plus r. buccalis lateralis VII (truncus infraorbitalis), ntr - posterior nasal tube or proximal part of lacrimonasal duct, n. pr - nervus profundus, pi - pineal organ, r. bac - ramus buccalis, r. mn, r. ln - ramus medialis and ramus lateralis narium n. profundus, r. mx - ramus maxillaris V, r. o. lat - ramus opthalmicus superfacialis VII, r. pal - ramus palatinus VII: r. prl, r. prm - ramus terminalis lateralis and medialis n. profundus; sac. n - olfactory sac; I - n. olfactorious; II - n. opticus.

Figure 5. Ethmoid of Eusthenopon from below; magnification: X 3/2 (Jarvik, 1937, fig. 16)

Psph - parasphenoid, Vo - vomer, art. aup - surface for articulation of palatoquadrate bone, fe. ch - notch of internal nares, fossa ap - apical pit, f. ap - apical aperture, iv. p - pit of intervomerine canal.

Figure 6. Diagram of the transformation of the fin of Rhipidistia into a pentadactyl limb.

1 - Eusthenopteron, 2 - transitional stage, 3 - primitive tetrapod stage (Jarvik, 1964, fig. 27); see text for discussion.

Figure 7. Diagram of the origin of tetrapods according to Gross (W. Gross, 1964, Abb. 3)

INDEX TO THE SCIENTIFIC NAMES
IN
"A POPULAR TREATISE ON THE COMMON INDIAN SNAKES"

by

FRANK WALL

1905-1919

Indexed by Simon M. Campden-Main

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From 1905 to 1919, F. Wall published a series of papers on Indian snakes, in 29 different issues of the Journal of the Bombay Natural History Society. It is uncertain how many complete sets of these papers have been brought together and bound, but the following index can be used either with bound sets or to find references throughout the original issues of the Journal. Each reference in the index gives the volume first, followed by the pages on which the scientific name is used. The plates were numbered consecutively throughout the series, so they are referred to only by number. The list below is a summary of the entire set of papers, with the dates given taken directly from the title page of the Journal. The dates should not be taken as definitive for nomenclatorial purposes.

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	2	447-475	17	31/3/12
	3	1009-1021	18	30/7/12
22	1	22-28	19	21/4/13
	2	243-259	21	30/9/13
	3	550-568		20/12/13
	4	749-760	20	31/3/14
23	1	34-43	22	30/6/14
	2	206-215	23	20/11/14
25	3	375-382	24	15/1/18
	4	628-635	25	10/6/18
26	1	89-97	26	20/12/18
	2	430-437	27	20/5/19
	3	803-810	28	20/10/19

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CRANIAL KINESIS IN LIZARDS; CONTRIBUTION TO THE PROBLEM OF THE ADAPTIVE SIGNIFICANCE OF SKULL KINESIS

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The term kinesis, when used as a reference to the skulls of tetrapods, is defined either as the movement of the upper jaw accompanied by specific elements of (or the entire) dermatocranium, or as movement of the olfactory region of the neurocranium with respect to the rear part of the axial skull (i.e., of the brain case formed of cartilage-replacement bones). This phenomenon was first described by Nitzsch in 1822, according to Bradley (1903), who discovered that the lizard skull was capable of movement in the fronto-parietal suture and in the articulation of the parietal bone with the occipital. Bradley studied the chewing musculature and accompanying movements in the skull of lizards. He formulated the first hypothesis of the functional significance of the movement of the upper jaw in relation to the axial skull (see below) and made the first attempt to correlate these movements with the functions of specific muscles. The term "cranial kinesis" was introduced by Versluys (1910) for a construction of the skull in which such movements would be possible, as well as the movements of the lower jaw. Versluys (1910, 1912, 1922, 1927) made a more thorough analysis of tetrapod cranial kinesis. He pointed out the prevalence of kinesis among most of the tetrapod groups, recent and extinct; classified various forms of kinesis, and proposed a theory of cranial kinesis, according to which the tetrapod skull was primitively kinetic; kinesis was inherited by the ancient tetrapods from fish-like ancestors and secondarily lost in several lines of tetrapod evolution.[1] From Versluys comes one of the most widely accepted hypotheses to date on the functional significance of cranial kinesis. Later contributions to the study of kinesis were made by Lakjer (1927), Marinelli (1928, 1936), de Jong and Brongersma (1927), Hofer (1960) and various other authors. Kinesis in crossopterygian fishes was shown by Romer (1937 per Frazzetta 1962) and in some stegocephalians (Pfannenstiel, 1932; according to Frazzetta, 1962). An exceptional amount of work on kinesis was devoted to the more specialized and unusual forms of birds and snakes. Comparatively little attention was given to kinesis in the more primitive forms of cranial kinesis (in lizards). A valuable contribution to the study of cranial kinesis in lizards was the work of Frazzetta (1962). Frazzetta by using motion pictures, demonstrated the connection between the movement of the upper jaw and the seizing and consumption of prey, and made the first biomechanical analysis of the work of the jaw muscles,

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responsible for movement of the upper jaw. Frazzetta presented a new hypothesis on the functional significance of cranial kinesis (see below). However, Frazzetta, in his analysis of cranial kinesis, focused his attention on one form (*Varanus*), giving less attention to the features of cranial kinesis of other forms studied by him. The type of cranial kinesis exhibited by *Varanus*, as our work has shown, cannot be considered as either the most primitive or the most widespread among lizards. For a clear presentation of the evolution of skull kinesis and its functional significance, a comparison of kinesis in various skulls beginning with the more primitive forms, is necessary.

MATERIALS AND METHODS

We have studied skull structure in *Sphenodon punctatus* and the following lizards: *Cyclura macleayi*, *Iguana sp.* (Iguanidae), *Agama caucasica**, *A. lehmanni*, *A. sanguinolenta**, *Phrynocephalus reticulatus* (Agamidae), *Lacerta media**, *L. agilis**, *Eremias arguta*, *E. grammica* (Lacertidae), *Eumeces schneideri**, *Mabuya aurata*, *Trachysaurus rugosus* (Scincidae), *Varanus griseus**, *V. niloticus* (Varanidae), *Teratoscincus scincus**, *Gecko gecko**, *Platydactylus guttatus*, *Gymnodactylus caspius** (Gekkonidae), *Ophisaurus apodus** (Anguidae), *Tupinambis sp.* (Teiidae), *Zonurus cordylus** (Zonuridae) from the material of the Zoological Institute of the Akademiia Nauk USSR, the Zoological Museum of Moscow University, the Chair of Vertebrate Zoology of Moscow University and from our own collections. We studied the details of cranial kinesis in the alcoholic (wet) connective tissue preparations of skulls of 11 species of lizards[2] (with skin removed) and also in the skulls of freshly killed species of Varanidae. In addition, the jaw musculature of nine other species of lizards was studied. Motion pictures of the eating of prey by *Agama caucasica* and *Lacerta agilis* were taken by an aide [assistant, or probationer] at the Paleontological Institute of the ANSSSR, N.N. Kalandadze, to whom the author is very indebted for his help in the work. We also wish to express our sincere thanks to B. S. Mateev and F. Ya. Dzerzhinskyj (chair of vertebrate zoology, Moscow University) for discussion of our results and for critical remarks, and for giving the opportunity to work with museum materials, the head of the herpetology division of the Zoological Institute ANSSSR, I. S. Darevskii, and head of the evolutionary morphology division, Zoological Museum, Moscow University, D. N. Hofmann.

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[1] An alternate hypothesis of the antiquity of the akinetic skull and independence of development of kinesis in various lines of vertebrate evolution was developed by Edgeworth (1935). Edgeworth's views do not survive serious criticism and have not received general acceptance.

[2] The names of these [11] lizards are designated by an asterisk in the list given above.

CRANIAL MOVEMENT OF LIZARDS

Following Bradley's work (1903), on lizard skulls, three fundamental segments [units] were distinguished: the occipital, maxillary, and mandibular. The occipital segment was reinforced in vertebrates and is considered to be immovable. It is formed of the occipitals and otic bones, and also the basi- and parasphenoids. The two other segments are movable relative to the occipital. Of interest to us here primarily is the movability of the maxillary segment, which is signified by the term "cranial kinesis". The relationships between the maxillary and occipital sections have already been described by Bradley, Versluys, Hofer, Frazzetta, Oelrich (1956) and Webb (1951) and we have confined ourselves only to their enumeration. These relationships include: the union of the quadrate, squamosal and the supra-temporal bones with the lateral ends of the paroccipital processes ("metakinetic axis" of Frazzetta), the parietal with the supra-occipital, the pterygoids with the basipterygoidal processes, sometimes of the epipterygoids with the prootic bones. Besides this, both segments are joined by the cartilaginous and membranous orbito-temporal elements of the brain case. All these connections allow a limited degree of movement of the maxillary segment relative to the occipital: first, as a whole, it turns around the metakinetic axis with the anterior end upward and forward (protraction) or downward and backward (retraction). Besides this, the maxillary segment during pro- and retraction changes configuration since it consists of a series of related divisions -- paired: (1) quadrate bones, (2) epipterygoids,

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(3) palatal divisions; -- and unpaired: (4) parietal division, and (5) the snout [muzzle], which always breaks down further into (5a) central and paired (5b) lateral parts. The composition of all these divisions with the exception of the quadrate and epipterygoid, differs as also differ the peculiarities of kinesis in the various forms of lizards (see table).

-- fig. 1 --

In general, in the skull of a typical lizard, the following movements take place (figs. 1-5). During retraction, the lower ends of the quadrate bones turn back and to the side [posteriolaterally]. The palatal segments, movably joined with the quadrates, are drawn to the back and side, sliding along the basipterygoidal processes and spreading the latter to the sides (drawing the palatine sections from the center line) [abduction]. The epipterygoid, attached by the articular hollows [surfaces] to the dorsal surface of the pterygoid, rotates its lower end back and to the side, as does also the quadrate, but at a lesser angle than the latter. The snout, as a whole, rotates its anterior end downward around the transverse axis, passing along the fronto-parietal suture ["mesokinetic axis" of Frazzetta]. The angle between the central part of the snout and the palatine section is somewhat increased; the angle between the frontals and the

-- fig. 2 --

parietals below is decreased. At this point, the lateral parts of the snout, together with the palatine sections, are diverted and their lateral margins rotate upward around the longitudinal axis passing approximately along the lines of juncture of the lateral and median parts of the snout. The parietal section, as Frazzetta correctly noted, and contrary to the opinion of Versluys, rotates

-- p. 1401 --

around the metakinetic axis with its anterior end upwards.[3] Finally, the lateral parts of the parietal section, participating in the movement of the entire section, also arch upwards, and, in forms with covered supratemporal fenestrae, rotate around the linear axis, passing along their articulation with the central part of the section, lateral margins upward.

In general, during retraction, the anterior end of the snout turns downward, the dorsal contour of the skull becomes more convex, the palatine arches, the lateral sections of the snout and the lower ends of the quadrate bones and the epipterygoids are shifted to the rear, drawn aside and rotated around the linear axis with the lateral edges upward. During protraction, an

-- fig. 3 -- -- fig. 4 --

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[3] In alcoholic connective-tissue preparations of lizard skulls may be found both variants of parietal division movements -- its rotation in the same direction as the snout, and the reverse, depending on the direction of force applied. Naturally, as examination shows, force applied to the lizard skull by the jaw muscles should be regarded as the latter variant of motion.

opposite movement of all the above-mentioned elements of the maxillary segment of the cranium takes place.

However, among the various forms of lizards, there are essential differences in the peculiarities of cranial kinesis and in the composition of the various sections of the maxillary segment (cf. table). First, the kinds of lizards studied fall primarily into two groups: (1) Cyclura, Agama, Lacerta, and Ophisaurus, in which the palatal unit is a solid shaft [core] participating in cranial movements as an indivisible integer [whole unit]--unquestionably a more primitive stage; (2) Eumeces, Varanus, Teratoscincus, Gecko, Gymnodactylus, and Zonurus, in which the palatine unit is articulated along the palato-pterygoidal juncture to the anterior and posterior parts, movable relative to one another. In lizards of the first group, the palato-pterygoidal articulation is a suture running as a whole very obliquely from postero-anteriorly medially and solidly uniting the two bones (Fig. 2), while lizards of the second group, a very loose syndesmosis runs more directly laterally [transversely], permitting rotation around the transverse axis (Fig. 4). In geckos, the palatine bone and the pterygoid hardly adjoin directly, being separated by loose connective tissue (mentioned by Lakjer, 1927). In lizards of the second group, during retraction, the palatine section is more or less bent upward: the region of the palatal-pterygoidal articulation is raised, and the descending angle between these bones is decreased.

-- Table, p. 1402--

--p. 1403--

The interior movement of the palatine section in lizards of the second group is correlated with the greater role of mesokinesis in the amphikinetic skull (Versluys terminology) than in lizards of the first group and is in general also correlated with the greater development of kinesis.

Within both groups of lizards there are some more pronounced differences among the various forms. Thus, in Cyclura (Fig. 1) and Agama, the

--fig. 5--

postorbital bones are closely joined not with the lateral element of the parietal division as in all the other forms, but with the lateral part of the snout, and take part in its movements. In Lacerta, the link between the quadrate bone and pterygoid (mentioned by Frazzetta) is very lax and in the amphikinetic skull, movements around the metakinetic axis predominate--mesokinetism is relatively weak. The most pronounced distinctness of movements of the central part of the parietal division and the upper temporal arches is in Lacerta and Ophisaurus. In Varanus, (Fig. 5) the zygomatic bone is closely connected with the palatine division and takes part in its movements (noted by Frazzetta), and has elements of rhynchokinetism (Hofer, 1960); i.e., the movability of the premaxillary bone in relation to the nasal. In the amphikinetic skull of Varanus, movement is predominantly around the mesokinetic axis--the parietal division shifts very little (but shifts nevertheless, contrary to the opinion of Hofer) with respect to the occipital segment. The gecko (Figs. 3-4) skull is the most kinetic among the skulls of the forms studied: the vomers move together along the central part of the snout--their articulation with the palatine bones is exceedingly mobile.

If we illustrate in the lizard skull lateral view, in a very simplified pattern, the leverage mechanism, in which straight lines represent individual units of the latter (movable only in relation to other units of the skull) and circles to represent the transverse axes around which the possible rotations of these units take place (not unlike the sketches Frazzetta presented for Varanus), then we obtain the following fundamental variants of the mechanisms (Fig. 6). In Varanus, in contrast to the simplified diagram of Frazzetta, we notice lines of flexion [folding] between the nasal and premaxillary bones, between the vomer and the premaxillary bones, and between the palatines and pterygoids. As is seen in the diagram, the cranial mechanism of Varanus is unique and significantly different from the primitive forms of cranial mechanisms to which lizards of the first group (among the forms studied) stand closest of all, especially Cyclura.

KINESIS IN LIVING LIZARDS

MOVING FORCES OF CRANIAL KINESIS

Hofer (1960) correctly pointed out that the anatomical data on the possibilities of motion in the skull, like data on kinesis, obtained on alcoholic connective-tissue preparations, cannot show the actual presence of correspondingly active motion in the cranium during the life of the animal, but show only the possibility of passive [enforced] motion.

--p. 1404--

In favor of the actuality of the motion observed in connective-tissue preparations of the skull is the fact that analogous movements on a much larger scale are more noticeable in the head of a freshly killed animal with fully preserved muscles, ligatures, etc., than in the connective tissues of preparations. Thus, the length of the skull of Varanus griseus from

--Fig. 6--

the end of the snout to the occipital condyle, varies accordingly: as much as 8.97% of median skull length (71.3 mm) during protraction and retraction in "fresh" heads, in three wet connective-tissue preparations of skulls of same size--on the average, only 2.45% (2.3 - 2.7).

For proof of active movement in the kinetic skull, examination of living lizards and analysis of the lines of force arising in the cranium during the contraction of cranial muscles is necessary. Direct examination of skull kinesis in lizards is difficult due to their great rapidity

--p. 1405--

of movement. Filming of eating prey by Agama caucasica and Lacerta agilis gave results that were hard to interpret; while grasping and swallowing prey these lizards repeatedly rotate the head around the longitudinal axis and to the side so that the kinetic movements of the skull are hard to pick out [distinguish] without the risk of taking the desired for the actual effect. The reason for this may be the small choice found in our selection of living forms. Both Lacerta and Agama belong to the first group of lizards, that is, they do not have movement within the palatine element and kinesis in them is generally less than in lizards of the second group. Thus in Lacerta, we see that the dominating movements of the maxillary segment are around the metakinetic axis, which is difficult to distinguish in a live lizard, and Agama has a very broad and low skull, thanks to which the dorsal contour is quite distorted during a slight lateral inclination. Frazzetta, with the aid of motion pictures, studied eating of prey by Gerrhonotus coeruleus. He noted that retraction takes place during closing of the mouth and compression of the lizard's jaws, while protraction takes place during the opening of the mouth. Frazzetta's observations were confirmed also by data of Boltt and Ewer (1964), on Varanus niloticus.

Frazzetta made a graphic analysis of the lines of force arising during the contraction of the jaw muscles in the cranium of Varanus. This analysis seems fundamentally accurate, but somewhat superficial, since Frazzetta did not study the jaw musculature of the lizard in detail, and did not try to assign a role to all the muscular parts. Protractors of the jaw mechanism in lizards appear in M. protractor pterygoidei and M. levator pterygoidei; retractors are primarily the fibers of the large M. adductor mandibulae externus (but never M. pterygoideus, despite Frazzetta's assertions). Various parts of the M. adductor mandibulae externus play completely different roles in the movements of the cranial mechanism: a large part of the fibers of the muscle have a retractive effect, some are neutral in relationship to the cranial mechanism and some manifest themselves as protractors. The summary effect of contraction of M. adductor mandibulae externus is retraction. Our studies of the jaw musculature of lizards showed that parts of M. adductor mandibulae externus, accepted in the works of Lakjer (1926), Lubosch (1933), I. Poglayen-Neuwall (1954), Oelrich (1956) and others, do not correspond with the functional and topographic units of the muscles. Furthermore, he (Frazzetta?) does not succeed well in identifying these parts in various forms in the order Sauria and, moreover, with parts with the same names in other reptiles. The scope of this article, unfortunately, does not allow us to add here a detailed analysis of the structure and function of lizard jaw muscles; we hope to do this in future publications.

In his analysis of the functions of the cranial mechanism of lizards, Frazzetta made one important error: according to his opinion, M. pterygoideus is a retractor, at least in the closing of the jaws on the prey. Actually, this muscle in lizards is neither a retractor or protractor of the cranial mechanism. Its force is applied to the pterygoids and to the lower jaw, forward and downward posteriorly of the jaw articulation. By such attachments, the contraction of M. pterygoideus does not change in conformity to the cranial mechanism. The movements associated with kinesis are in no way affected by the length of M. pterygoideus (Fig. 7; it corresponds to Fig. 11 in Frazzetta's paper). M. pterygoideus might be a retractor with fulfillment of two conditions: (1) flexibility of the palatine arch (at least in the juncture of the palatine bone and the pterygoids); (2) the origin of M. pterygoideus anterior of the hinge* line of the palatine arch from the palatine bone or the bones of the snout. (*cf. Geologicheskii Slonan-Sofiano, p. 223). The second condition is not fulfilled in lizards. The role of M. pterygoideus in retraction of the maxillary segment lies in the transfer of the retraction force component in the contraction of M. adductor mandibulae externus from the lower jaw to the palatine arch (for birds - see Marinelli, 1936).

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THE PROBLEM OF THE FUNCTIONAL SIGNIFICANCE OF CRANIAL KINESIS

The phenomenon of cranial kinesis has been known for about 150 years, but one problem has not been finally solved--what is the functional significance of this wide-spread complex adaptation in vertebrates? In general, all are agreed that kinetism is correlated with feeding and chiefly with the capture of food. But, in regard to the definite value of cranial kinesis, there are several different hypotheses.

Frazzetta convincingly showed the inadequacy of Versluys' hypothesis, according to which cranial kinesis served as a means of increasing the size of the gape of predatory animals, through a greater spread between the upper and lower jaws. In the monokinetic metakinetic cranium, protraction does not change the vertical range of the gape, and during amphikinesis or in the monokinetic-mesokinetic skull, it decreases the gape.

--Fig. 7--

Bradley's hypothesis is also untenable; it proposed that kinesis, during the opening of the mouth for grasping prey, permits adduction of the palatine elements for holding the prey between them. The evolution of lizards has gone particularly in the direction of increasing the width of the inter-pterygoideal cavity [depression] and the reduction of the palatal teeth, that is, in a direction diametrically opposed to that which would have been expected if such a kinetic function were present. In addition, the protractor muscles are comparatively weak and cannot produce the considerable compressive force between the left and right elements of the palatine arch necessary for holding of prey between them.

Romer's hypothesis on the amortizational role of kinesis (1937) on the impact of jaws cannot be discarded so decisively. Frazzetta was inclined to display skepticism as regards this hypothesis, since in the capacity of amortizators in the kinetic cranium, one must include the contraction of the retractor muscles, i.e., the above-noted jaw adductors. The flexibility of the cranial bones in the lower forms of lizards might, according to Frazzetta, with the same success play the amortizational role without the aid of the complex structure provided by kinesis. But, skull kinesis is strongly developed even in small lizards. We can add that from the point of view of this hypothesis incomprehensible is the role of the protractor muscles according to which, during the opening of the mouth (before the clamping of the jaws) the maxillary segment of the skull is elevated and thus bending the spring at the end.

According to Frazzetta's hypothesis, cranial kinesis serves for attaining the simultaneous closing of the jaws in seizing the prey. The gape is oriented so that the rising lower jaw and lowering upper jaw are simultaneously applied to the prey, by which means the risk of the prey's escape is lessened, as compared with the condition in the akinetic skull, where the prey is "caught" by the lower jaw only. It seems to us, however, that Frazzetta lost sight of the fact that the orientation of the jaws in relationship to seizing the object is not attained by kinetic movements, but by movements of the neck and by turning the head at the occipito-cervical joint, i.e., movements which take place also in the akinetic cranium. The simultaneity (or near simultaneity) of contact with the prey by the upper and lower jaws might be attained in the akinetic skull by the lowering of the head simultaneously with the raising of the lower jaw. It is unlikely in predators with an akinetic skull (and of such there are very many, discounting the mammals),

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that, after contact of the prey by the upper and lower jaws, sufficient time elapses for the escape of the prey. Even in rushing at concealed prey from ambush a predator discloses itself sooner than its jaws (both together or one of them a split second earlier) grasp the prey. It seems to us that kinesis is not of any essential benefit either in gaining a "moment of surprise" in seizing prey nor for the catching of prey in general.

--Fig. 8--

In movements of the kinetic skull, the inequality of the forces produced during protraction and retraction is significant. The protractors are two very comparatively weak muscles, while the retractors are powerful jaw adductor muscles. Therefore, the active movement bearing the functional load should likely be retraction. Strange as it seems, beginning with Bradley and Versluys, most scientists have sought the functional significance in protraction. Only Marinelli (1936) hinted at the functional significance of the closing of the beak in birds, since the opening of the beak (according to his opinion) was only a preparatory step in the process of movement in the upper jaw. Kinesis, according to Marinelli, is permissible in the case of necessity of shifting the place of principal pressure by the jaws closed on the prey closer to the end of the beak or corner of the mouth.

It seems to us that the advantage of the kinetic skull in comparison to the akinetic is not in any kind of capture, but in holding the still living, moving prey. The kinetic and akinetic jaws can be identically effective in catching prey. But it is easier for kinetic jaws to hold it. We can note that akinetic straight jaws during the holding of prey will push forward on the object caught (Fig. 8-1); and the resultant forces applied by them to the object held will also be directed forward. In the akinetic skull this load lies in holding prey by the teeth. This may be avoided by the convex form of jaw, but then the jaws would always be "bent down" to some prey of limited size and could not hold smaller prey. Kinesis provides the predominantly bent jaws with more effective jaw pressure on any item seized, and eliminates their [the jaws] deficiencies (Fig. 8, 2). Akinetic jaws may be analogized to claws; the kinetic, to fingers; since fingers are more suitable than claws for holding objects, so kinetic jaws are more suitable than the akinetic for the same purpose. The complexity of the movements of cranial kinesis is a result of the complexity of the cranial structure.

In grasping prey, the kinetic skull has other advantages over the akinetic (analogous to the advantages of fingers over claws): the kinetic upper jaw can transfer the prey along the lower jaw, crushing its resistance and killing it. During squirming of the prey, the kinetic jaws holding it can relax slightly, without releasing the victim, and finally exhausting it in the struggle (the "spinning? principle"). The amortizational hypothesis also does not contradict this role of kinesis. All these functions of kinesis can exist together, as kinesis has a complex significance, serving as the best means of holding prey.

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From this point of view, the relative weakness of the protractor muscles is understandable; their fundamental role is to return the maxillary unit of the skull from the operative retractive position to the normal position necessary for compact closing of the oral cleft. Also, protraction is accomplished somewhat farther along than the "normal" central position of the maxillary segment and always accompanies the opening of the mouth and the closing of the jaws. Therein is the truth of the hypothesis of Boltt and Ewer (1964) which says that protraction serves for freeing the upper teeth, stuck in the victim during the grasping of the prey and for momentum in swallowing it.

We ought to give here an explanation of the history of the very numerous cases in the history of vertebrates of loss of cranial kinesis, which occurred independently in various lines of evolution. The loss of kinesis is to be expected in (1) animals which do not need to hold squirming prey--for them, kinesis is useless (all specialized vegetarian forms, Diadectidae and Pareiasaurs among the Cotylosauria; many Chelonia and many Ornithischia; even Versluys remarked about this, giving a different explanation, however, for the loss of kinesis in vegetarian forms); (2) those forms which require maximum pressure on the food being chewed--kinesis in this case would even be harmful (as in some forms of vegetarians, but especially in mollusk eaters and other such forms, for example Placodontia, also noted by Versluys); (3) in some situations in which the preservation of the adaptive values of kinesis would be advantageous, but when some other kind of competing adaptation is more important for a given form, excluding the possibility of retaining kinesis. This situation occurs in forms for which the development of the secondary palate has proven to be especially important, apparently eliminating kinesis; it also occurs in the case of specialized feeding on very small or large prey. Kinesis is advantageous (in its unspecialized forms) in specific forms of predation, and especially for the generalized predators that feed mainly on prey small (but not very small) relative to its own size; prey of that size may be seized in the predator's jaws, such as insects, by lizards, and small vertebrates by the larger [predators]. When prey is considerably smaller than the predator, the advantage of kinesis for seizing it is not so essential, since for seizing it, long, relatively thin, pincher-like jaws are advantageous. Typical cases of this kind are: Crocodilia, Phytosauria, Ichthyosauria, Mesosauria, dolphins and others (Iordanskii, 1963). Kinesis in the form of metakinesis cannot be maintained in the species with long jaws due to the lesser firmness of the linkage of the long jaws to the brain case (Versluys, 1912). The loss of kinesis in Pterosauria is probably associated with this. It should be pointed out that in the presence of mesokinesis and prokinesis, kinesis in that case can be preserved; an example of this would be the long-beaked avian ichthyophages. The above pertains only to the more primitive forms of kinesis, meta- and amphikinesis.

If a predator specializes in feeding on coarser prey, subequal to itself or larger, the load on the cranium during the capture, killing and chewing [of food] is so great that kinesis is disadvantageous, through lessening the solidity of the skull. Kinesis may be advantageous in absence of food mastication by the jaws but it becomes disadvantageous for more or less prolonged chewing of the food requiring, as said above, rather firm pressure on the object processed. The loss of kinetism in the Therapsida line is associated with this fact. Snakes occupy a special position. In snakes, a more highly specialized form of kinesis developed with an extreme degree of movability of elements of the maxillary segment in relation to each other, which aids in swallowing large prey whole. As a consequence, snakes in many cases kill their prey by constriction or by poison, and the jaws do not exert mechanical pressure in holding, killing and chewing the prey.

The reduction of kinesis in chameleons is evidently correlated with feeding on small prey, captured by the aid of the tongue.

The question of kinesis or akinesis in Sphenodon remains open at this time. Recently Ostrom (1962) showed that in several types of Hatteria the protractor muscles are well developed and in a mature state. Ostrom suggested that in various populations of Sphenodon, kinesis can be lost or preserved in the adult state depending on the feeding peculiarities of a given population. Our study of the skulls of Hatteria leads to the conclusion that metakinesis in these forms and their ancestors must essentially be distinguished from the scheme of metakinesis proposed by Versluys (1910, 1912). Versluys proposed that in metakinesis, the maxillary segment of the skull moves as a single unit, in which the palatine arch, the bones of the snout and the skull roof are all rigidly joined to each other. However, the structure of the skull of Hatteria shows that retraction in this form should take place in the abducting elements of the palatine arch (pterygoids, palatines, epi- and ectopterygoids, and vomers). This means that in this metakinetic skull, movement of the lateral parts of the maxillary segment in relation to its central part should take place, similar to those noticed in the amphikinetic lizard skull. Whether during retraction the movements of the palatal arch and the lateral elements of the dermatocranium are independent, as in lizards, or whether those and others were displaced relative to the middle elements of the maxillary segment, we cannot determine from available museum materials. In any case, retraction of the metakinetic skull type is accompanied by diversion and rotation around the linear axis, lateral margins upward, of elements of the palatine arch, by the lateral part of the superposed skull armor. It seems to us permissible to presume that these movements might be characteristic of the metakinetic skull type in general. But examination of the problems of evolution of cranial kinesis exceeds the scope of the present paper.

CONCLUSIONS

(1) Among the various lizard species, there exist essential differences in the peculiarities of cranial kinesis and in the composition of various parts of the maxillary segment. Cranial kinesis of Varanus, used as the basis for analysis of lizard skull kinesis by Frazzetta (1962), is neither the most primitive nor the most prevalent form of cranial kinesis among lizards.

(2) The most primitive type, among the forms studied, is in the Cyclura, Agama, Lacerta, and Ophisaurus, in which the palatine section of the maxillary segment is a tough core [stout shaft], taking part in the movements of the skull as a single unit.

(3) In the presence of strengthening of cranial kinesis in lizards, in the palatine unit there is developed movability of its anterior part in relation to the posterior part.

(4) The M. pterygoideus, which functions as a retractor in the cranial mechanism in Frazzetta's opinion, actually in lizards cannot produce any kind of retractor movements by the latter.

(5) It seems probable that cranial kinesis provides the best means of holding prey [which is trying to escape] in the predators jaws. Protraction can serve to release the teeth of the upper jaw during seizure of prey or in swallowing.

(6) Kinesis of the skull in its unspecialized forms is especially advantageous for the universal [generalized] predator feeding on prey [which is] small relative to its own size, but not too small prey.

(7) Most of all, in the metakinetic type of skull, retraction and protraction of the maxillary segment are accompanied by abduction and adduction of the palatal arches, and the lateral elements of the superposed skull and by their rotation around the longitudinal axes, that is, definite movement taking place within the maxillary segment of the skull, despite the pattern of metakinetism proposed by Versluys (1910, 1912).

Movable elements in the skull of various forms of lizards

Segments and divisions of the skull			Cyclura, Agama	Lacerta, Ophisaurus	Eumeces	Varanus	Teratoscincus, Gecko, Gymnodactylus
Occipital Segment			Basioccipital, exoccipital, supraoccipital, basisphenoid, parasphenoid, prootic, and opisthotic bones				
Maxillary segment	Palatine Division		Pterygoid, palatine and transverse bones, vomers, and septomaxillaries		Posterior unit		
					Pterygoid and transverse bones	Pterygoid and transverse bones	Pterygoid and transverse bones
					Anterior unit		
					Vomers, palatines and septomaxillaries		Palatines
	Snout	Lateral unit	Supramaxillaries, prefrontal, postorbital, lachrymal	Supramaxillaries, prefrontals, zygomatic, lachrymal		Supramaxillaries, prefrontal, and lachrymal	Supramaxillaries, prefrontal, and zygomatic
		Median unit	Premaxillary, nasal, frontal, postfrontal	Premaxillary, nasal, and frontal		Anterior unit: premaxillary bone	Premaxillary, nasal, frontal and vomers
						Posterior unit: nasals & frontal	
	Parietal Division		Parietal, squamosal, supratemporal	Supratemporal arch: squamosal, postorbital, postfrontal	Parietal, squamosal, postorbital, postfrontal, and supratemporal		Parietal, postfrontal and supratemporal
				Median unit: parietal and supratemporal			
	Epipterygoid division—Epipterygoid						
	Quadrate division		Quadrate bones				

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*Broken lines designating divisions taking part to some extent jointly in skull kinesis action.

TABLE OPPOSITE PAGE 1403

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TAXONOMIC INDEX TO ANDERSSON AND LÖNNBERG PAPERS ON PRESENT LOCATION OF LINNAEAN REPTILE AND AMPHIBIAN TYPES

Index prepared by Paulo E. Vanzolini

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In a series of three papers published near the end of the nineteenth century, Lönnberg and Andersson annotated the present place of deposition of many of the types of species described by Carolus Linnaeus. It has always been difficult to use these papers, however, because the arrangement is by institution holding type material, and one must search through all three papers when seeking information on a single Linnaean species. This index will permit one to find all information on a single species in any of the three papers. Under each species listed the user will find first a Roman numeral referring to the paper, and then the pages within that paper on which the species is discussed. The three papers, with their reference numbers, are as follows:

I. Lönnberg, Einar. Linnean Type-Specimens of Birds, Reptiles, Batrachians and Fishes in the Zoological Museum of the R. University in Upsala. Bihang till K. Svenska Vet.-Akad. Handlingar, band 22, afd. 4, no. 1, 1896, pp. 1-45.

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1898-1928

Prepared by

Simon M. Campden-Main

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BIBLIOGRAPHY OF THE CHAMELEONTIDAE

1864 - 1964

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INTRODUCTION

No comprehensive bibliography dealing with the Chameleontidae has ever been published. This listing is designed to serve as a single source of information on chameleons and contains most major papers for the one hundred year period indicated. Included are 520 citations, some of which are not entirely devoted to chameleons. In these, references to chameleons are indicated by the page numbers and plate numbers included within brackets. Papers which refer in their entirety to chameleons will contain no such indication.

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It is hoped that a table of contents and index to this listing will eventually be completed; a compilation of sources prior to 1864 is in progress.

In spite of the assistance, errors of omission are my own and, for these, I apologize. I would greatly appreciate assistance in locating these errors, and encourage those noting any to tell me about them.

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March, 1969

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DISTRIBUTION OF SEA SNAKES IN THE SOUTH CHINA SEA AND EAST INDIAN OCEAN

by V. P. Shuntov

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The Russian fishing trawler SESKAR cruised the South China Sea from January through March 1964. A. I. Chigirinskiy and Yu. M. Maksimov observed about 70 snakes and collected 75 specimens belonging to 7 species. V. G. Osipov, when cruising the South China Sea and East Indian Ocean in November and December 1963 and January through March 1964 on the fishing trawler ORLIK, observed about 100 sea snakes. These specimens were processed by the Pacific Research Institute of Marine Fishery Management and Oceanography in Vladivostok.

Data of all the counts of sea snakes have been reduced to one denominator--the number of individ- / 1883 / uals observed per hour when the speed of the vessel is 10 knots (Figs. 1, 2, 3).

It is known that sea snakes gravitate in their distribution toward shallow coastal areas. The distribution of sea snakes presented in Fig. 1 confirms the above statement. Indeed, most of the samples taken from the open water of the East China sea, in the central part of the South China sea and northeast of the Philippine Islands did not contain any sea snakes at all; whereas the sample taken from the southern belt of the South China Sea, notably in the Gulf ofSiam, as well as between Sumatra and Kalimantan Islands, contained many sea snakes. Out of 45 samples, 38 contained snakes. In 15 samples the number of snakes varied from 1 to 5; in 10 samples from 5 to 10, and in 11 samples from 10 to 25 snakes per hour of trawling with the speed of the vessel being 10 knots (Fig. 2). Because the snakes are expert divers and spend considerable time under water, the listed figures indicate only their relative quantity in these areas. Also in the Gulf of Tonkin, north of the Gulf of Siam, the number of sea snakes was considerable (according to our observations conducted in 1961).

The number of samples taken from the Indian Ocean is, of course, too small for the elucidation of regularities in the distribution of snakes in this vast area. However, the data listed in Fig. 1 show quite clearly that in the open ocean the snakes are seldom seen. Here they usually are observed not farther than 60-70 miles from the coastline. Only on December 7 1963 were four individuals of *Pelamis platurus* observed in the central sector of the ocean about 800-850 miles from Ceylon land Sumatra.

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As a rule, the snakes are encountered in places with bottom depths less than 90-100 m. The main mass, however, is limited to depths less than 75 m. This is conspicuously confirmed by the character of distribution of sea snakes in areas with shoals of varying sizes. Where the shelf is narrow, the snakes are seldom observed at a distance of several tens of miles from the coast. However, in the Gulf of Tonkin and in the southern South China Sea, where the shelf is very wide, sea snakes occur in large numbers at distances of 70-100 miles off the coast (Figs. 1 and 2).

Especially large numbers of snakes are observed in shallow gulfs. The reason for this is that in places with very indented coastal line, the currents create eddy circulations which help keep mature snakes (which are not good swimmers) in a definite location and prevent the young from being transported beyond the boundaries of the shoals.

The tropical Australian and Asian Seas are most favorable for sea snakes. In addition to many shoals and gulfs, there is an abundance of fish and invertebrates in the seas, on which the sea snakes depend for food. Because of these facts, this region has become a center of abundance of qualitative and quantitative of sea snakes (as to the latter cause, one must also take into consideration historical reasons).

At our disposal were only 75 snakes obtained from several stations in the Gulf of Siam. Therefore, it is impossible to plot distribution schemes for individual species because the absolute number of species cannot be estimated by visual observations. The only exception is *Pelamis platurus*, which is a unique color and can be readily identified at a greater distance. In the Gulf of Siam area this species was most numerous (Fig. 3), making up 55% of the snakes.

Our observations conducted in 1961 in the Gulf of Tonkin (Shuntov, 1962) demonstrate that in the open sectors of the Gulf, *P. platurus* was also most numerous of the snakes. Of several tens of samples examined by V. G. Osipov in the Indian Ocean (mainly over great bottom depths at distances exceeding 50-70 miles from the coast) only 10 samples contained snakes, 8 of which consisted of only *P.* / 1885 / *platurus*. The absence of this species from samples taken in the extreme south of the South China Sea between Sumatra and Kalimantan Islands was unexpected (Fig. 3).

In the Gulf of Tonkin, *P. platurus* inhabits waters where the salinity exceeds 32%. Therefore, the quantity of these snakes sharply decreases in the NW part of the gulf where the water is diluted by rivers. Off Hainan Island, however, where the water is quite saline, *P. platurus* is found in the littoral water (Shuntov, 1962). In the Gulf of Siam the species is more widely distributed than in the Gulf of Tonkin. The possible reason for such a distribution is the river discharges at the tip of the gulf. However, it has not yet been established how the dilution affects the distribution of *P. platurus* because no observations have been conducted north of 12°N.

Other species of snakes were less often observed in the given areas; out of 75 snakes caught in the Gulf of Siam, *P. platurus* made up 53, *Astrotia stokessii* (Gray) 8, *Lapemis hardwickii* Gray 4, *Hydrophis spiralis* Shaw 3, *Praescutata viperina* (Schmidt) 3, *Hydrophis fasciata* Guenther 2, *Microcephalophis cantoris* Schm. 2 individuals.

In the southern South China Sea and in the Gulf of Siam, several observations were conducted in various seasons. This enables us to conclude roughly about the migrations of snakes. Yu. M. Maksimov observed concentrations of snakes in the eastern part of the Gulf of Siam and in the southern part of the sea between Sumatra and Kalimantan Islands at the beginning of Feburary 1964. V. G. Osipov had observed such concentrations by the end of 1963 in the same areas. Snake concentrations in these areas were considerable at the end of March 1964 (see Figures 2 and 3). In the Gulf of Siam area one could observe migration toward the gulf. In a number of species, the migration to more concealed areas could be associated with the birth of young. This is, in a way, confirmed by the snakes that were caught during 17-20 March 1964 at three stations in the Gulf of Siam.

It is seen from the table that the females with embryos were observed only in the upper part of the Gulf. The listed data show that P. platurus reproduced during the observation period. Four young P. platurus were observed at two stations; the length of their bodies equaling that of the embryos. Undoubtedly, they were born in March. A part of the snake population would probably reproduce during April.
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It should be noted that the reproduction of sea snakes has been little investigated. For the majority of species, we do not even know the time of reproduction. According to M. Smith (1926), most of the snakes that inhabit the Gulf of Siam bear young in March and April. The data listed in the table confirms that the P. platurus reproduces at this time. On the basis of data at our disposal it is seen that Hydrophis spiralis also reproduces in the spring. We dissected three females of this species, which were caught on 17 and 18 March 1964 at the first and second stations. One of them (150 cm.) contained 8 embryos, the other (135 cm.) 5 embryos, 28-30 cm. long. Microcephalophis cantoris evidently reproduced by the end of summer. A female caught at station 2 on 18 March 1964 was 98 cm. long and had three embryos 2-3 cm. long. The reproduction of Astrotia stokessii occurs evidently in the winter. This is confirmed by samples caught on 18 March 1964: six young snakes were 37, 38, 41, 40, 40 cm. long.

Lapemis hardwickii and Hydrophis fasciatus evidently reproduce in the winter or autumn. Females of these species were observed in August and September of 1961 in the Gulf of Tonkin; they contained large embryos (10-15 cm. long).

All of the sampled snakes were molting. Evidently, the molting, in contrast to reproduction, occurs at the same time in all the species. P. platurus that were observed during summer in the Gulf of Tonkin had a contrasting color with a brilliant yellow hue. P. platurus, which were caught in March 1964 in the Gulf of Siam, had a rather monotonous color with a pink hue. A new yellow skin could be observed through the epidermis by the beginning of summer.

The stomachs of the individuals that were caught in the Gulf of Siam contained only fish (mainly young sturgeons). Some individuals contained 5-7 small sturgeons, 2-6 cm. long. The main food of the snakes inhabiting the Gulf of Siam consisted of sturgeons--evidently, because these are the most numerous fishes in the area.

TABLE

DATA ON THE DISSECTION OF FEMALE P. PLATURUS
CAUGHT DURING 17 - 20 MARCH 1964

No. of Stations	Coordinates	Number	Mean Length	No. of Newly-Born and Their Length in CM	No. of Females With Embryos and The Length of Embryos in CM
1	9°07' N. 102°52' E.	10	35.0	2 (23.5; 20.0)	--
2	11°21' N. 102°31' E.	12	42.0	--	2 (18.0; 18.5; 17.0; 16.0; 16.0; 8.5)
33	12°00' N. 101°08' E.	12	40.0	2 (20.0; 24.5)	2 (20.0; 22.0)

/From 1883/

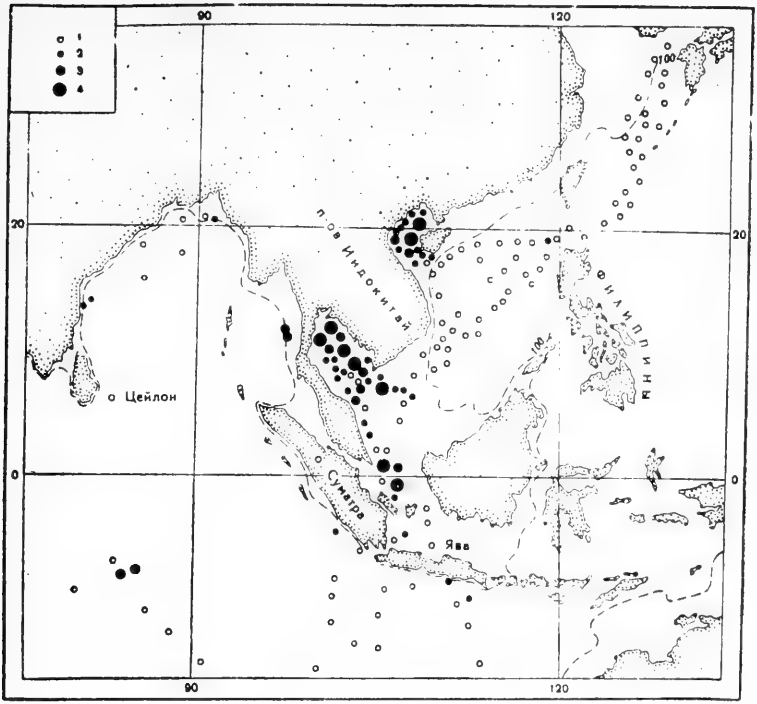

FIG. 1. Distribution of Sea Snakes in the South China Sea and East Indian Ocean From November 1963 through March 1964 (For the Gulf of Tonkin, the data pertain to 1961).

1 - Snakes have not been noticed; 2 - 1 to 5 snakes;
3 - 5 to 10 snakes; 4 - 10 to 25 snakes per 1 hour with the speed of vessel being 10 knots.

/from 1884/

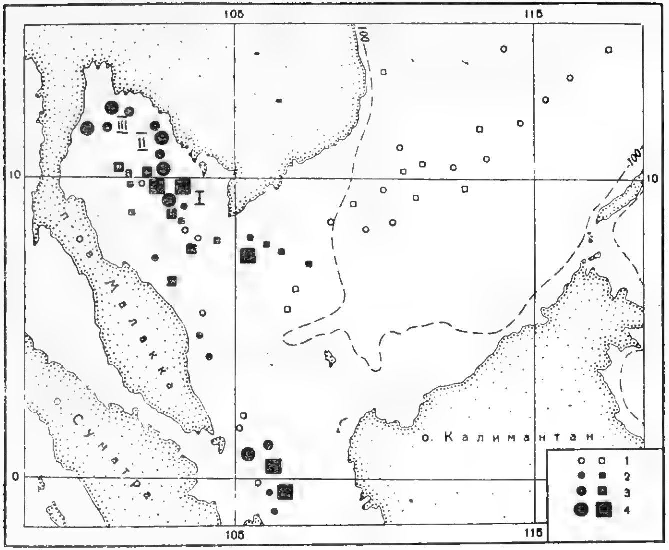

FIG. 2. Distribution of Sea Snakes in the South China Sea during February and March 1964.

1 - no snakes seen; 2 - from 1 to 5 snakes;
3 - from 5 to 10 snakes; 4 - from 10 to 25 snakes per 1 hour with the speed of vessel 10 knots.
Squares denote February, Circles March; the Roman numbers (I - III) show the locations of light stations.

/from 1885/

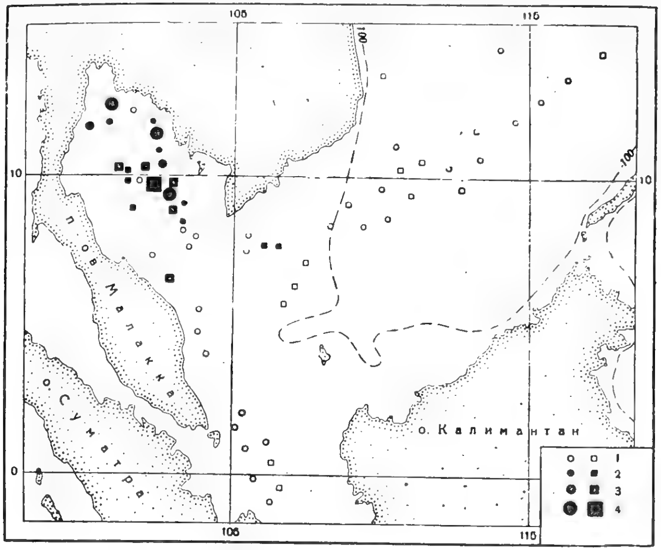

FIG. 3. Distribution of P. platurus in the South China Sea in February and March 1964.

1 - no snakes; 2 - 1 to 5 snakes; 3 - 5 t0 10 snakes;
4 - 10 to 25 snakes per hour with the speed of vessel being 10 knots.

Index

THE
SALAMANDERS
OF
THE
FAMILY
PLETHODONTIDAE

(by Emmett Reid Dunn)

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INDEX TO THE SCIENTIFIC NAMES IN "A CONTRIBUTION TO THE ZOOGEOGRAPHY OF THE WEST INDIES WITH ESPECIAL REFERENCE TO AMPHIBIANS AND REPTILES"

by

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-1

THE EVOLUTION OF THE HYOBRANCHIAL APPARATUS IN THE LARVAE OF AMPHIBIA

by A. S. Severtzov

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INTRODUCTION

The present work is a part of the investigation being conducted in the laboratory of Evolutionary Morphology in the Zoological Academy of Sciences, in the Academy of Science of the USSR. It deals with the problem of the origin of terrestial vertebrates which "pertains to the most complex and interesting divisions of phylogeny and relates to many general questions of evolution" (Schmalhausen 1964). In these investigations by methods of comparative embryology we studied a series of systems of organs with the goal of explaining the transformation which took place in the course of the evolution of vertebrates from the ancestral Tetrapoda to contemporary Amphibia. The morphobiologic and the functional analysis (with the addition of data from paleontology) permits us to understand the adaptive significance of the transformations in organization, and thus to point out and explain the basic directions of evolution in the lower Tetrapoda. The latter point is particularly significant since there are now two mutually exclusive theories on the origins of the Tetrapoda. According to the theory of monophyletic origin of the terrestrial vertebrates, the Tetrapoda arose as a single branch from the rhipidistian crossopterygian fishes. All of the variations in extinct and extant forms is based upon their adaptive radiation into the terrestrial and aerial sphere of life. On the other hand, the majority of advocates of the theory of polyphyletic origin of the Tetrapoda, which was worked out primarily by the Swedish paleontological school, consider that those amphibians which have tails and legs arose from one of the branches of Rhipidistia, i.e., the Porolepiformes, and the tailless amphibian, **Gymnophiona,** and all the amniotes arose from another branch, the Osteolepiformes.

Our present work deals with the evolution of the hyobranchial apparatus in the larvae of Amphibia and investigates the transformation which took place in the course of development of the lower Tetrapods. By the term hyobranchial apparatus, we mean that complex of morphologic structures which occupies the area from the hyoid to the last gill arch inclusive, and all the muscles connected therewith. Ontogenesis of this morphofunctional system is concluded at the stage at which the larval hyobranchial apparatus is functioning and its morphogenesis ceases before metamorphosis. The evolution of the hyobranchial apparatus in the larvae of Amphibia as a single unit in connection with its function, which has not been investigated by anyone prior to this time, should be interesting for two reasons: first, from the time the vertebrates came up to dry land the basic direction in the evolution of adult Amphibia has consisted of their adaptation to the terrestrial and aerial spheres. The larvae of most Amphibia have continued to live in water. The study of the hyobranchial apparatus in the larvae hence gives us material which is more favorable for explaining the origin of this system in amphibia. Second, such investigation can shed light not only on the origin of the hyobranchial apparatus in the larvae of the extant Urodela and Anura but also on those processes which led to the structures seen in Recent forms.

The problem in the present dissertation is the explanation of the following questions: 1. What function or functions does the hyobranchial apparatus fill in the larvae of Amphibia? 2. How is this function manifested, in other words, what is the mechanism of action of the hyobranchial apparatus? 3. How did the evolution of the hyobranchial apparatus take place in connection with its functions? 4. What was the origin of the mechanism of action for this system?

The resolution of the principal questions was facilitated by the fact that in the literature the functions and in part the mechanism of action for the hyobranchial apparatus of fish, primarily Teleostei, have been described. The construction of the hyobranchial apparatus is known for both fishes and the larvae of amphibians to the degree that homology of the majority of its elements is no longer in doubt. Also, the basic features of the phylogenetic connections of the lower tetrapods have also been explained. In addition, the mechanism of the expulsion phase of the buccal pump has been reconstructed by M. M. Voskoboenikov, (1932) and I. I. Schmalhausen, (1964). The mechanism for the suction phase in the respiration of crossopterygian fish is facilitated by the movements of the hyobranchial apparatus, the structure of which was described by Jarvik (1954, 1963, 1967).

MATERIALS AND METHODS

Larvae of four families of Urodela and six families of Anura were investigated. Following is a list of species (Ranodon sibiricus, Hynobius keyserlingii, Ambystoma sp., Tritutus cristatus, T. bulgaris, Pleurodeles waltlii, Salamandra maculosa, Necturus sp., Proteus anguineus, Xenopus laevis, Bombina bombina, B. orientalis, Pelobates fuscus, Rana temporaria, R. esculenta, Bufo bufo, B. viridis, Hyla arborea, H. japonica). The structure and development of the hyobranchial apparatus was studied in slide preparations and in a series of sections from which were made microphotographs, sketches, graphic and plastic reconstructions. Four hundred and twenty-three larvae at various stages of development were examined with morphologic methods. Analysis of functions and of the mechanism of action of hyobranchial apparatus was carried out on the basis of obser-

vations of living larvae as well as with the help of electrical excitation of individual muscles (in large axolotls). To observe the movements of the hyobranchial apparatus living larvae were placed in a chamber with a mirror bottom. A binocular microscope was focused on the reflection of the base of the oropharyngeal cavity through which the contours of the cartilage and muscle were visible through the skin. Through a large number of observations, a clear picture of the movements of the hyobranchial apparatus was compiled. In addition, observations were made on the movement of the hyobranchial apparatus in the fry of pike and in addition three series of sections from the larvae of Neoceratodus and Protopterus were studied as well as preparations of skulls of neotenic stegocephalid (Dvinosaurus primus Amalitzki No. 39, 40, 41 and Tungussogyrinus bergi) from the collection of the Paleontological Museum of the Academy of Sciences of the USSR.

CHAPTER 1

THE EVOLUTION OF THE HYOBRANCHIAL APPARATUS IN THE LARVAE OF URODELA.

All Urodelan larvae which are "waiting predators" generally feed on zooplankton. The prey is captured at a distance with the aid of a stream of water which is induced by depression of the base of the oro-pharyngeal cavity and opening of the mouth. Upon entry of the prey the gill arches are closed by the gill flaps. The depression of the floor of the oro-pharyngeal cavity occurs by the action of the hyobranchial apparatus. The constriction of M. sternohyoideus elicits a retraction of the copula. The hyoid, which is suspended from the skull on two ligaments, then turns due to the presence of the free moving hyocopulatory articulation with its anterior or forward end downward. The copula is lowered simultaneously without changing its horizontal position. The forward portion of the base of the oro-pharyngeal cavity is consequently depressed. At the same time the M. ceratohyoideus exterior, a muscle which at this moment has a point of support on the hyoidal arch and is fixed by the contraction of M. sternohyoideus and by position of the hyoid ligaments, is contracted. The posterior, (i.e., dorsal) end of the ceratobranchiale I extends ventrally but its action extends to all of the gill arches so that the ventral and dorsal ends of ceratobranchiale are united by cartilaginous ridges -- junturae proximales and comissurae terminales. During the action of the M. ceratohyoideus exterior the back portion of the floor of the oro-pharyngeal cavity is depressed. A similar action is seen in all of the forms investigated, except for Proteus anguineus, in which M. sternohyoideus, because of its greater development and more extensive area of attachment to the mucilaginous floor of the oro-pharyngeal cavity, may act both on the forward portion of the floor of the oro-pharyngeal cavity, by means of the turn of the hyoid, and on the floor of the gill region; thus it sharply strengthens the whole action of depression. After the prey has entered the mouth the jaws close. During the action of the hyobranchial apparatus the floor of the oro-pharyngeal cavity begins to rise and pushes almost all of the water which entered the mouth during the capture of the prey through the opening gill slit. This lifting movement takes place more slowly than the movement of depression. The M. intermandibularis posterior and the Mm. interhyoidei anterior and posterior play a primary role in this movement. During their contraction the floor of the oro-pharyngeal cavity swells and at the same time rises. The M. intermandibularis posterior has a point of attachment on the lower jaw, the M. interhyoideus anterior on the posterior end of the ceratohyale and through the above mentioned ligaments onto the skull, and the M. interhyoideus posterior is connected on the end of ceratobranchiale I which is connected with the skull only by means of the M. levator arcus branchialis I. In the motion of lifting the Mm. levatores arcuum branchialum also play a role and they extend upward to the dorsal ends of the gill arches and the Mm. subarcuales obl. II, III facilitate a protraction of the ceratobranchiale. A significant role in the described movement is played by M. geniohyoideus, which in pulling the copula defines the movement of the hyoidal arch to its original position. The protraction of the copula during the action of the M. geniohyoideus is conditioned by the fact that it rests on the symphysis of the lower jaw, which is fixed at this moment as a consequence of the contraction of M. intermandibularis anterior.

The ingestion of food takes place at the end of the upward motion of the floor of the oro-pharyngeal cavity. At this time the gill arches close under the action of M. transversus ventralis IV. The pressure of the water remaining in the oro-pharyngeal cavity has increased due to the lifting of the floor, and the contained food goes to the region of lower pressure, that is, to the esophagus whence it is swallowed. The M. subarcualis rect. I serves as a sinergist in this motion, and this muscle in fixing the gill arches to the hyoidal creates a point of support for the M. transversus ventralis IV.

This mechanism for the capture of food is used by the larvae of all Urodela investigated. We were not able to observe the movements of the hyobranchial apparatus which are especially connected with breathing. The external gills, organs for gas exchange in the larvae of Urodela, move independently of the hyobranchial apparatus; movements of the latter

assist the capture and swallowing of food but not breathing. The mechanism of action of this system is based on rotation of the hyoidal arch in the sagittal plane. We were able to show that the mechanism for depressing the floor of the oro-pharyngeal cavity derives from the buccal pump and this is also true for the mechanism of raising the floor of the oro-pharyngeal cavity. Consequently, the mechanism for respiratory motions in the ancestors of the terrestrial vertebrate was transformed into a mechanism for the capture of food by the larvae of Urodela. This conditioned a high degree of homology of the hyobranchial apparatus in fish and the larvae of tailed Amphibia. Nonetheless, it was mainly the loss of the breathing function that determined the major sequential transformations of the hyobranchial apparatus, as shown both in a comparison of the larvae of Urodela with fishes as well as in comparisons of the larvae of the investigated species one with another. Already in Rhipidistia the reduction of the dorsal regions of the gill arches (pharyngeal and epibranchial) is connected with the transition to pulmonary respiration (Schmalhausen, 1964) and this reduction in the larvae of Urodela is supplemented by a reduction of ventral elements. In all of them the fifth arch has completely disappeared (in the Proteidae, the IV arch as well) and the hypo-element of the IV arch also disappears, the hypo-elements of the III arch are reduced (a rudiment of the hypobranchiale III is found only in the larvae of Hynobiidae and Cryptobranchidae) and even II (in Proteidae). This process led to the disappearance of the posterior gill slits. In the larvae of Urodela there are three slits which are situated between I and II, II and III, III and IV ceratobranchialia (in the Proteidae two slits remain between I and II, and II and III). Thus the most posterior gill arch in the fish which is located between the IVth and Vth arches (in the Proteidae the preceeding one as well) and the most forward slits between the hyoid and the first gill arch are reduced. The position of this arch is occupied by the ceratohyoideus exterior as a homolog to the M. opercularis in fishes.

The reduction of the hyobranchial apparatus occurs together with several changes associated with the perfection of the mechanism for the capture of food. First of these was a modification of the movement most responsible for this process, namely the depression of the floor of the oro-pharyngeal cavity. The union of the urohyale and basibranchiale from independent elements of the hyobranchial skeleton in the Rhipidistia to a single copula in the larvae of Urodela facilitated a better transmission of the action of Mm. sterno- and geneohyoidei to the hyoidal arch. The transformation of the M. opercularis into the M. ceratohyoideus exterior and the associated appearance of commissurae terminalis in the larvae of Urodela created a possibility for depressing the posterior part of the floor of the oro-pharyngeal tract.

The mechanism for lifting the floor of the oro-pharyngeal cavity remained virtually unchanged; apparently the speed with which water is expelled through the gill slits does not have great biological significance, since the capture of food is not determined by this. The perfection of the mechanism for closing the gill slits during the capture of food is connected with the differentiation of M. subarcularis rect. IV. In the larvae of Hynobiidae, this muscle has one concavity which extends from the fourth to the first gill arch and it is thus a common constrictor of the gill slits. In the larvae of Ambystomidae and Salamandridae there are two supplementary portions of the M. subocularis rect. IV which unite the IV arch directly with II and III. Crests on the ventral ends of ceratobranchialia serve to strengthen all three parts.

The reconstruction of the hyobranchial apparatus driven by the need for perfection of the prey captive mechanism is most clearly seen (among the investigated forms) in the Proteidae. Here a progressive development of the M. sternohyoideus and M. ceratohyoideus exterior facilitates a stronger depression of the floor of the oro-pharyngeal cavity than is possible in the larvae of other Urodela. The extension of the area of support of M. sternohyoideus on the soft floor of the oro-pharyngeal cavity was made possible by the high degree of reduction of the gill arches. The distinctiveness of the structure and mechanism of action of the hyobranchial apparatus of Proteidae is explained by the particular biology of this blind cave form which is required to feed on very mobile and quickly moving Crustacea. There is time for a proteid to make only one ingesting movement, at the moment the tip of the snout touches the prey, and this movement must be strong enough to promote a high probability of capture.

It is thus evident that differences in the construction of the hyobranchial apparatus are insignificant among the investigated forms. The larvae of higher families (Ambystomidae and Salamandridae) are only distinguished from the larvae of the primitive families (Hynobiidae) by the disappearance of the rudiment of hyobranchiale III and by the acquisition of a more highly differentiated apparatus for closing the gill slits. Only in the Proteidae was there a more significant reconstruction of the hyobranchial apparatus. Thus the stability in the construction of this system corresponds to the stability of the mechanism for the capture of food.

Comparative embryological investigation of the hyobranchial apparatus of Urodelan larvae permitted us to estimate its evolutionary development, i.e., the establishment of the basic qualities of organization which define the above mentioned mechanism of action.

The mesenchymal layers of the arch of the hyobranchial skeleton in the larvae of all the investigated forms initially rests in a transverse position. Then, to the degree that there is relocation of the stomadeum from the ventral side of the embryo to the end of the snout (in actively feeding larvae the mouth is terminal), the hyoid and the gill arches change their position. As a result they are situated obliquely with relationship to the longitudinal axis of the body (the dorsal end of each arch is located significantly more caudal than the lower). This creates the possibility of turning of the hyoid arch in the sagittal plane and at the same time the whole mechanism of action of the hyobranchial apparatus.

Parallel with the change in position of the arches, the hyobranchial skeleton differentiates and the muscles which control it develop further. The copula forms in the medial part of the floor of the oro-pharyngeal cavity. In the majority of the forms investigated it arose immediately in the form of a single element. Only in *Ranodon sibiricus* at one of the stages of development were we able to discover a branchial segmental-like formation of the copula, which is encountered only in Acanthodii (Watson, 1937). The *branchiale basalia* already fuse in the following stage. This shows that the evolution of the basalia elements of the hyobranchial skeleton involved fusion rather than reduction. This, as well as the fusion of the *basalbranchialia* and *urohyale* during the transition from fishes to tetrapods, facilitated a better transmission of the action of the *M. sternohyoideus* to the hyoid arch.

In the initially continuous mesenchyme formation of the hyoid and gill arches independent centers of cartilage are differentiated and these correspond to the later division of the arches into hypo- and cerato- elements. During the early stages of development of hynobiid larvae the *hypohyalia* lie under the edge of the *ceratohyalia*. This bend disappears as in the Rhipidistia (Jarvik, 1954, 1963), and the hyoid assumes a definite form for the larvae of Urodela. In the larvae of Ambystomidae and Salamandridae the hyoid is formed directly without the above mentioned curve. *Commissurae terminales* which unite the posterior ends of the *ceratobranchiali* arise as outgrowths from these after the gill arches have been completely formed, that is, their development occurs by means of positive anabolism, extensions of the final stages of development of their *ceratobranchiali*. These elements of the hyobranchial skeleton are distinctive only for the larvae of Amphibia; the elements are new formations, and hence not homologous to the *epibranchia* of fish as suggested by Fox (1954). By means of a positive anabolism the supplementary portions of *M. subarcularis rect. IV* and of the crest which serve for their strengthening have also developed in the larvae of the higher Urodela. The reduced parts of the hyobranchial apparatus (4th and 5th gill slits, *hyobranchiale* III) evolved through negative anabolism. Consequently, the evolutionary transformation of the hyobranchial apparatus in the larvae of Urodela which are connected with the loss of the breathing function took place by means of a negative anabolism and the transformation which conditioned the perfection of the mechanism for food capture, by means of the positive mode of phyloembryogenesis.

CHAPTER II

THE HYOBRANCHIAL APPARATUS OF THE STEGOCEPHALIDS

The study of the structure of the hyobranchial skeleton in the stegocephalids was restricted to representatives of Labyrinthodontia (groups which are considered to be the ancestors of Anura). In the literature there is information on the structure of the hyobranchial skeleton of representatives of one family of Lepospondyli (*Lysorophus coctinus*) and four families of Labryinthodontia (*Dvinosaurus*, *Platyceps*, *Gerrothorax*, *Trimerorhachis*, *Micropholis*, *Branchiosaurus*). All of these stegocephalids are neotenic forms and possess larval structures of the hyobranchial apparatus.

The number, form, and correspondence of elements of the hyobranchial apparatus (with the exception of the well-developed *hyobranchiale* III in series of representatives from both groups) were the same as in the larvae of Urodela. The arches of the hyobranchial skeleton were always situated obliquely with respect to the longitudinal axis of the body. In *Dvinosaurus* the hyoid was suspended by ligaments from the skeleton (Bystrov, 1938, 1939). Epibranchials were absent in all of the above mentioned stegocephalids. There were three gill slits, the same number as in the larvae of extant Urodela (the first and the last gill slits of the ancestral tetrapods were absent). In addition, evidence of external gills was found in some stegocephalids. *Dvinosaurus* was also noted to have external gills (Bystrov, 1938). The similarity of the structure of the hyobranchial skeleton in both the larvae of stegocephalids and the larvae of extant Urodela presumes a similarity in their mechanism of action. The presence of external gills indicates that the hyobranchial apparatus of stegocephalids as well as of the larvae of urodelans serves for the capture of food. Thus, we were able to explain that despite variations among the several representatives, the hyobranchial apparatus of the larvae of Labryinthodontia and the larvae of Lepospondyli was constructed and functional on the same principle as that of the larvae of the extant Urodela.

CHAPTER III

THE EVOLUTION OF THE HYOBRANCHIAL APPARATUS IN THE LARVAE OF ANURA

I. I. Schmalhausen (1964) has suggested that the hyobranchial apparatus of tadpoles was formed under conditions of rapid flow of mountain streams

poor in zooplankton. The following associated characteristics appeared in the larvae of Anura: an apparatus of lip cartilage which serves for the capture and chewing of the growing plants that serve as basic food, a long convoluted intestine which is suitable for the digestion of this food, and an external gill concavity which facilitates the acquisition of a streamlined body form. The origin of the last item caused loss of the external gills and the development of hidden homologous gills situated on the *ceratobranchialia* as in fishes. We were not able to observe the motion which specially serves for breathing. For this reason the mechanism for the transport of food, even though there are peculiarities imposed by the development of concealed gills

Such an interpretation of the function of the hyobranchial apparatus in the tadpoles is confirmed by the absence of gills in the larvae of *Xenopus laevis* and by the observation that the motion of the hyobranchial apparatus serves only for the transport of food.

The large food masses entering the mouth in dispersed condition require a change in the motion pattern of the hyobranchial apparatus. In tadpoles, as distinct from the larvae of Urodela, ingestion occurs by means of frequent oscillations which are not of great amplitude. These oscillations create a weak constant stream of water which facilitates the transport of food into the interior of the oro-pharyngeal cavity. Food is not captured at a distance. In none of the investigated forms do the oscillations of the hyobranchial apparatus occur in the sagittal plane as in the larvae of Urodela, but rather in the transverse plane.

The depression of the floor of the oro-pharyngeal cavity takes place during the motion of the *ceratohyalia* and the gill chambers (*ceratobranchialia*) with the medial edges downward. The *M. orbitohyoideus* and *M. suspensoriohyoideus* draw the lateral ends of the hyoid upward. *Ceratohyalia* turn in the geoquadrate articulation which serves as the only connection of the hyobranchial apparatus of tadpoles with the skull. During this turning, the medial ends of the ceratohyals, which are spread and thickened, are depressed; together with the *copula* I *pars reuniens* and *copula* II which are situated along the medial line of the body. The *Mm. levatores arcuum branchialium* also contract, drawing upward the back and posterior regions of the gill chambers. As a result, the latter turn and the hyobranchial disc which is furthermore connected immoveably with *copula* II is depressed. The forward region of the ventral wall of the esophagus in the tadpoles of Phaneroglossa is connected to the posterior region of the hypobranchial disc. For this reason, the esophagus opens when the hypobranchial disc is depressed. As a result of the complex of described motions, the entire median region of the floor of the oro-pharyngeal cavity curves upward and the water which has poured in through the oral opening carries the elements of food from the lip cartilage into the depths of the cavity. During the depression of the oro-pharyngeal cavity the gill arches close due to the contraction of *Mm. constrictores branchiales*, i.e., the oro-pharyngeal cavity is isolated from the external gill chamber. The latter chamber is isolated from the outside by a dropping of the walls of its efferent canal and this wall plays the role of a valve. The return movement of the *ceratohyalia* with the medial ends upward takes place during the action of *M. interhyoideus anterior*. This muscle contracts and at the same time lowers the lateral ends of the hyoid. Together with the medial ends of the *ceratohyalia*, the *pars reuniens* and both copulae are raised. However, the *M. interhyoideus anterior* draws the ends of the hyoid not only ventrally but caudally as well attempting to join them horizontally.

Copula I is hindered by this movement and it supports the medial ends of the ceratohyals. Simultaneously with the contraction of the *M. interhyoideus anterior*, the *Mm. subarcuales recti* and *obliqui* contract and turn the gill chambers with a movement which is counter to the movement of depression. The simultaneous contraction of the above mentioned muscles raises the median portion of the floor of the oro-pharyngeal cavity. With this a stream of water carrying food material changes its direction and enters the gill slits while the particles of food are retained due to the presence of a special filter apparatus.

In the larvae of Phaneroglossa the filtered water exits through the gill slits into the external gill chamber, sweeping over the gill branches in the process. During the next intake pulse the retained food material is drawn into the esophagus, while the next lifting of the buccal floor causes the water to be filtered again. After entering the external gill chamber the last batch of water is expelled. Thus each successive drop of the floor of the oro-pharyngeal cavity will cause the water that enters into the esophagus to be further enriched by the food particles which remained in the oro-pharyngeal cavity during the previous elevation of its floor.

The mechanism of action of the tadpole hyobranchial apparatus is characteristic for all the investigated forms. It is remarkable that one cannot detect elements of the breathing movement of fish in it. The external gill concavity thus does not participate in the pumping of the water. In contrast to the condition in fishes the water is not sucked through the gill slits but passes them passively. The two-cycle pump of the larvae of Anura thus works as a one cycle pump in the larvae of Urodela. Investigation of the ontogenesis of the higher hyobranchial apparatus in anuran larvae permits us to explain the particular features of its construction and function which are connected with the change in the plane of oscillation. As in the urodelan larvae the mesenchymal formations of the arches of the hyobranchial skeleton are initially positioned in the transverse plane. The same complement of elements of

the hyobranchial skeleton develops in tadpoles as in urodelan larvae. The single new element is *copula* I. Shortly after the arches are laid down the formation of the long convoluted intestine begins. The latter literally forces the heart into the region of the hyobranchial apparatus, changing its configuration and the entire course of its further development. The hyobranchial skeleton moves somewhat rostrally, consequently the hyoid comes in contact with the quadrate cartilages. At this spot the quadrate articulation develops. *Copula* II (we succeeded in showing the homologue of the copula in urodelan larvae) having lost the possibility for growing caudally remains arrested as a short cartilage throughout the entire larval life of Anura, of a size equivalent to that seen in the early stages of larval development in the Urodela.

Hypobranchialia I and II approach one another and fuse. In the larvae of Phaneroglossa the mouth remains ventral until metamorphosis. Consequently the arches of the hyobranchial skeleton retain their initial transverse position. The change of configuration and topography of the hyobranchial skeleton observed in the anuran larvae must then have arisen as a result of a deviation from the course of development characteristic for the urodelan larvae. This deviation apparently results from interactions in forming the intestine and the heart and the lack of any tendency by the mouth to translocate. In tadpoles the hyobranchial apparatus then acts differently as the plane of its oscillation changes (since the arches lie in a transverse position rotation of the hyoid in the sagittal plane cannot lower the floor of the oro-pharyngeal cavity). It must be emphasized that this deviation arose by means of a changed construction in correlated mutual relationships (co-adaptation) of the hyobranchial apparatus with the organs surrounding it. The transformation of the hyobranchial apparatus took place not as a result of direct adaptation to the changed character of the food but indirectly, because of a change in other organs.

The deviation described above determined all further evolution of the hyobranchial apparatus. *Hypohyalia* noted in the beginning stages of development of the hyoid under the edge by the *ceratohyalia* (as in the hynobiid larvae) do not change their position, but spread out and fuse forming the *pars reuniens*, which is not cartilaginous but remains prochondrial for the entire larval life. Consequently the *pars reuniens* (which arises as the result of deviation in the development of *hypohyalia* particular to the larvae of Urodela) is the homologue of these elements of the hyobranchial skeletons and is not basal as believed by the majority of investigators. The *pars reuniens* serves as an elastic connection between the *ceratohyalia* when these move in the transversal plane. *Copula* I which possesses the most primitive construction in pelobatid tadpoles (it is lacking in the tadpoles of *Xenopus laevis*) arose in the process of evolution of the larvae of Anura of arcolaxis and has no homologue among the ancestors of the tailless amphibians. The remaining elements of the hyobranchial skeleton in the larvae of Anura are changed because of a deviation evolved by means of positive anabolism. The transport of dispersed food material required an increase in the amount of water circulated through the oro-pharyngeal cavity. With this a proportional increase of the medial parts of the *ceratohyalia* occurred, leading to the restructuring of the *ceratobranchialia* of the gill chambers and the fusion of *hypobranchialia* into a broad disk. Among the forms investigated, the tadpoles of Discoglossidae and Pelobatidae are more primitive in several structures of the hyobranchial system than are the tadpoles of the Ranidae, Bufonidae and Hylidae. Maximal spreading of the hyoid and the gill chambers is noted in the tadpoles of *X. laevis*; the latter characteristically feed on decaying matter and phytoplankton and hence require increased amounts of water to pass through the oro-pharyngeal tract.

The transformation of the hyobranchial skeleton is paralleled by the transformation of its musculature. The *M. ceratohyoideus exterior*, which lowers the *ceratobranchialia* in the larvae of Urodela, disappears. New muscles develop, namely the *Mm. orbita* and *suspensoric hyoidea*. The *Mm. levatores arcuum branchialium* expand and in the tadpoles of *X. laevis* may even fuse into a single muscle layer. The *Mm. constrictores branchiales* develop in anuran larvae as a result of the development of the concealed gills and the reduction of the gill flaps (which in the larvae of Urodela close the gill slits during the intake of water into the oro-pharyngeal tract cavity). The presence of these muscles in the tadpoles of *X. laevis* attests to the fact that gill breathing has in this species disappeared for a second time. The development of *Mm. constrictores branchiales*, which close the gill slits, is the single characteristic that conditioned the unification of the functions of breathing and food transport in the hyobranchial apparatus of tadpoles.

The muscles which participate in the raising of the floor of the oro-pharyngeal cavity have been subjected to just as great a transformation. The *M. interhyoideus posterior* is well expressed in the larvae of Pelobatidae, but absent in a series of investigated forms. The *M. interhyoideus anterior* is wide in the larvae of Urodela; but appears as a narrow strip in connection with the transverse location of the hyoid in the larvae of all the Phaneroglossa. In the larvae of *X. laevis* it is again broad. The *M. intermandibularis anterior* and *M. geniohyoideus* which determine the protraction of the hyoid and copula in the larvae of Urodela are in tadpoles kept from this function by the hyobranchial apparatus, and instead participate in the mechanism of action for the lip cartilage. The *Mm. subarcuales obl.* II and III are independent in the larvae of Urodela. In tadpoles (with the exception of **those *Hyla***) they are fused into a single muscle and in *X. laevis* they furthermore lose their connection with the copula. The evolutionary transformations of

the musculature of the hyobranchial apparatus of tadpoles occurred primarily through positive anabolism which could be clearly traced in a whole series of instances. The transformation of the M. intermandibularis posterior and M. sternohyoideus occupies a particular place. These muscles play a leading role in the mechanism of action for the hyobranchial apparatus in the larvae of Urodela, but do not function in tadpoles; for this reason they are always incompletely developed although they have not disappeared completely in any of the investigated forms. The preservation of the primordia for M. intermandibularis posterior and M. sternohyoideus is explained by the fact that they induce movements of the hyobranchial apparatus in adult Anura (A. S. Severtzov, 1961). Consequently one observes not a reduction but a retardation in anuran larvae, a temporary restraint in the development of these muscles which is elicited by their exclusion from the mechanism of action of the larval hyobranchial apparatus and by the necessity of preserving them for future function. Speaking more generally, retardation may begin when any component is excluded from the functioning of the provisional or temporary system even though the component is preserved for functioning at subsequent stages of ontogenesis. The offered conception to a certain degree explains the adaptive significance of regulated retardation in ontogenesis - a very little studied class of heterondria. Thus in the larvae of Anura a mechanism of action of the hyobranchial apparatus is developed. The evolution of the latter proceeded primarily by means of positive modes of phyloembryogenesis.

CHAPTER 4

HYOBRANCHIAL APPARATUS OF RHIPIDISTIA

In the investigation of mechanism of action of the hyobranchial apparatus in the larvae of Amphibia, the elaborate descriptions and reconstructions of the structure of the hyobranchial apparatus of Rhipidistia (Jarvik, 1954, 1963, 1967) give us the possibility to reconstruct the mechanism of action for this system in the crossopterygian fishes and also to weigh the arguments in favor of the theory of polyphyletic origins of the tetrapods advanced by Jarvik. The structure and location of the pulmonary discs in Glyptolepis and Holoptychius (Porolepiformes) and in Eusthenopteron (Osteolepiformes) is such that they condition the mobility of the floor of the oro-pharyngeal cavity and hence the rising and falling movements that assure the oscillation of the hyobranchial apparatus. The structure of the hyobranchial skeleton of Eusthenopteron and in particular of Glyptolepis is similar to the structure of this system in the larvae both of the stegocephalids and of the extant Urodela (the most important shared characteristic is the oblique or slanting location of the hyoid and gill arches which shows that the oscillations of the hyobranchial apparatus must have taken place in the sagittal plane during the action of the M. sternohyoideus). Consequently the mechanism of action of the hyobranchial apparatus in Rhipidistia, which served primarily for breathing, was similar to such mechanisms in the larvae of the stegocephalids and the larvae of the extant Urodela, but not in the larvae of Anura. One of the arguments used to substantiate the theory of the polyphyletic origin of the tetrapods advanced by Jarvik (1963, 1967) is based on his homology of a series of elements of the hyobranchial skeleton of Eusthenopteron and the larvae of Anura. In his opinion the sublingual pivot is homologous to copula I, the basibranchiale I to copula II and the basibranchiale II to the median fissure of the hyobranchial disc. The cited homologous features allowed Jarvik to come to the conclusion that the hyobranchial apparatus of the larvae of Anura developed on the basis of the structure of this system in Eusthenopteron. We succeeded in showing that of the homologous features advanced by Jarvik only the comparison of basibranchiale I in Eusthenopteron and of the basal elements of the hyobranchial skeleton of the tadpoles copula II was justified. Copula I is a new formation which is characteristic only of the larvae of Anura (see chapter 3) and the medial fissure of the hyobranchial disc arose during the process of the proliferation and fusion of the hypobranchialia and does not have anything in common with the basal elements. Nor is it possible, as presumed by Jarvik, to reconstruct the musculature of the hyobranchial apparatus of Eusthenopteron using the correspondences to analogous muscles in the larvae of Anura; all that is further emphasized by this is the similarity of the forms compared. The muscles of the hyobranchial apparatus of the tadpoles are highly changed as a result of the origin of a new mechanism of action. The presence of a sublingual pivot (which is not known in any of the extinct or contemporary forms) and a series of other characteristics in the construction of the hyobranchial skeleton attest to the specialization of Eusthenopteron. Thus the structure of its hyobranchial apparatus cannot be considered as a prototype for the structure of this system in the larvae of Anura and it is not possible to confirm or establish the theory of the polyphyletic origins of the tetrapods by means of such comparison.

CONCLUSIONS

In summary we must characterize the basic factors which determine the transformation of the hyobranchial apparatus and its evolutionary trends in the larvae of Amphibia. The evolution of the hyobranchial apparatus in the larvae of stegocephalids and the larvae of the extant Urodela is characterized by the loss of its function in breathing and its perfection as a mechanism for prey capture. The loss has permitted the reduction in a series of elements of the hyobranchial skeleton and the disappearance of several gill openings, as well as several

progressive transformations of the hyobranchial apparatus. The high evolutionary stability of this apparatus is explained by the fact that its action permits the animal to capture prey at a distance; it thus represents the perfection of the basic function of feeding. Both reduction and progressive transformation of the hyobranchial apparatus are most noticeable in the Proteidae, in which only two pairs of gill openings are preserved. Theoretically reduction might be expected to have proceeded further in the urodelan larvae, since only the single anterior pair of gill openings is necessary for expulsion of water from the oro-pharyngeal cavity. However, the hyobranchial apparatus cannot be reduced further. The complete loss of gill openings, observed in some adult Amphibia, would if carried out in all stages mean a basic transformation of the mechanism of hyoid action. Thus the tendency for a reduction of the hyobranchial apparatus in the evolution of urodelan larvae is offset by the need to perfect its action in other functions. The hyobranchial apparatus in the larvae of Anura arose by modification of the hyobranchial apparatus in the larvae of stegocephalids and was formed according to the same principle as in the larvae of extant Urodela. The appearance of the breathing function in the hyobranchial apparatus of the tadpoles seems to have had no effect on its evolution. The transformation of this system took place as a result of a change in the correlated connections of the hyobranchial apparatus and the organs surrounding it in the ontogenesis of anuran larvae. The deviation which is defined or determined by a change in the area of oscillation for the tadpole hyobranchial apparatus is a most important factor which determined its further evolution. It seems to have led to the perfection of a new mechanism for action, that is to a proliferation of cartilage and a corresponding reconstruction of the musculature. The most extreme expression of this tendency among the forms is the construction of the hyobranchial apparatus in the tadpoles of the species _Xenopus_ _laevis_. In all of our work, the data obtained on the ontogenesis and the morphology of the hyobranchial apparatus in amphibian larvae and the comparison with the structure of the hyobranchial apparatus of stegocephalids and crossopterygian fishes confirm the theory of monophyletic origin of the Tetrapoda.

In our investigation of the evolution of the hyobranchial apparatus in amphibian larvae we examined the evolution of the caenogenetic system, i.e., the complex provisional or temporary adaptations which serve only in the course of the larval period of life. At the time of metamorphosis, the hyobranchial apparatus becomes subject to the basic morpho-functional reconstruction. The mechanism for the evolutionary transformation of temporary traits has not previously been investigated. The proofs gathered from our work that embryonic adaptation evolved by means of phyloembryogenesis. They also let us extend the boundaries of the theory of phyloembryogenesis. Now it can be said that not only the characteristics or traits of definitive organization but also of embryonic adaptation are subject to the ordered manner of development which was determined by A. N. Severtov.

HERPETOLOGY

by I. S. Darevskii

From Chapter Nine, Vertebrate Zoology, in Fifty
Years of Soviet Science and Technology, Moscow,
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Interest has increased in the past ten years in the study of our native amphibian and reptilian fauna. Current works in this area represent a continuation of the traditional herpetological research of Russian zoologists of the pre-revolutionary period, characterized by the three-volume monograph of A. M. Nikol'skiy, "Reptiles and Amphibians" (1915-1918), from the series "Fauna of Russia". This basic summation, however, demonstrated an obvious lack of data on our native herpetofauna, especially with regard to its ecology.

By the end of the 20's the basic direction of our herpetological research was more or less clearly determined, i.e., faunistic research and, closely related to it, work on classification and zoogeography, the study of the mode of life of the separate species and morphological-ecological research, all undergoing further development in subsequent decades. In addition, at the present time the question of the study of amphibians and reptiles as intermediate and reservoir hosts for some parasites of man and useful animals has become more urgent, and the study of poisonous snakes as producers of poisons has found growing applicability in our pharmacological industry.

Beginning in the 20's and 30's there was a broad flowering of faunistic research embracing the whole of the territory of the Union, which assisted in pinning down the geographic distribution of many species of amphibian and reptile (see the collected articles of S. A. Chernov, 1945, and of P. V. Terent'yev, 1957).

For a long time and most thoroughly the territory of the European part of the USSR had been covered in the herpetological sense. More than one hundred special works had been dedicated to the distribution and in part to the ecology of the species found there.

The rich amphibian and reptilian fauna of the Caucasus has repeatedly attracted the attention of our herpetologists. Reports and private studies have been published on the herpetofauna of Armenia, Azerbaidjan, Georgia, Dagestan and other regions of the Caucasus and Trans-caucasus. A great contribution has been made by Soviet experts toward the study of the extremely interesting herpetofauna of Kazakhstan and Central Asia. The latter was made possible as a result of the increase of native cadres of zoologists and the activity of the zoological institutes of the republican academies. Much research has also been conducted on the herpetofauna of Siberia and the Far East.

A series of varieties, including several new ones in the study of lizard species and subspecies, were first recorded in our country. While A. M. Nikol'skiy reported only 23 species of amphibian and 127 species of reptile, at the present time in the USSR 33 of the former and 132 of the latter are known.

The distribution of several rare species of lizard and snake was examined, only 1-2 specimens of which had earlier been identified, and many of which were discovered far beyond the limits of the boundaries of their previously known habitats. It was not excluded that some of these findings, especially in the southern regions of the USSR, resulted as a consequence of the generally observed warming of the climate and subsequent expansion of the habitat of the heatloving varieties toward the north.

The basic results of the aforementioned increased faunistic research and questions of the formation of herpetofauna of the many natural zones of the USSR are reflected in relevant sections of the five-volume work - "The animal world of the USSR", compiled by the Zoological Institute of the Academy of Sciences of the USSR (1936-1958).

It should be noted that along with their study of native fauna Soviet experts also devoted part of their attention to the herpetofauna of some foreign countries (see, for example, A. G. Bannikov, 1958).

With the usual effect of the accumulation of knowledge concerning the distribution of amphibians and reptiles, a broadening of the research in the field of taxonomy has taken place, which we are even now, however, not developing sufficiently. Primarily, such research has had the task of defining the status of unclear areas in the systematic relationship of groups, i.e., the green frog (Rana), the round-headed lizard (Phrynocephalus), or the Colubridae (adder) snake (Eirenis). In recent times the attention of the taxonomist-herpetologist has been drawn more and more to questions of geographic and population variations of the distinct varieties. Thus P. V. Terent'yev (1957) came to the conclusion that many taxonometric indicators concerning amphibians, considered constant, consist in actuality of a stage in a series of gradual changes now known as clinal variation. Terent'yev even theorized that, in many cases when studying geographic variations, one must renounce the concept of sub-species. S. A. Chernov has published a series of articles on the classification of the various genera of snake of our fauna.

A small number of research projects on zoogeography are being conducted principally on the clarification of the genesis of the herpetological fauna of various regions of the USSR, particularly Central Asia, the Caucasus and Crimea. In the course of these projects attempts are being made to explain in the light of paleogeographic data the abrupt breaking-out from the habitat by some widely distributed species of reptiles. Thus, S. A. Chernov (1954) explained the distribution break-out of some species of lizard and snake in the northern Caspian Sea area by the fluctuation of the latter body during the Quaternary period. I. S. Darevskiy (1959) demonstrated the possibility of the penetration into the Caucasus of the series of Turan (Central Asian)

elements of herpetofauna by means of a dry-land bridge, which at one time united the Apsheronskiy and Krasnovodskiy Peninsulas. The problem of the influence of the glacial period on geographic variability was examined by Terent'yev (1948). The 1949 book by Terent'yev and Chernov presents a zoogeographic outline of all of our native herpetofauna.

A significant place among the works of the Soviet herpetologists is occupied by the study of the biology of amphibians and reptiles, during which much work was done relating to their nutrition. Following the well-known research of N. V. Krasavets (1945-51), dozens of articles have been written on the subject, analyzing the qualitative and quantitative side of the eating habits of many species. In particular, it was shown that there was no really significant selective capability in the feeding habits of the majority of the lizards studied, i.e., the qualitative composition of their food depended in the first place on the makeup of the entomofauna in the biocoenosis, changing relative to the season of the year. Secondly, the nature of the food intake of many species of lizard show a gradual adjustment of eating habits to the consumption of particular types of output during the periods when the latter are most plentiful. In addition, the positive role of the lizard as a destroyer of harmful insects was also clarified. It should be stated here, however, that the broad conclusions drawn by some authors as to the "helpful" or "harmful" roles of one or another reptile in the majority of cases are very artificial, inasmuch as their evaluations are based only on an analysis of the contents of the stomach, completely ignoring either the biomass and the number of living things abroad serving as food for the reptile, or the strength and level of the energy metabolism of the predator itself. Some conclusions are expected from a parallel study of the availability of a specific food supply for the predator and his hunting area.

Data were received from a fishing industry study of frogs and water snakes, and what was of special interest was the fact that there is a lack of food competition between the young of amphibians and young fish.

In recent years for many species of amphibian and reptile the time of gonadal development, the duration of the incubation period, the number of eggs in the clutch or the number of young in the litter, the time of the onset of sexual maturity, etc., have been determined. A portionality (sic) of the clutch of a series of arid and semi-arid lizards was discovered, and the existence in some of these of a second, autumnal peak in gonadal development, accompanied by a renewal of sexual activity in the Fall. During a parallel study of the seasonal dynamics of the fatty body and the gonad of the lizard, a connection between the nature of nutrition and reproduction was established.

New in principle for reptiles and higher vertebrates in general was the discovery of normal parthenogenic reproduction, and related to it polyploids in some Caucasian rock lizards of the polymorphic species - Lacerta saxicola. Many problems, such as the dynamics of numbers, seasonal and daily migrations, "homing instinct", individual dwelling areas, alarm procedure, growth, age and some other aspects of amphibians and reptiles are still not being studied sufficiently. A continuation is necessary of the work begun by A. A. Sergeyev on body temperature and thermoregulation in reptiles.

The study of the dynamics of the development and morphology of amphibians was introduced in our country primarily in the work of I. I. Schmalgauzen and his school, in significant part collected in his monograph "The Genesis of Terrestrial Vertebrates" (1964). The study of the phylogeny of present-day lizards on the basis of an analysis of the musculature of the extremities is being successfully carried forward by V. B. Sukhanov at the Paleontological Institute of the Academy of Sciences of the USSR, which has made some interesting additions to the classical scheme of Kemp. He has done original research on the locomotion of lizards and has clarified the role of the latter in the formation of the system of movement of terrestrial vertebrates in general. To the functional morphology of reptiles is dedicated several works of I. S. Darevskiy, who first reported, in particular, on the skin glands of lizards and explained some of the principles of the evolution of the concrescence of the eyelid in the Lacertae and Scincidae.

The biomechanics of reptilian armor has been studied by L. I. Khozatskiy (1948-1964).

Numerous works on the fossil types of amphibians and reptiles discovered on the territory of the USSR are collected in a volume devoted to them, i.e., "The Fundamentals of Paleontology (1964)".

The bases for the study of poisonous animals and their poisons were already established in our country in the first years of the Soviet era by Ye. N. Pavloskiy. This lead has been carried forward with success (Bogdanov, 1965). Work on the study of poisonous snakes, the biochemistry and toxicology of their poisons has been effectively conducted primarily in the Institute of Zoology and Parasitology of the Academy of Sciences of the Uzbek SSR. Here were developed the optimal conditions for the maintenance of poisonous snakes in nursery conditions, which noticeably increased the production of snake poisons. Several studies of this institute were published in the collection "Questions of Herpetology and the Toxicology of Snake Poisons (1966)". Our national pharmacological industry has done well in the production of the requisite anti-snakebite serums and other medicinal preparations, for the production of which the poisons of many types of snake of our native fauna were used.

Amphibians and reptiles are apt subjects for the numerous research projects in the fields of physiology, biochemistry and cytology, particularly in the fine work of B. P. Ushakov and his colleagues on the thermostability of the cells and proteins of amphibians and lizards.

In prospect for Soviet herpetology is a broad field of activity in the area of each of the aforementioned categories. In the Far East and the southern regions of Central Asia we can still anticipate the discovery of new species of native fauna. On the agenda in the field of taxonomy have been placed the study of intraspecific and population variability of a growing number of varieties and the formation of objective phylogenetic systems. A complete review and many "hard jobs" are ahead involving the taxonometric relationships of groups, i.e., the roundhead and Eremias among the lizards. A broadening of ecological research is needed, especially work in the field of population ecology with the application of morphological, physiological, biochemical and other modern methods. Also necessary is the study of the biocoenotic role of amphibians and reptiles, and an examination of the ecological and physiological differences of closely related species living in the same biotype. Much interesting and primarily new material is expected as well from morpho-ecological research. The use of amphibians and reptiles as biological models during research in the field of bionics is also anticipated. For many reasons both classes of animal are also especially well suited for the study of variety-generation and questions of species.

Our national herpetology has published a series of monographs, recognized even at home for their broad scope. The "Guide to Reptiles and Amphibians" of P. V. Terent'yev and S. A. Chernov, the third edition of which (1949) was translated into English, is a comprehensive summary of the data on classification, distribution and the mode of life in the amphibians and reptiles of the USSR. The monograph of P. V. Terent'yev, "The Frog (1956)" has become a reference book for Soviet herpetology. His "Herpetology (1961)" was the first textbook of world herpetology.

In the last two decades alone in our country four doctoral and fifteen master's dissertations on herpetological themes have been successfully defended. Corresponding subjects are ever more in evidence in the scientific zoological institutes and the departments of the Institutes of Higher Learning (VUZ).

In 1964 in Leningrad the First, and in 1966 the Second All-Union Herpetological Conferences were convened, gathering together many participants from the various ends of the Earth. The conferences determined and then discussed the course of further development of herpetological research in our country.

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"THE INFLUENCE OF SOUND ON THE BEHAVIOR OF AMPHIBIANS AND REPTILES"

by

Charles M. Bogert

From "Animal Sounds and Communications," A.I.B.S.

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PATHO-MORPHOLOGICAL AND HISTOCHEMICAL CHANGES IN THE ORGANS OF TURTLES ON BOARD THE "ZOND-5" PROBE

by N. A. Gaidamakin, G. P. Parfenov, V. G. Petiukhin,
V. V. Antipov, P. P. Saksonov, and A. V. Smirnova

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Translated from Russian by Morris D. Friedman

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Some reptiles, particularly turtles, are convenient for specific biological investigations in space for a number of reasons. The organization level in these animals is not much lower than in mammals, moreover, no complex special systems are needed, and they may be fixed rigidly on board the spacecraft. Taking account of seasonal differences, the subject is accessible for research at any time of the year. For these general considerations, tests with turtles were included in the space biology research program.

Steppe turtles (Testudo horsfieldi Gray) were on the "Zond-5" which flew around the moon together with other biological subjects. In all 8 adult turtles 6-7 years old, and 340-400 g in weight, were examined. Two animals (the test group) were on the probe (Fig. 1), two (the control group) were transported to the cosmodrome and back, and four turtles (intact) were in a vivarium.

The animals were delivered to the laboratory two months before the beginning of the experiment. During this time, the turtles were weighed repeatedly, the peripheral blood was investigated and an EKG was recorded at three standard terminals. Moreover, the alimentary activity of the animals was observed carefully. Their daily ration was meat (2 g), cabbage (10 g), carrots (10 g), bread (10 g).

The experimental animals were placed in individual narrow cages on the probe, in which they were practically unable to move. Contained in these same cages were the control animals. The experimental and control turtles received no food or water throughout the whole experiment, the intact turtles were in free cages in a customary environment.

The turtles were put on board the "Zond-5" on 2 September 1968. From that time on they ceased to receive food. As is known, lift-off was on 15 September. After the circumlunar flight and a return to earth, the probe splashed down on 21 September in the Indian Ocean. The subject reached Bombay 3 October, and was returned to Moscow on 7 October. Patho-morphological investigations on the turtles were carried out on 11 October.

As is seen from the cited sequence of carrying out the experiment, the test animals were subjected to 39 days of starvation, flight factors lasting 7 days, the effect of a tropical climate and conditions associated with a stay in the ocean after splashdown, and with transportation via ship and aircraft. According to results of dosimetry conducted on the probe, the total radiation dose received by the test animals did not exceed 3.5 rad.

Excluded from the control group was the influence on the animals of not only space flight factors, but also the tropical climate and additional transportation conditions.

The biological effect of the complex of space flight factors and other conditions originating during the experiment was estimated by using some hematological tests, electrocardiography, a number of patho-morphological and histochemical methods of investigation. The electrocardiography was carried out prior to the beginning of the experiment, after circumlunar flight, and return of the animals to the laboratory.

During dissection of the animals, combined tissue blocks from pieces of intestine, spleen, testes and seminal vesicle, liver, kidney, and heart were formed by an original method developed specially for subsequent histological and histochemical investigations.

The principle behind the method of combined tissue blocks is that an organ taken from the test animal is glued to filter paper together with the same organ removed from a control and intact animal. The tissue blocks thus prepared are frozen in dry ice and combined sections are prepared in a cryostat for histochemical investigations. Analogous blocks, not frozen, are placed in a fixing mixture, carried out by dehydrating and compressing media to obtain sections treated by histological methods. Preparation of the sections on a microtome of combined blocks, enclosed in paraffin and stained by appropriate methods, was carried out in the customary order. Therefore, under one cover glass we had an identical thickness, prepared under identical conditions, of combined sections of organs of the different animals. This permitted a reliable comparison between the structural changes in the organs of the test, control and intact animals. The sections were colored by hematoxylin-eosin, ribonucleic acid (RNA) was revealed by methyl green pyronine according to Brash, glycogen according to Shabadash, lipides by scarlet, iron according to Perls. Also assayed were the activities of succinate-dehydrogenase (SDG) according to Nachlas et al., monoaminooxidase (MAO) according to Glenner, alkaline phosphatase (AP) according to Gomor (E. Pierce, 1962), and of alpha-glycerophosphate dehydrogenase according to D. Quadlino et al. (1960) in a modification by R. P. Nartisissov (1968).

Externally, and in behavior, the animals of all three groups displayed no differences at the time of examination.

The alimentary activity in both the test and control animals flying to the cosmodrome and in the intact animals in the vivarium was identically high. Weight loss of the animals that flew in the probe was about 10%. Weight loss of the control animals was only 5%. No substantial differences in the peripheral blood of the examined animals was detected.

An analysis of the electrocardiograms recorded at different times before and after the flight did not disclose any noticeable differences in the cardiac activity of either the test or control animals. According to our data, the frequency of cardiac contraction in the animals in the active

state in the vivarium fluctuated between 14 - 48 contractions per minute. A definite arrhythmia evidently of vague origin is characteristic for turtles. In our observations the R-R interval fluctuated between 20-49 sec. The repetition of cardiac contractions by 10-12 beats per minute occurred under a greater stimulus (injection by a needle in the gastrocnemius). Return of the pulse frequency to the original level occurred relatively quickly, in about 1-2 minutes.

On the 21st day after termination of the flight an EKG was recorded and some results of this investigation are presented in Table 1 and Fig. 2.

TABLE 1. CHARACTERISTICS OF CARDIAC ACTIVITY OF TURTLES WHO FLEW IN "ZOND-5"

No.	Animal Number	Heart Contraction Frequency per Minute	R-R Interval in sec. Drawing Rate 15 mm/sec
1	22 Test	28	30-49
2	37 Test	28	32-34
3	49 Control flying to cosmodrome	32	29-31
4	47 Control in vivarium	30	22-23

As is seen from the Table and the EKG, no substantial differences between the test and control were detected in a number of the indices studied, (cardiac contraction frequency, R-R interval). As regards the change in the individual EKG peaks, it is impossible to make any definite conclusions because of insufficient data.

In a macroscopic investigation of the internal organs it was clear that the thickness of the intestine diminished over the whole extent of the test and control turtles. The liver surface in the test animals was intensely brown; in the intact turtles, it was dark cerise; and was intermediate between these colors in the control animals.

Significant differences were observed in a comparative microscopic investigation of the organs of the experimental and the intact turtles. The diameter of the intestine and the thickness of the muscle layer diminished in the test animals, the villi were shortened in places (Fig. 3). The mitotic activity of the epithelial crypts was suppressed. Certain epithelial cells had a pycnotic nucleus (Fig. 4). The cells of the stroma of the villi in the cytoplasm and some epithelial cells contained clumps of brown pigment not discernable in the intact animals. The content of the PAS - positive substances was diminished (Fig. 5). The number of beaker-like cells diminished, particularly in the depth of the crypt, the MAO and alpha-glycerophosphate dehydrogenase (GFD) activity decreased.

The spleen follicles were diminished and none contained mitotic figures. Some lymphocytes had pycnotic nuclei, which were not noted in the intact animals.

The seminiferous tubules in the testes were diminished in diameter (Figs. 6, 7), and brown pigment accumulated in the interstitial tissue. It was manifest only in individual cells in the intact animals. This pigment was also detected in many remaining germ cells, had a dark orange tint in uncolored preparations, gave a negative reaction on iron, and was colored moderately by sudan. Conglomerates of the pigment possessed birefringence. The number of germ cells and the concentration of RNA therein diminished considerably (Figs. 6, 7). The SDG activity increased somewhat, but the MAO and alpha-GFD activity decreased.

The seminal vesicles of the test turtles were destroyed (Fig. 8), their lumen was filled with spermatozoids (Fig. 9) in the intact animals. The RNA concentration and ferment activity in the seminal vesicles was changed as compared with the intact control animals exactly as in the testes.

A diminution in the size of the hepatocytes and their nuclei was observed in the liver, the cell cytoplasm became basophile (Fig. 10). The quantity of brownish, big-clump pigment was increased at places where the endothelial-reticular cells accumulated, and dustlike granules of trivalent iron increased in the lumen of the bile capillaries. Ribonucleic acid was contained in the nucleoli of liver cells and in a small quantity in the perinuclear zone. The RNA concentration was negligible, but higher than in the intact animals. The glycogen content (Figs. 11, 12) in not only the hepatocytes but also in the peripheral blood cells was also elevated, principally in the leucocytes and in the free reticular cells in the lumens of the vessels. Fat vanished from the liver cells, while it appeared in a significant amount (Fig. 13) in the intact animals. In the liver of the intact turtles there was almost no outcropping of formazane corresponding to the SDG activity, they appeared in some hepatocytes in the test animals, in many Kupfer cells, the vessel walls, and the bile ducts; the AP activity was also elevated. On the other hand, the MAO activity in the hepatocytes was clearly reduced (Fig. 14), and suppressed altogether in the peripheral blood elements.

The volume of cell nuclei of the epithelium of the twisted ducts was diminished in the kidneys, some nuclei became pycnotic, the cell outlines unclear, grains of brown pigment sometimes appeared in the cell cytoplasm, which gave no reaction with iron and was not colored by sudan, and dustlike granules of an iron-containing pigment appeared. Moreover, RNA appeared more weakly in the nucleoli in the epithelium cells of many twisted ducts. The SDG activity, and to a lesser degree, the AP activity, was elevated, while the MAO and alpha GFD activity was lowered.

No changes were noted in the hearts of the test animals.

The same changes were outwardly noted in the control turtles which reached the lift-off point of the probe and were subjected only to the effect of hunger, as in the test animals. The degree of the changes in some organs was less evident. There were less cells with hyperchromic nuclei in the epithelial crypts of the intestine in the control turtles, single mitoses were evident in the crypts of one of the turtles. The mitotic activity of the cells was noted also in the spleen follicles, which while they were diminished as compared with the spleen follicles of the intact animals, they were still somewhat coarser than in the test animals, i.e., the size of the ducts and the number of germ cells were diminished, and an increase in lipofuscin was observed in the interstitial tissue. In the seminal vesicles of the control animals, in contrast to the test turtles, spermatozoids were present (Fig. 15). Moreover the SDG, AP, alpha GFD activity in the testes and walls of the seminal vesicles changed slightly. Less definite changes in the fermentative activity, particularly of MAO, were detected in the liver also.

Therefore, the diameter of the intestine, the thickness of the muscle layer, and the length of the villi of the mucosa diminished in the test and control turtles. Cells with pycnotypic nuclei and lipofucsin inclusions appeared in the epithelial crypt, the number of beaker-like cells diminished. All this indicates the development of atrophy of the intestine connected with starvation. Its functional activity was reduced, as shown by the suppression of the mitotic activity of the epithelial crypts, and the reduction of the RNA concentration in the epithelial cells of the mucosa.

Starvation and dehydration of the organism caused changes of atrophic character in other organs also: disappearance of lipids from the liver; diminution in the magnitude and volume of liver and kidney cells; accumulation of lipofucsin in these organs, particularly in the interstitial tissue of the testes; diminution in the diameter of the sperm channels and the number of germ cells of the spermatogenic epithelium; disappearance of spermatozoids from the seminal vesicles.

In our opinion, a certain increase in the RNA concentration and the glycogen content in the liver cells is associated with the decrease in the cell volume and with their dehydration.

The rise in iron content in the liver and kidneys is possibly associated with hemolysis of the erythrocytes, as well as with the diminution in its demand for hematopoesis purposes, which are suppressed during starvation.

Atrophy is caused by changes in the fermentative activity of the tissues: in the intestine walls, in the testes, liver and kidneys the SDG activity increases, as to a lesser degree does the AP activity, while the MAO and alpha-GFD activity is reduced.

However, all the listed changes in the turtle organs cannot possibly be explained by just the effect of starvation. The fact is that changes were less definite in the control turtles which were starved at the same time as the test animals. Thus, pycnotypic cells were rarely encountered in the epithelial crypt of the intestines in the control animals; single figures of mitosis could be encountered. Spermatozoids were detected in the seminal vesicles in almost the same quantity as in the intact turtles. The diminution in follicle volume was less definite. Mitotic cell fission was manifested in some follicles. The activity of the ferments in the tissues also changed less noticeably.

Apparently such a difference should be explained by the additional effect of the space flight factors. A higher degree of reduction in the MAO activity in the organs of the test animals can indicate this in particular. As is known, monoaminooxidase is a self-oxidizing ferment, participating in the regulation of the exchange of biologically active compounds, including serotonine. The serotonine level in the blood changes under the influence of individual flight factors such as overloads, vibrations, penetrating radiation (V. V. Parin, et al., 1964-1965; V. V. Antipov, et al., 1967).

If peculiarities in ecology, the quite definite seasonal fluctuations in physiological activity which is elevated in turtles during the warm part of the year, are taken into account, then it is here impossible to exclude also the influence of residence of the animals under tropical climate conditions. Also, ship transportation conditions from the splashdown point could be important.

Therefore, the results obtained indicate that the complex of space flight factors combined with starvation caused changes of atrophic nature in the turtle organs: a diminution in the intestine walls and in the diameter of the sperm channels, in the volume of liver and kidney cells, and in the number of germ cells of the epithelium of the testes, an accumulation of lipofucsin in the organs, suppression of the mitotic activity of the epithelium of the mucous of the intestine, and the hematopoetic tissue of the spleen. Also the fermentative activity of the cells changed. Starvation and transportation to the cosmodrome resulted in less definite atrophy of the tissues.

A comparison of the changes occurring in the test and control animals showed that the fundamental structural changes in the turtles were caused by starvation, and to a lesser degree, by space flight factors.

FIGURE LEGENDS

Fig. 1. Turtles Nos. 22 and 37 on board the "Zond-5" during flight to the moon.

Fig. 2. Electrocardiogram of the turtles (Second terminal, tape rate 30 mm/sec). 1 - Turtle No. 22 (Test); 2 - Turtle No. 47 (control)

Fig. 3. Intestine. Combined tissue block. Intestine diameter and layer thickness diminished, villi shortened in test turtles (Brashe, lens enlargement.)

Fig. 4. Test turtle intestine. Cells with hyperchromic nuclei, some of which "drop out" in intestine lumen, are seen in the epithelium crypt (Hematoxyline-eosine. Gom. IV, ob. 40, 800 X magnif.)

Fig. 5. Intestine. Combined tissue block. In test turtles PAS - positive reaction deep in the crypt clearly weakened (Shabadash, lens enlargement.)

Fig. 6. Testes of turtles on board the "Zond-5". Duct diameter diminished, embryo epithelium thinned, united by cells. Considerable outcrops of brown pigment in interstitial tissue (Brashe, Gom. VI, ob. 20, 240 X)

Fig. 7. Testes of intact turtles. Compare with Fig. 6 (Brashe, Gom. VI, ob 20, 240X)

Fig. 8. Seminal vesicles of turtles on board the "Zond-5". Spermatozoids missing from lumen. (Brashe, GOM. VI, ob. 16, 115X)

Fig. 9. Seminal vesicles of intact turtles in the vivarium. Lumens filled with spermatozoids. (Brashe, Gom. VI, ob. 16, 115X)

Fig. 10. Liver. Combined tissue block. In turtles on board the "Zond-5" the cell size diminished, their cytoplasm is darker and basophilic; the amount of pigment is increased (Hematoxyline-eosine. Gom VI, ob. 40, 470X)

Fig. 11. Liver of intact turtles. Glycogen in cells in moderate quantity (Shabadash, Gom. VI, ob. 40, 470X)

Fig. 12. Liver of test animals. Glycogen content increased. Compare with Fig. 11. (Shabadash, Gom. VI, ob. 40 470X)

Fig. 13. Liver. Combined tissue block. In turtles on "Zond-5", no fat in cells. (Scarlet red. Gom. IV, ob. 40, 800X)

Fig. 14. Liver. Monoaminooxidase activity in turtles on the "Zond-5" reduced (a) and significant (b) in intact animals. (Glenner et al., Gom. VI, ob. 16, 115X)

Fig. 15. Seminal vesicles of turtles at the cosmodrome. Small quantity of spermatozoids remain in lumens. (Brashe. Gom. VI, ob. 16, 115X)

The figures are not reproduced in this translation.

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COMMENTS ON THE TYPES AND SOME OTHER INTERESTING AMPHISBAENIANS IN THE COLLECTION OF THE ZOOLOGICAL INSTITUTE AT LENINGRAD

by Carl Gans

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In 1881 Alexander Strauch published what he described as a preliminary report of his studies of amphisbaenians--a small group of reptiles allied to the lizards and snakes. This important paper was based upon a reexamination of most of the types in European museums. Strauch's success in clarifying the concept of a number of species rested to a large extent upon his willingness to travel in order to examine the original types rather than to expend major efforts in extrapolating a concept from the often inadequate original descriptions. Four of the six new species described in his study were based upon specimens then in the collection of the St. Pétérsbourg Academy of Sciences, which is now the Zoological Institute, and have apparently not been reexamined until this time.

It is truly unfortunate that Strauch was only able to publish the text of his revision (both in the Bulletin and the Mélanges Biologiques of the Academie des Sciences de St. Pétérsbourg) but that the illustrations could not be printed. His intention to include them in a later, perhaps more extensive study is indicated by the existence in the library of the Zoological Institute of a plate labelled A. Strauch, Amphisbaeniden Tab. I and Mem. Acad. Sci. VII Serie. This document includes views of nine species (Fig. 1, *Trogonophis wiegmanni*; Fig. 2, *Bipes canaliculatus*; Fig. 3, *Amphisbaena fuliginosa*; Fig. 4, *A. alba*; Fig. 5, *A. pretrei*; Fig. 6, *A. leucocephala*; Fig. 7, *A. mertensi*; Fig. 8, *A. vermicularis*; Fig. 9, perhaps *A. prunicolor*--this illustration does not seem to pertain to any of the forms described in Strauch, 1881), but the paper for which it was intended was apparently never published.

Another important collection was apparently purchased in 1885 from the "Linnea" Institute. The small collection ascribed to "Paraguay, Amer. merid." included five important amphisbaenians that were catalogued with the ascription "Original" by names described by Boettger (1885) as from a "Linnea" collection. As best can be determined now, the "Linnea" was a commercial company which purchased specimens from foreign collectors (in this case, H. Rohde), had them identified and published on (often paid for on a "per species" basis), and then sold the specimens to various museums such as London, Wien, and apparently Leningrad. Until 1885, Linnea was located in Frankfurt am Main, but records in the British Museum disclose that it moved to Berlin in that year and apprently became defunct about a decade later (cf. Gans, 1966a).

My colleague, Dr. Ilja Darevsky, had earlier informed me of the existence in the Leningrad collection of five specimens of amphisbaenids purchased from "Linnea" in 1885 and ascribed to the five new species described in Boettger's 1885 paper. Since Boettger had only a single specimen of each form, since no other specimens with these data were found in any European museum, and since it was unlikely that two collections of equivalent composition would appear in a single year, I have already predicted (Gans, 1966a, 1967) that Strauch acquired all five types. It is now possible to confirm this. Not only are the entries marked "original" in the old Academy catalog, but the specimens agree with the original descriptions in many significant details.

The Leningrad collection, furthermore, contains the holotype of Nikolskij's (1907) *Diplometopon zarudnyi* deposited there together with the rest of the Iranian collection described by that author. Besides these specimens Strauch was also able to exchange paratypes and syntypes of various species described by Boulenger and others. All of these are referred to in the list given below, together with their current status and comments upon the specimens where indicated. The sequence follows that of my checklist of the Amphisbaenia (Gans, 1967), except for the species of *Leposternon*, which are listed in the order of their description.

I am most grateful to my colleague, Dr. Ilya Darevsky for permission to examine these materials in his care, for hospitality during my stay in Leningrad, and for arranging to translate these notes.

LISTING

TROGONOPHIDAE

Pachycalamus brevis Günther, 1881 (Z.I.L. No. 6678), from Socotra, presumably a paratype exchanged by the British Museum in 1885.

Diplometopon zarudnyi Nikolski, 1907 (Z.I.L. No. 10341), labelled "East Persia, Djibel-Tnie, neighbourhood Nasrie and Achvas." Holotype.

AMPHISBAENIDAE

Amphisbaena albocingulata Boettger, 1885 (Z.I.L. No. 6660), from "Paraguay." Holotype purchased from Linnea, 1885. The specimen has 193 body, 3 lateral, and 24 caudal annuli, 16 dorsal and 11-12 ventral segments per midbody annulus, and a snout-vent plus tail length of 72 plus 10 mm. The posterior part of the head shields are asymmetrical as is the mentomalar region. Other characteristics are in good agreement with the description and the name is properly assigned as *Amphisbaena prunicolor albocingulata* (cf. Gans, 1966b).

Amphisbaena fenestrata (Cope), 1861 (Z.I.L. No. 5106), from "St. Jean." marked as exchanged from Reinhardt (Copenhagen), 1878; may be one of the paratypes of *Amphisbaena antillensis* Reinhardt and Lütken, 1862.

Amphisbaena gracilis Strauch, 1881. The holotype of this species is supposed to be Z.I.L. No. 5517, without locality. The specimen appears to have become lost or destroyed which is unfortunate since the description in not immediately assignable and the status of the name remains in doubt.

Amphisbaena leucocephala Peters, 1878 (Z.I.L. No. 5569), from Bahia. This specimen, correctly identified by Strauch, is only the third known individual of the species (cf. Gans, 1965). The specimen is faded, but it is still noticeable that the head was light colored and the darker brown pigment covers the dorsal surface from the neck to the tail only. The specimen has 233 body, 4 lateral and 25 caudal annuli with the autotomy site on the 6th caudal. Supra- and infralabials number 4 and 3, the first and second postgenial rows have 2 and 5 segments, and there are 9 postmalars. Ten precloacal pores occur, and a midbody annulus has 19 to 21 dorsal and 20 to 21

ventral segments. Snout-vent plus tail length is 314 plus 45 mm and midbody diameter 12 mm. Particularly the yellow head, the low number of body annuli, the high number of precloacal pores, and the relatively short tail length of this, now somewhat dried, specimen are in good agreement with those for the two previously reported specimens, and the former differs mainly in the enlargement of the post-frontal head segments, which are quite small in the third specimen.

Amphisbaena mertensi Strauch, 1881 (Z.I.L. No. 311). The holotype actually has 230 body, 5 lateral and 27 caudal annuli (as contrasted to the 231, 3, 32 in the original description). All other meristic characters are in excellent agreement with the original description. Rather than being only light brown dorsally and lighter ventrally, as stated by Strauch, this specimen indeed shows the anterior half of each segment pigmented all around the trunk. The name clearly belongs with the species to which it has been assigned.

Amphisbaena pretrei Duméril and Bibron, 1839 (Z.I.L. Nos. 1197, 1199, 1200, 5563 from Bahia; Nos. 1202, 1203, 5563 without data). Several of these specimens appear to have the pigmentation more clearly expressed than those previously examined (Gans, 1965). The anterior part of the body has the individual segments markedly pigmented, while the zone lateral to the cloaca shows each segment with a dark dot. Both are characteristics seen also in A. vermicularis.

Amphisbaena ridleyi Boulenger, 1890 (Z.I.L. No. 7856), from Fernando Noronha, Brazil may be part of the original syntype series and hence a lectoparatype. It was exchanged with the British Museum in 1889.

Amphisbaena s. steindachneri Strauch, 1881 (Z.I.L. No. 312). The lectoparatype bears only the designation Brazil and is in exceedingly rotten condition. As far as can be determined the assignment is correct.

Blanus s. strauchi Bedriaga, 1884 (Z.I.L. No. 5903). The collection contains a single lectoparatype obtained from Bedriaga and in good agreement with the original description.

Blanus s. bedriagae Boulenger, 1884 (Z.I.L. No. 6679). This syntype from "River Xantus, Asia Minor" is in good agreement with the original description.

Leposternon rostratum Strauch, 1881 (Z.I.L. Nos. 314 and 315). The first of these two syntypes collected in 1837 by Luschnath is here named lectotype since Strauch indicated that it formed the basis for the description. The head scalation of the lectoparatype is considerably more irregular. For reasons given in the revision of the genus (Gans, 1971) the name belongs in the synonymy of Leposternon infraorbitale.

Leposternon crassum Strauch, 1881 (Z.I.L. No. 316). The holotype from "Basilien" is in good condition and its counts agree quite well with those of the original description. Analysis of the characteristics suggests that this is a very large specimen of Leposternon microcephalum probably taken in the vicinity of the city of Rio de Janeiro and it has hence been placed in the synonymy of that species (Gans, 1971).

Leposternon guentheri Strauch, 1881 (Z.I.L. No. 313). The holotype is in good condition and its characteristics suggest that it is a specimen of of Leposternon microcephalum presumably taken from the frontier region between Rio Grande do Sul and Corrientes (Argentina) (Gans, 1971).

Leposternon boulengeri Boettger, 1885 (Z.I.L. No. 6656). This is the first of four names in this genus described by Boettger and assigned to specimens derived from"Paraguay." The type is in good agreement with the original description and the name belongs in the synonymy of Leposternon microcephalum (Gans, 1971).

Leposternon strauchi Boettger, 1885 (Z.I.L. No. 6655). No specimen with this label was initially found in the collection. However, there were two specimens labelled L. onychocephalum (Z.I.L. No. 6653) with one of the labels in the new format using the Cyrillic alphabet. Since Boettger described only one specimen of onychocephalum and the specimen with the new lable agrees exactly with Boettger's description, it is assumed to be the holotype. The name belongs in the synonymy of Leposternon microcephalum (Gans, 1971).

Leposternon affine Boettger, 1885 (Z.I.L. No. 6654). The holotype agrees well with Boettger's description and the name belongs in the synonymy of Leposternon microcephalum (Gans, 1971).

Leposternon onychocephalum Boettger, 1885 (Z.I.L. No. 6653). The holotype is in good agreement with the original description and the name belongs in the synonymy of Leposternon microcephalum (Gans, 1971). This or some of the other names here assigned to Lepostenon microcephalum might be resurrected if it should ever prove desirable to assign names to geographic races of Leposternon microcephalum.

[Please consult the original paper for the literature citations in the text.]

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STUDIES OF REPTILE LIFE IN THE ARID SOUTHWEST

by

L. M. Klauber

Bulletin no. 14, San Diego
Zoological Society, 1939

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ARTHUR NORRIS BRAGG

(1897-1968)

BIOGRAPHY AND BIBLIOGRAPHY

by

C. J. McCoy
(Carnegie Museum of Natural History)

and

Jeffrey Howard Black
(Oklahoma Baptist University)

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No. 27

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ARTHUR NORRIS BRAGG
(1897-1968)

"Regardless of how what I have done in my thirty or more years of the study of Amphibia in Oklahoma may appeal to later generations, of what false deductions and inadequate interpretations may appear in my papers or of the many mistakes made, anyone interested in the development of natural history in the Southwest must necessarily take what I have done (good, so-so, or bad) into account."[1] The author of these humble words, Arthur Norris Bragg, was born in Pittsfield, Maine on 18 December 1897, and died in Norman, Oklahoma on 27 August 1968, less than two months after his retirement from active teaching at the University of Oklahoma.

Arthur N. Bragg was the fourth child of Nathan and Emma Bragg. When Bragg was six years old his father died, and his mother was forced to support herself and her children. His early schooling was irregular, because the family had to move frequently from place to place, living where Emma Bragg could find work. Because of this unsettled life, his interest in unpopular things, and his clumsiness at group activities he had few friends and was never popular as a boy. But life in rural Maine provided ample opportunity for early development of an interest in observing nature. At the age of eight he first heard a strange sound in a roadside ditch, which in later years he identified as the call of Rana clamitans melanota. He recalled being much impressed at age nine by his first Clemmys guttata, which he called his "polka-dotted turtle."

Bragg's academic progress was slowed by almost overwhelming financial difficulties, but he never gave up his goal of getting a college education. He graduated from highschool at 21, and entered Bates College, in Lewiston, Maine in 1919. During these years he supported himself by working as a chef at summer resorts in Maine and New Hampshire, as a cook for a logging crew, and by working in a wooled factory, among other jobs. Following his sophomore year he spent one year as principal of a grade school, then returned to graduate from Bates in 1924. Bragg married Mary Kierstead on 24 December 1924.

The next year Bragg went to Johns Hopkins University, where he became interested in protozoans after taking classes under H. S. Jennings and S. O. Mast. After one year at Hopkins he took a job as Assistant Professor of Biology at Marquette University. During an eight-year stay at Marquette his interest in invertebrates broadened, and he completed the manuscript for a textbook, unfortunately never published, on invertebrate zoology. One summer was spent on the Maine coast, making illustrations for the book from living animals.

Leaving Marquette, Bragg went to Boston University for his M.A., and studied animal behavior and entomology. His thesis topic was food vacuoles and selection of food by Paramecium, and his first publications dealt with Paramecium. Bragg entered the University of Oklahoma in 1934 to work on a Ph.D. under A. Richards. He collected his first breeding pairs of Bufo cognatus in April, 1935, for research on the mitotic cycle and mitotic distribution in early embryos. During the research for his Ph.D, which he received in 1937, Bragg found yolk platelets in amphibian eggs and developed a technique for determining the amount of cell division occuring at various places in an embryo of any stage. This method (mitotic index) had never been applied to any amphibian, nor to any embryo derived through holoblastic cleavage. His findings were published in well-known journals in 1938 and 1939, yet the general disregard of this work by others bothered him throughout his life.

During the early days in Oklahoma two events of great importance occurred in the life of A. N. Bragg. One was a developing friendship with Charles Clinton Smith, Sr., and the other was the start of his interest in the genus Scaphiopus. In Smith, Bragg found an enthusiastic and sympathetic associate, and their joint field trips set a pattern for the remainder of Bragg's life. In later years he frequently told of the collecting trips when they would be out for days, catching naps in corn fields or in the weeds beside a countyroad during the day, and hunting amphibians all night. Regardless of how many hours he went without sleep, Bragg was never late for his classes, sometimes returning with just enough time to clean up and go to the classroom. Bragg's interest in spadefoots started unexpectedly. He had thousands of Bufo cognatus tadpoles in a large tank, and agreed to share the tank with another graduate student, Minnie Trowbridge, who was studying the development of Scaphiopus. To their amazement, the Scaphiopus tadpoles ate the Bufo tadpoles: thus began the interest in Scaphiopus that became the dominant theme of Bragg's scientific work.

In the early 1940's Bragg developed progressive deafness, and had to wear a hearing aid. During the last 15 years of his life he suffered from serious coronary disease, cataracts, and other medical difficulties. These physical problems, and advancing age, made it necessary for him to work at a slower pace, but he never failed to answer the call of the toads. Every spring except one, and every summer except three between 1935 and 1968 he studied amphibians in the field in Oklahoma and adjacent areas. He visited every county in Oklahoma at least once, and most of them many times. Thousands of specimens were collected at all stages of development, and behavior and distribution were observed and

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[1] We thank Mrs. Mary Kierstead Bragg for permission to use material from Bragg's unpublished autobiography "The making of a naturalist."

studied in the majority of forms. During much of this time he virtually lived with the amphibians. Bragg claimed to be able to "think" like a toad, and his students and friends sometimes referred to him as "Mr. Toad" or "*Bufo*" Bragg. He seemed to know every pool, permanent and temporary, almost to the smallest buffalo wallow, and he could determine with amazing accuracy whether it had been used for breeding by *Scaphiopus*, *Bufo*, *Rana*, *Hyla*, or other amphibians. Despite the scope and intensity of his work on the amphibians, his research was always run on a "shoestring" budget, supported principally by the Oklahoma Biological Survey, which he served as herpetologist.

Bragg published more than two hundred papers, and a book on the spadefoot toads. His papers were not entirely devoted to herpetology, but also covered subjects such as protozoans and other invertebrates, religion and science, and biography. He has been criticized for putting out so many short notes, some perhaps superficial or not "scientifically" written, in obscure journals. These criticisms did not appear to bother Bragg. He never worried about where he published, and did not consider this important. He frequently remarked that a person could publish a number of short papers and then later review and discuss these in a longer paper, or save all the data and publish a single long paper. He once said that if something had happened to him, and these small notes had not been published, then we would not have known most of what he had learned about spadefoots. Like many field biologists, he carried an enormous amount of unpublished information and observations around in his head.

Few contemporary herpetologists met Bragg, although he corresponded with many. He was active in the Oklahoma Academy of Science and rarely missed a meeting, but it was unusual for him to attend a national scientific meeting. This was in part due to the financial troubles that plagued him into later life, by which time his health prevented long journeys to meetings. Bragg had many interests outside herpetology. He was at one time active in the Presbyterian Church. He liked to read a wide variety of subjects, and could converse on practically any topic. During later years, when he could read only with the aid of a magnifying glass, he would have his graduate students read aloud favorite selections from the books of poetry that were always at hand. He actively collected stamps, and had a postmark collection.

Arthur N. Bragg enjoyed living, and impressed his sense of enjoyment on those who knew him. Concerning his studies, he wrote: "I firmly believe that one does best what one likes best to do," and "I was made for a field naturalist, not for a laboratory man." His life's work stands as a monument to the accuracy of this self-analysis.

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1950j Salientian range extensions in Oklahoma and a new state record. *In* Researches on the Amphibia of Oklahoma, Univ. Okla. Press. pp. 39-44.
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1965b Gnome of the Night. Univ. Penn. Press, Philadelphia. 127 p.
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1966a Rememberances of the Ortenburgers. The Biol. 48 (1-2):10-14.
1966b Longevity of the tadpole stage in the Plains Spadefoot (Amphibia: Salientia). Wasmann J. Biol. 24 (1):71-73.
1966c Further notes on predation by tadpoles of the Plains Spadefoot. Proc. Okla. Acad. Sci. 46:25-26. (A. N. Bragg and J. Nelson).

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KEYS TO THE HERPETOFAUNA OF THE EASTERN HEMISPHERE

PART I INTRODUCTION AND GENERAL LIST

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EDITOR'S NOTE

How often have we all been frustrated when identifying reptiles and amphibians by our poor memory of the critical publication or, even worse, not even knowing a key existed? This review of identification sources is aimed at the reduction of such frustrations.

George began this project to summarize the literature of the Oriental region. His initial enthusiasm pushed him into adjacent regions, and, once committed, his momentum carried him through the entire Eastern Hemisphere. The size of the resulting manuscript requires that we publish it in seven parts: I. Introduction and General List, II. Africa, III. Asia, IV. Asia Minor, Atlantic Ocean and Islands, and Australia, V. Europe, Indian Ocean and Islands, and Indo-Australian Archipelago, VI. Madagascar, Pacific Ocean and Islands, and Philippine Islands, VII. Bibliography. These, as all other SHIS publications, will appear at irregular intervals. G. Zug

INTRODUCTION

This paper is a compilation of keys and synopses found in the herpetological literature from 1850 to the present, early 1974.[1] It covers the Eastern Hemisphere and includes the Atlantic and Pacific oceans and the Galapagos Archipelago. The other coastal islands of North and South America and the Caribbean have been omitted. The major portion of the world literature has been examined, but readers may find other references which they may wish to add. However, the citations contain a means to identify almost every described reptile and amphibian within the geographical limits of this paper, given the locality where found or collected.

Both keys and synopses have been listed and can be used for identification, although it should be remembered that keys as artificial arrangements are developed solely for identification of specimens and synopses, often found in key format, are developed to show interrelationships. Ultimately, the researcher will have to go into the literature in depth to be certain of an exact and accurate identification of the specimen. For purposes of this paper, keys and synopses have not been differentiated. Accordingly, all of the referenced works should be treated as containing keys and used as such.

The keys cited are meant to afford a quick, fairly accurate and tentative identification of an herpetological specimen. Most of the keys are arranged for the analysis of species, but many are arranged for genera and a few for families only. Higher taxa are mentioned, but in general, keys to orders and suborders have not been emphasized. In some of the older literature classification breakdown to sections, tribes, etc. are found and have been listed for their historical value.

Most of the references are to keys of the couplet type, some of the older ones are a mixture of the couplet, multiple choice, and even bracket multiple choice. These latter also have been listed for historical purposes.

The work has been divided into sections based on political and/or geographical designations under which taxa are listed. An introductory general listing is presented, comprised of keys to those amphibians and reptiles which are widely distributed over two or more land masses, or to those animals where the distribution should not or could not be pinpointed. In some ways this list is a "catch-all" - but necessary. It is suggested that this list be referred to concurrently with the others.

Under each of the major political-geographical land and ocean masses, including the general list, are listed taxa of forms which occur over the whole area or those which have not been identified within a specific smaller political or geographical area. Beneath this section subdivisions of each major area are then listed alphabetically by country (an attempt was made to use the most modern name of the country). Subdivisions of countries into smaller units also have been listed.

The political-geographical areas for which the keys are lised are:

I. Africa
    - Afars and Issas
    - Algeria
    - Angola (including Cabinda)
    - Burundi
    - Cameroon
    - Central Africa (may include area from Ethiopia and Somali Republic west to Senegal and south to Angola and Mozambique)
    - Chad
    - Congo Republic
    - Dahomey
    - East Africa (Somali Republic south to Mozambique)
    - Egypt (including Sinai Peninsula)
    - Ethiopia
    - Gabon
    - Ghana
    - Guinea
    - Ivory Coast
    - Kenya
    - Liberia
    - Libya
    - Malawi
    - Mali
    - Mauritania
    - Morocco
    - Mozambique
    - Niger
    - Nigeria
    - North Africa (Morocco east to Egypt, southeast to Ethiopian coast and Somali Republic's northern coastal area; Barbary Coast)
    - Northeast Africa (Egypt, Sinai, Sudan east to north Kenya and Somali Republic)
    - Rhodesia (Southern Rhodesia
    - Rwanda
    - Senegal
    - Somali Republic
    - Southern half of Africa (10° N. lat., south)
    - South and southern Africa (Angola east to Mozambique, south to South Africa)
    - Southeast Africa (Mozambique, Rhodesia, eastern South Africa)
    - Southwest Africa (Angola, Southwest Africa, western South Africa)
    - Subsahara Africa
    - Sudan
    - Tanzania
    - Togo
    - Tropical Africa
    - Tunisia
    - Ubangi-Shair
    - Uganda
    - Upper Volta
    - West Africa (countries of the western coast of Africa from 5° N. lat., south to western South Africa)

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[1] A few earlier works have been cited, especially those of John Edward Gray.

- Zaire
- Zambia

II. Asia
- Assam
- Bay of Bengal islands
- Burma
- Bonin Islands
- Ceylon
- China
- India
- Japan (and adjacent islands)
- Korea
- Malaya (including Malayan Peninsula and adjacent islands
- Nepal
- Pakistan
- Ryukyu Islands
- Sakhalin
- Siberia
- Sikkim
- Singapore
- Southeast Asia (Indochina)
- Southwest Asia (Southeast U.S.S.R., Central Asia, Afghanistan, Turkmen S.S.R., Turkestan, Usbek S.S.R., Kazakh S.S.R., Western Kinkiang; Kirghiz S.S.R.)
- Soviet Central Asia (Kazakh S.S.R., Kirghiz S.S.R.)
- Taiwan
- Thailand
- Western Asia (Western China, Soviet Central Asia, Southwest Asia, Afghanistan, Pakistan)

III. Asia Minor
- Afghanistan
- Arabia
- Baluchistan
- Iran
- Iraq
- Israel
- Jordan
- Syria

IV. Atlantic Ocean
- Canary Islands and eastern Atlantic islands

V. Australia
- Melbourne area
- New South Wales
- North Australia (20° S. lat., and northward)
- Northern Territory
- Queensland
- South Australia
- Southeastern Australia (Victoria and New South Wales)
- Southwestern Australia
- Tasmania
- Victoria
- Western Australia

VI. Europe
- Austria
- Balearic Islands
- Belgium
- Central Europe
- Cyprus
- Denmark
- France
- Germany
- Great Britain
- Greece
- Greek Islands
- Hungary
- Italy
- Mediterranean Islands
- Jugoslavia
- Netherlands
- Poland
- Portugal
- Romania
- Southeastern Europe (Greece, Turkey, and vicinity)
- Spain
- Switzerland
- U.S.S.R.

VII. Indian Ocean
- Aldabra
- Comoros
- Mascarenes
- Mauritius
- Seychelles
- Socotra

VIII. Indo-Australian Archipelago
- Borneo
- Celebes
- Indonesia
- Moluccas
- Natuna
- New Guinea, Papua (and adjacent islands)
- Sarawak
- Sumatra
- West Irian

IX. Madagascar

X. New Zealand

XI. Pacific Ocean, Oceania
- Galapagos Archipelago
- Melanesia (Bismark, Fiji, Loyalty, New Britain, Solomon islands, New Caledonia)
- Micronesia (Marianas, Palau)
- Polynesia (Hawaiian Islands)

XII. Philippine Islands
- Mindanao
- Palawan

Under each political or geographical designation, each taxon, which has a key, has been listed alphabetically as follows: 1) Amphibia, Reptiles; 2) all taxa designations below class to, but not including family; 3) family and lower taxa. After each taxon, the level of the key (to species, genus, family, etc.) is given followed by the author of the paper containing the key and an abbreviated literature citation. A full citation is given in a "References Cited" section. Where the taxonomic level of the key has been omitted, species level is inferred.

Some abbreviations have been used, al obvious (e.g., sp. for species, fam. for family). The abbreviation "diff." has been used to refer to a key differentiating a series of animals, two subspecies, or two or more taxa.

Wherever possible currently accepted nomenclature and spelling have been used, although the older term has been referenced. This has been done only for family and genus and not for species or subspecies. Such detail has been left to the researcher.

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GENERAL LIST

AMPHIBIA	Dumeril & Bibron, 1843-54
fam.	Gunther, Cat. Bat. Sal. 1858
ord.	Greene, J. Proc. Linn. Soc. 5:218, 1861
ord. to gen.	Hoffman, 6:1, 1873-78
subord. to sp.	Gadow, 8, 1901
fam. to gen.	Terentjev, Moscow 1961/Israel 1965
REPTILIA	Fitzinger, 1826; Dumeril & Bibron, 1834-54
ord. after Owen	Greene, J. Proc. Linn. Soc. 5:218, 1861
fam. to sp.	Gadow, 8, 1901
fam. to gen.	Terentjev, Moscow 1961/Israel 1965
AMPHISBAENIA sp.	Gray, Cat. Tort. Croc. Amphis. 1844; Strauch, Bull. Ac. St. Peter. 11:355, 1882
ANURA	Gray, Cat. Amph. 11, 1850
arcifera fam. to gen.	Cope, J. Ac. N.S. Phila. 6:67, 1866
sect. to groups	Mivarts, P.Z.S. Lond. 280, 1868
gen. to sp.	Boulenger, Cat. Bat. Sal. Ecuad., 1882
APODA	See Gymnophiona
CAUDATA fam. to sp.	Gray, Cat. Amph. II, 1850
gen.	Strauch, Mem. Ac. St. Peter. 16:1, 1870
gen. to sp.	Smith, W. H., Ph.D. diss. 1877
fam. to sp.	Boulenger, Cat. Bat. Grad. 1882
fam., w/gill or slits	Valentine, Copeia 582, 1964
CROCODILIA sp.	Gray, Cat. Tort. Croc. 1844
sp.	Gray, An. Mag. N.H. 10:365, 1862
gen. to sp.	Boulenger, Cat. Chel. Rhyn. Croc. 1889
fam. to gen.	Hoffman, 6:443, 1890
fam.	Wermuth, Mitt. Zool. Mus. Berl. 29:375, 1953
fam. to subord.	Wermuth & Mertens, Berlin 1961; Kimura, Fukada, Tokyo 1966
GYMNOPHIONA gen.	Smith, W. H., Ph.D. diss. 1877
gen.	Peters, W., Monat. Ak. Berl. 924, 1879-80
fam. to sp.	Boulenger, Cat. Bat. Grad. 1882
gen.	Boulenger, A., Mag. N.H. 12:161, 1883
gen. to sp.	Boulenger, P.Z.S. Lond. 401, 1895
fam., subfam.	Taylor, U. Kans. Sci. Bull. 48:297, 1969
LACERTILIA fam. to sp.	Gray, Cat. Liz. 1845
fam.	Boulenger, Am. Mag. N.H. 14:117, 1884
subord. to sp.	Boulenger, Cat. Liz. I-III, 1885-87
subord. to gen.	Hoffman, 6:443, 1890
div. to fam.	Camp, Bull. A.M.N.H. 48:289, 1923/rprnt 1971
SERPENTES fam. to sp.	Gray, Cat. Snakes 1849

fam., gen.	Dumeril, 1853
gen., sp.	Jan, Milano 1863
forms to gen.	Hoffman, 6, 1890
gen., sp.	Boulenger, Cat. Snakes I-III, 1893-96
fam.	Noquchi, Carnegie Inst. Wash. 1909, after Boulenger op. cit.
infraord.	McDowell, J. Herp. 8:1, 1974
TESTUDINES fam. to sp.	Bonaparte, Mag. Zool. Bot. 2:58, 1837-38
fam. to sect.	Fitzinger, Zool. Abh. An. Wien I, 1841
sp.	Gray, Cat. Tort. Croc., 1844
fam. to sp.	Gray, P.Z.S. Lond. 165, 1869
tortoise gen.	Gray, P.Z.S. Lond. 722, 1878
fam. to sp.	Boulenger, Cat. Che. Rhyn., 1889
fam., gen.	Hoffman, 6:1, 1890
fam.	Siebenrock, Sitz. Ak. Wien 116:527, 1907
subord. to subsp.	Wermuth & Mertens, Berlin 1961
sea turtles sp.	Bustard, Lond.-Sydney 1972
ABLEPHARINE gen.	Fuhn, Rev. Roum. Biol. 14:23, 1969
ABLEPHARUS sp.	Strauch, Bull. Ac. St. Peter. 6:533, 1868
AELUROGLENA, Meizodon, Coronella, Coluber diff.	Bogert, Bull. A.M.N.H. 77, 1940
AGAMIDAE gen., sp.	Boulenger, Cat. Liz. 1, 1885
ALLIGATOR sp.	Vaillant, Nou. Arch. Mus. Paris 10:143, 1898
ALLIGATORIDAE gen. sp.	Gray, Trans. Zool. Soc. Lond. 6:125, 1869
gen. sp.	Wermuth, Mitt. Zool. Mus. Berl. 29:375, 1953
ALLIGATORIDAE, Gavialidae, Crocodilidae diff.	Gray, Trans. Zool. Soc. Lond. 6:125, 1869
ALSOPHYLAX sp.	Strauch, Mem. Ac. St. Peter. 35:1, 1887
AMBLYCEPHALIDAE	See Dipsadinae
AMPHISBAENIDAE gen. sp.	Boulenger, Cat. Liz. II, 1885
subfam., gen.	Vanzolini, Herpetologica 7:113, 1951
AMPHISBAENIDAE, Trogonophinae diff.	Gray, P?Z.S. Lond. 442, 1865
ANELYTROPIDAE, Lacertidae, Gerrhosauridae, Scincidae, Dibamidae diff.	Boulenger, Cat. Liz., 1887
ANILIIDAE gen. sp.	Boulenger, Cat. Snake I, 1893
ATHERIS sp.	Strauch, Mem. Ac. St. Peter. 14:1, 1869
BOIDAE gen., sp.	Boulenger, Cat. Snake I, 1893
BUFONIDAE, Pelobatidae, Leptodactylidae as a group diff. from Pipidae, Discoglossidae, Hylidae	Proctor, P.Z.S. Lond. 197, 1921
CAECILIIDAE, Typhlonectidae, Caeciliinae, Dermophinae, Ichthyophidae, Scolecomorphidae diff.	Taylor, U. Kans. Sci. Bull. 48:297, 1969
CAECILIINAE fam., subfam. diff.	Taylor, U. Kans. Sci. Bull. 48:297, 1969
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CHELONIIDAE gen.	Carr, Proc. New Eng. Zool. Club 21:1, 1942
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CISTUDININAE	See Emydinae

CISTUDO See Terrapene

CLEMMYS sp. Siebenrock, Sitz. Ak. Wien 112:439, 1903

CNEMASPIS sp. Loveridge, P.Z.S. Lond. 817, 1935

COLUBER, Coronella, Meizodon, Aeluroglena diff. Bogert, Bull. A.M.N.H. 77, 1940

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  Opisthoglyphae, Proteroglyphae gen., sp. Boulenger, Cat. Snakes III, 1896
  Copes divisions subfam. Taub, Bull. A.M.N.H. 138, 1967,
  Dunn's modification of Cope subfam. Taub, op.cit.
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CORDYLIDAE gen., sp. Boulenger, Cat. Liz. II, 1885

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  Pipidae-Hylidae group diff. from Pelobatidae-Bufonidae-Leptodactylidae Proctor, P.Z.S. Lond 197, 1921

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fam. diff. Boulenger, Cat. Liz. III, 1887

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GYMNOPHTHALMIDAE See Teiidae

HOMALOPSIDAE (Homalopsinae?) sp. grouped Jan, Arch. Nat. 27:87, 1861

HYLIDAE gen. Goin, An. Carnegie Mus. 36:5, 1961
gen., sp. Nieden, Das Tier I, 1923
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gen. sp. Parker, London, 1934

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OMYCHOCEPHALUS See Typhlops

OPHTHALMIDION See Typhlops

PELOBATIDAE gen., sp. Nieden, Das Tier I, 1923
Bufonidae-Leptodactylidae group diff. from Pipidae-Discoglossidae- Hylidae
Proctor, P.Z.S. Lond. 197, 1921

PELOCHELYS, Chitra, Trionyx diff. Siebenrock, Sitz. Ak. Wien III:807, 1902

PIPIDAE-Discoglossidae-Hylidae group diff. from Pelobatidae-Bufonidae- Leptodactylidae
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PLEURODELIDAE	See Salamandridae
PODARCES	See Lacerta
POTAMOPHILIDAE (Homalopsinae, Tropidonotus?) gen.	Jan, Arch. Zool. Anat. 3:201, 1865
PRISTIDACTYLIA	See Lacertidae
PYXIDEA	See Cyclemys
RANA subgen.	Boulenger, Rec. Ind. Mus. 20:1, 1920
esculenta subsp.	Terentjev, Zool. Anz. 74:82, 1927
migromaculata subsp.	Terentjev, Ibid.
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gen.	Boulenger, Cat. Liz. III, 1887
subfam.	Mittleman, Smith. Misc. Coll. 117:1, 1952
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SCOLECCOMORPHIDAE fam., subfam. diff.	Taylor, U. Kans. Sci. Bull. 48:297, 1969
SEIRANOTIDAE	See Salamandridae
TARENTOLA sp.	Strauch, Mem. Ac. St. Peter. 35:1, 1887
TEIIDAE slender tongued gen.	Gray, An. N. H. 2:331, 1839
TERRAPENE, Cyclemys, Cuora, Emys, Notochelys gen. sp.	Gray, P.Z.S. Lond. 173, 1863
TRIONYCHIDAE gen., sp. grouped	Gray, P.Z.S. Lond. 38, 1873
gen., sp.	Siebenrock, Sitz. Ak. Wien 111:807, 1902
gen.	Siebenrock, Ibid. 116:1741, 1907
TRIONYX, Pelochelys, Chitra diff.	Siebenrock, Sitz. Ak. Wien 111:807, 1902
TROGONOPHIDAE	See Trogonophinae
TROGONOPHINAE diff.	Gray, P.Z.S. Lond. 442, 1865
TYPHLOPIDAE	Peters, Sitz. Nat. Berl. 69, 1881
gen.,sp.	Boulenger, Cat. Snake I, 1893
TYPHLOPS sp.	Peters, Monat. Ak. Berl. 77, 1861
UROPELTIDAE sp.	Boulenger, Cat. Liz. I, 1885
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ZONURIDAE	See Cordylidae

KEYS TO THE HERPETOFAUNA OF THE EASTERN HEMISPHERE

PART VII BIBLIOGRAPHY

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KEYS TO THE HERPETOFAUNA OF THE EASTERN HEMISPHERE

PART II AFRICA

GEORGE JACOBS

RESEARCH ASSOCIATE
DIVISION OF REPTILES & AMPHIBIANS
NATIONAL MUSEUM OF NATURAL HISTORY

SMITHSONIAN
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1975

Division of Reptiles & Amphibians
National Museum of Natural History
Washington, DC 20560

AFRICA

Amphibia fam. to subsp.	Dourmeque, Amsterdam reprnt 1972
Amphisbaenia sp.	Gray, P.Z.S.Lond. 442, 1865
Anura (smaller toads)	Loveridge, Occ.Pap.BostonS.N.H. 8:43, 1932
Caudata fam. to sp. adults & larva	Thorn, Paris, 1968
	Maxwell Busack Ibid., transl. Bull.Md.Herp.Soc. 7:95, 1971
Cryptodira fam. to subsp.	Loveridge, Williams, Bull.M.C.Z. 115:161, 1957
Gymnophiona sp.	Nieden, Sitz.Ak.Berl. 3:186, 1912
gen., sp.	Nieden, 37, Berlin, 1913
fam. to sp.	Taylor, Lawrence, Kans., 1968
Serpentes fam. to sp.	Villiers, IFAN, 2:1, 1950
fam. to subsp.	FitzSimons, An.Transv.Mus. 25:35, 1966
Testudines gen.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Ablepharus sp.	Werner, Denk.Ak.Wien 96:437, 1919
Adenorhinos, Bitis, Atheris sp. diff.	Marx, Rabb, Field.Zool. 44:161, 1965
Acontias sp., subsp.	Broadley, Greer, Arnoldi 4:1, 1969
Aeluroglena, Coronella, Coluber, Meizodor diff.	Bogert, Bull.A.M.N.H. 77:107, 1940
Agama sp.	Werner, Mitt.Nat.Mus.Hamb. 30:1, 1913
agama turuensis & a. elongis diff.	Loveridge, Bull.M.C.Z. 74:195, 1933
cyanogaster subsp.	Klausewitz, Senck.Biol. 35:137, 1954
Algiroides, Lacerta diff.	Loveridge, Bull. M.C.Z. 91:235, 1942
Amblyodipses sp.	Broadley, Occ.Pap.Nat.Mus.Rhodesia 4:629, 1971
Amphisbaena, Trogonophis Bipes, Leposternon gen. diff.	Strauch, Bull.Ac.St.Peter. 11:355, 1882
Amphisbaenidae gen., sp.	Loveridge, Bull.M.C.Z. 87:351, 1941
	Werner, Mitt.Mus.Hamb. 27:1, 1910
fam.diff.	Gray, P.Z.S.Lond. 442, 1865
Ancyclocranium barkeri, A. somalicum diff.	Loveridge, Proc.Biol.Soc.Wash. 59:73, 1946
Aparallactus sp.	Boulenger, An.Mag.N.H. 16:171, 1895
	Loveridge, Bull.M.C.Z. 95:119, 1944
lineatus, anomalus, niger diff.	Loveridge, Proc.New Eng. Zool.Club 17:49, 1938 after Boulenger P.Z.S. Lond. 267, 1919
Arthroleptides sp.	Loveridge, Bull.M.C.Z. 79:1, 1935
Arthroleptis sp.	Boulenger, An.Mus.Genoa 42:157, 1905-06
	Noble, Bull.A.M.N.H. 49:147, 1924
ogoensis & rouxi diff.	Loveridge, P.Z.S.Lond. 763, 1925
Aspidelaps scutatus subsp.	Broadley, Arnoldia 4:1, 1968
Atheris sp.	Marx, Rabb, Field.Zool. 44:161, 1965
Atheris, Bitis, Adenorhinos, sp. diff.	Marx, Rabb, Filed.Zool. 44:161, 1965
Atractaspis sp.	Boulenger, An.Mus.Congo 2:7, 1901; Werner, Mitt.N.M.Hamb. 30:1, 1913; Laurent, Mem.Roy.Sci.Nat.Belg. 38, 1950
Bitis sp.	Marx, Rabb, Field.Zool. 44:161, 1965
Boaedon sp.	Gunther, An.Mag.N.H. 1:322, 1885; Boulenger, An.Mus.Genoa, 32:5, 1892
sp., subsp.	Roux, Esteve, Guibe, Bull.Mus.Nat.Paris 36:371, 1964
Boodon - see Boaedon	
Breviceps sp.	Power, An.S.Afr.Mus. 20:451, 1926
uluguruensis, rugosus, usambaricus diff.	Barbour, Loveridge, Mem.M.C.Z. 50:87, 1928
Brookesia sp.	Loveridge, Bull.M.C.Z. 106:175, 1951
Brookesia, Chamaeleo, Rhampholeon diff.	Loveridge, Bull.M.C.Z. 74:195, 1933; Boulenger, Cat.Liz., III, 1887
Bufo sp.	Boulenger, P.Z.S.Lond. 545, 1880; Noble, Bull.A.M.N.H. 49:147, 1924
micranotis, anotis diff.	Loveridge, P.Z.S.Lond. 763, 1925
Cacosternum sp.	Hewitt, An.Natal Mus. 5:435, 1926; Inger, S.Afr.Anim.Life, 6:510, 1959
Calamelaps sp.	Loveridge, Bull.M.C.Z. 95:119, 1944
Cardioglossa sp.	Noble, Bull.A.M.N.H. 49:147, 1924
Chaleides ocellatus subsp.	Mertens, Senck. 3:116, 1921
Chamaeleo sp.	Werner, Zool.Jb. 15:295, 1902
three horned sp.	Rand, Breviora 99, 1958
bitaeniatus sp. group	Rand, Bull.M.C.Z. 130:1, 1963
dilepis (males) subsp.	Loveridge, Bull.M.C.Z. 79:207, 1936
Chamaeleo, Brookesia, Rhampholeon diff.	Loveridge, Bull. M.C.Z. 74:195, 1933
Chamaeleonidae gen., sp.	Gray, P.Z.S.Lond. 465, 1864
gen.	Werner, 27 Berlin, 1911
Chamaeleontidae - see Chamaeleonidae	
Chamaelyeus sp.	deWitte, Copeia 634, 1963
Chamaesaura sp.	Boulenger, P.Z.S.Lond. 722, 1894
Cherainella sp., Peltastes diff.	Gray, P.Z.S.Lond. 615, 1872
Chilorhinophis sp., subsp.	Loveridge, Bull. M.C.Z. 106:175, 1951; Loveridge, 119:1, 1958
Chiromantis sp.	Werner, Verh.Zool.Bot. Wien 72:62, 1922(1923); Noble, Bull.A.M.N.H. 49:147, 1924
	Ahl, Zool.Anz. 80:27, 1929; Ahl, SitzFreundeBerl. 211, 1931
Chlorophis sp.	Schmidt, Bull.A.M.N.H. 49:1, 1923; Hecht, Zool.Amz. 81:329, 1929
irregularis, heterolepidotus diff.	Loveridge, Proc.A.N.S.Phila. 89:265, 1937 - see Boulenger P.Z.S.Lond. 193, 1915
Chlorophis, Philothamnus sp.	Gunther, An.Mag.N.H. 15:526:1895
diff.	Loveridge, Bull.M.C.Z. 119:1, 1958
Cinixys mogueyi & belliana diff.	Siebenrock, Sitz.Ak.Wien 112:439, 1903
Cnemaspis sp.	Loveridge, P.Z.S.Lond. 817, 1935; Angel, Bull.Mus.Nat.Paris 15:163, 1943; Angel, Guibe, Lamotte, Mem.IFAN 40:371, 1954

Coluber, Coronella, Meizodon, Aeluroglena diff. Bogert, Bull.A.M.N.H. 77:1, 1940
Colubridae gen. grouped Bogert, Bull.A.M.N.H. 77:1, 1940
gen.,sp. deWitt, Mem.Inst.Roy.H.N.Belg. 29, 1947
Colubridae (based on Bogert's arrangement) gen. Aaron, Bull.A.M.N.H. 138:1, 1967
Conraua sp. Lamotte, Perret, Bull.IFAN 30:1603, 1968
Cordylidae gen. to subsp. Loveridge, Bull.M.C.Z. 95:1, 1945
Cordylosaurus, Platysaurus, Pleurostrichus, Gerrhosaurus diff. Gray, P.Z.S.Lond. 640, 1865
Coronella, Coluber, Meizodon, Aeluroglena diff. Bogert, Bull.A.M.N.H. 77:107, 1940
Crocodilidae - see Crocodylidae
Crocodylidae gen., sp. Schmidt, Bull.A.M.N.H. 39:385, 1919
Crocodilus - see Crocodylus
Crocodylus cataphractus & vulgaris, Osteolaemus tetraaspis diff. Monard, Mem.IFAN 1:123, 1951
miloticus subsp. Deraniyagala, Spol.Zeyl. 25:1, 1948
vulgaris & madagascariensis, Philas johnstoni diff. Gray, P.Z.S.Lond. 177, 1874
Crotaphopeltis hotamboeia tornieri & hotamboeia diff. Loveridge, Bull.M.C.Z. 75:195, 1933
werneri shrevei & w. werneri diff. Loveridge, P.Z.S.Lond. 133:29, 1959
Cyclamorbis, Emyda, Cycloderma diff. Siebenrock, Sitz.Ak.Wien 111:807, 1902
Cycloderma, Cyclamorbis, Emyda diff. Siebenrock, Sitz.Ak.Wien 111:807, 1902
Dasypeltis sp. Gans, An.Mus.Roy.Congo Belg. 74:237, 1959
Dendroaspis jamesoni jamesoni & j. kaimosae diff. Pitman, Uganda J. 5:93, 1937 - see also Loveridge, Proc.Biol.Soc.Wash. 49:63, 1936
Dromophis sp. Loveridge, Bull.M.C.Z. 95:119, 1944
Duberria sp. Loveridge, Bull.M.C.Z. 95:119, 1944
lutrix lutrix & l. shiranum diff. Loveridge, Bull.M.C.Z. 74:195, 1933
Echis sp. Strauch, Mem.Ac.St.Petersb. 14:1, 1869
Elapsoidea sunderwalli subsp. Loveridge, Bull.M.C.Z. 95:119, 1944
Emyda, Cyclanorbis, Cycloderma diff. Siebenrock, Sitz.Ak.Wien 111:807, 1902
Eremias sp. Boulenger, P.Z.S.Lond. 920, 1896
Eryx sp. Tsarewsky, An.Mus.St.Petersb. 20:340, 1915
colubrinus subsp. Loveridge, Bull.M.C.Z. 79:207, 1936
Eumeces sp. Taylor, Bull.U.Kans. 33:1, 1935
Feylinia sp. Schmidt, Bull.A.M.N.H. 39:385, 1919
Gastropholis sp. Werner, Zool.Anz. 27:461, 1904
Gekkonidae gen., sp., subsp. Loveridge, Bull.M.C.Z. 98:1, 1947
Gerrhosauridae gen., sp. Boulenger, Cat.Liz. III, 1887; Loveridge, Bull.M.C.Z. 89:483, 1942
Gerrhosaurus flavigularis subsp. Loveridge, P.Z.S.Lond. 131, 1920 - see also Schmidt, Bull.A.M.N.H. 39:385(579), 1919
major gecki & m. major diff. Loveridge, Bull.M.C.Z. 74:195, 1933
Gerrhosaurus, Pleurostrichus, Platysaurus, Cordylosaurus diff. Gray, P.Z.S.Lond. 640, 1865
Glauconia - see Leptotyphlops
Glauconidae - see Leptotyphlopidae
Grayia sp. Schmidt, Bull.A.M.N.H. 49:1, 1923
Heleophryne sp. Hewitt, An.Natal Mus. 5:435, 1926
Hemidactylus brookii goegraphic forms Loveridge, Copeia 245, 1941
Hemisus sp. Noble, Bull.A.M.N.H. 49:147, 1924
marmoratum marmoratum & m. guineensis diff. Loveridge, Bull.M.C.Z. 74:195, 1933
Holaspis guentheri laevis & g. guentheri diff. Loveridge, Bull.M.C.Z. 110:141, 1953
Homopholis wahlbergii wahlbergii & w. arnoldi diff. Loveridge, Proc.Biol.Soc.Wash. 57:1, 1944
Homopsus sp. Siebenrock, Zool.Anz. 34:623, 1909
Hylambates sp. Boulenger, An.Mus.Genoa 42:157, 1905-06; Noble, Bull.A.M.N.H. 49:147, 1924
Hymenochyrus sp., subsp. Arnoult, Lamotte, Bull.IFAN 30:270, 1968
Hyperolius sp. Noble, Bull.A.M.N.H. 49:147, 1924; Ahl, Mitt.Zool.Mus.Berl. 17:1, 1931
Ichnotropis sp. Schmidt, Bull.A.M.N.H. 39:385, 1919
Ichnotropis capensis capensis & c. longipos diff. Loveridge, Bull.M.C.Z. 110:141, 1953 - see also FitzSimons, Transv.Mus.Mem. 1, 1943
Ilysiidae - see Anillidae
Kassina sp. Noble, Bull.A.M.N.H. 49:147, 1924
sp., subsp. Ahl, Zool.Anz. 88:277, 1930
Kimixys beliana subsp. Laurent, Breviora 176, 1962
Kinixys sp., Kinothorax diff. Gray, P.Z.S.Lond. 192, 1863
Kinothorax, Kinixys sp. diff. Gray, P.Z.S.Lond. 192, 1863
Lacerta sp. Schmidt, Bull.A.M.N.H. 39:385, 1919
Lacerta (allied to L. muralis) sp. Boulenger, Trans.Zool.Soc.Lond. 21:1, 1916
Lacerta, Algiroides diff. Loveridge, Bull.M.C.Z. 91:235, 1942
Lacertidae sp. Dungar, Niger.Field. 32:117, 1967
Latastia sp. Werner, Mitt.N.H.Hamb. 30:1, 1913
johnstonii, siebenrock diff. Loveridge, Bull.M.C.Z. 74:195, 1933
Leptodira sp. Werner, Sitz.Ak.Wien 116:1823, 1907 (1905); Werner, Zool.Jhb. 27:595, 1909
Leptopelis sp. Noble, Bull.A.M.N.H. 49:147, 1924; Ahl, Sitz.Freunde Berl. 185, 1929
Leptotyphlopidae gen., subgen. Peters, Sitz.Freunde Berl. 4:69, 1881; Boulenger, Cat.Snake I, 1893
Leptotyphlops sp. Boulenger, Am.Mag.N.H. 6:91, 1890; Werner, Mitt.Zool.Mus.Hamb. 34:191, 1916 (1917)
emini emini & e. pembae diff. Loveridge, Proc.Biol.Soc.Wash. 54:175, 1941
longicauda, & emini diff. Loveridge, Bull.M.C.Z. 74:195, 1933
Liopholidophis sp. Parker, An.Mag.N.H. 16:390, 1925
Lophosaura sp. Power, P.Z.S.Lond. 209, 1932
Lycodonomorphus sp. Loveridge, Bull.M.C.Z. 119:1, 1958
laevissimus subsp. Raw, An.Natal Mus. 21:713, 1973

Lycophidion sp.	Parker, Am.Mag.N.H. 12:544, 1933
sp., subsp.	Laurent, Bull.M.C.Z. 136:461, 1968
Lygosoma sp. groups	Smith, Rec.Ind.Mus. 39:213, 1937
Mabuya sp.	Werner, Denk.Ak.Wien 96:437, 1919
maculilabris group sp.	Broadley, Arnoldi 6(23), 1974
planifrons & taitana diff.	Loveridge, Bull.M.C.Z. 79:207, 1936
quinque taeniata obsti & q. margaritifer diff.	Loveridge, Bull.M.C.Z. 110:141, 1953
striata ellenbergi & binotata diff.	Loveridge, Bull.M.C.Z. 110:141, 1953
Megalixalus sp.	Noble, Bull.A.M.N.H. 49:147, 1924
fornasinii & dorsalis diff.	Parker, P.Z.S.Lond. 897, 1930
Meizodon, Coronella, Coluber, Aeluroglena diff.	Bogert, Bull.A.M.N.H. 77:107, 1940
Mioden sp.	Loveridge, Bull.M.C.Z. 95:119, 1944
Monopeltis sp.	Werner, Mitt.Mus.Hamb. 27:1, 1910
Naja sp.	Ferriera, Bull.Antiven.Inst.Am. 4:53, 1930
melanoleuca subsp.	Bruno, An.Mus.G.Doria 4:1, 1968
melanoleuca & nigricollis diff.	Bruno, An.Mus.G.Doria 4:1, 1968
Natricinae gen.	Malnate, Proc.Ac.Phila. 112:41, 1960
Natriciteres sp.	Loveridge, Bull.M.C.Z. 119:1, 1958
Natrix anoscopus anoscopus & a. gendrii diff.	Loveridge, Proc.U.S.N.M. 91:113, 1941
olivacea subsp.	Loveridge, Bull.M.C.Z. 79:1, 1935
Nectophryne sp.	Roux, P.Z.S.Lond. 58, 1906; Noble, Bull.A.M.N.H. 49:147, 1924
Nucras sp.	Boulenger, An.S.Afr.Mus. 13:195, 1917
Osteolaemus sp.	Vaillant, Nouv,Arch.Paris 10:143, 1898
Osteolaemus tetraaspis, Crocodylus cataphraetus & vulgaris diff.	Monard, Mem.IFAN 1:123, 1951
Panaspis sp	Fuhn, Rev.Roum.Biol. 15:379, 1970
Paranaja multifasciata subsp.	Loveridge, Bull.M.C.Z. 95:119, 1944
Pelomedusidae gen.	Boulenger, An.Mag.N.H. 1:346, 1888
gen. to subsp.	Loveridge, Bull.M.C.Z. 88:465, 1941
Peltastes sp.	Gray, P.Z.S.Lond. 653, 1870; Gray, P.Z.S.Lond. 615, 1872
Peltastes, Cherainella sp. diff.	Gray, P.Z.S.Lond. 615, 1872
Pelusios sp.	Gray, P.Z.S.Lond. 192, 1863
Pelusios migricans subsp. diff.	Loveridge, Bull.M.C.Z. 74:195, 1933 - see also Siebenrock, Zool.Jb. 3:558, 1909
Petropedetes sp.	Ahl, Zool.Anz. 58:81, 1924
Phelsuma sp.	Loveridge, Bull.M.C.Z. 89:437, 1942
Philas johnstoni, Crocodylus vulgaris & madagascariensis diff.	Gray, P.Z.S.Lomd. 177, 1874
Philothammus sp.	Loveridge, Bull.Inst.Roy.Soc.Belg. 27:1, 1951; Loveridge, Bull.M.C.Z. 119:1, 1958
hoplogaster, battersbyi diff.	Loveridge, Bull.M.C.Z. 119:1, 1958
irregularis subsp. diff.	Loveridge, Bull.M.C.Z. 106:175, 1951
Philothammus, Chlorophis sp.	Gunther, An.Mag.N.H. 15, 1895
diff.	Loveridge, Bull.M.C.Z. 119:1, 1958
Phrynobatrachus sp.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908); Werner, Denk.Ak.Wien 96:437, 1919
Phrynobatrachus pakenhami & acridoides diff.	Loveridge, Proc.Biol.Soc.Wash. 54:175, 1941
Phrynopsis sp.	Ahl, Zool.Anz. 60:269, 1924
Phyllodactylus sp.	Loveridge, P.Z.S.Lond. 133:29, 1959
Pipidae gen.,sp.	Nieden, I, 1923
Platysaurus, Cordylosaurus, Pleurostrichus, Gerrhosaurus diff.	Gray, P.Z.S.Lond. 640, 1865
Pleurostrichus, Platysaurus, Cordylosaursus, Gerrhosaurus diff.	Gray, P.Z.S.Lond. 640, 1865
Pristurus sp.	Boulenger, An.Mus.Genoa 36:545, 1896; Laurent, Bull.Mus.Roy.Belg. 23:1, 1947
Probreviceps macrodactylus macrodactylus, m. loveridgei, & P. uluguruensis diff.	Parker, An.Mag.N.H. 8:261, 1931
Pseudocordylus sp.	Broadley, An.Natal Mus. 16:99, 1964 - after FitzSimons, Transv.Mus.Mem. 1:528, 1943
Prosymma sp.	Chabanaud, Bull.Mus.Nat.Paris 22:433, 1916; Loveridge, Bull.M.C.Z. 119:1, 1958
ambigua subsp. & P. meleagris diff.	Laurent, Mus.Dondo 23, 1954
Psammophis sp.	Boulenger, P.Z.S.Lond. 530, 1895; Werner, Denk.Ak.Wien 96:437, 1919; Loveridge, Bull.M.C.Z. 87:1, 1940
tritaeniatus tritaeniatus & t. multisquamis diff.	Loveridge, Proc.Biol.Soc.Wash. 45:83, 1932; Uthmoller, Zool.Anz. 135:225, 1941 - after Loveridge, op.cit.
Ptychadena sp.	Poynton, Senck.Biol. 45:193, 1964
Ptyodactylus sp.	Anderson, London 1898
Rana sp.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908)
angolensis & mutti diff.	Parker, P.Z.S.Lond. 897, 1930
fasciata fasciata, f. fulleborni, f. merumontana & R. stenocephala diff.	Barbour, Loveridge, Mem.M.C.Z. 50:87, 1928
mascareniensis subsp.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908)
venusta, gondokorensis, mascareniensis & schillukorum diff.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908)
Rhacophoridae gen., sp.	Ahl, III, 1931
Rhammophis sp.	Schmidt, Bull.A.M.N.H. 49:1, 1923; Loveridge, Bull.M.C.Z. 95:119, 1944
Rhampholeon sp.	Werner, Zool.Jb. 15:295, 1902
Rhampholeon, Brookesia, Chamaeloe diff.	Loveridge, Bull.A.M.N.H. 74:195, 1933 - see also Boulenger Cat.Liz. III, 1887
Riopa sundwallii sundwallii & s. modestum diff.	Loveridge, Bull.M.C.Z. 74:195, 1933
Scincidae gen., sp.	deWitte, Laurent, Mem.Mus.Roy.Belg. 26, 1943
Simocephalus sp.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908)

Spalerosophis sp.	Marx, Field.Zool. 39:347, 1959
Stenodactylus sp.	Anderson, J.Lond. 1898
Tancredii (supersp.) sp.	Siebenrock, Zool.Anz. 26:191, 1903; Fuhn, Rev.Roum.Biol. 15:379, 1970 - see also Panaspis
Tarbophis sp.	Bogert, Bukl.A.M.N.H. 77:1, 1940
Thelotornia kirtlandii subsp.	Loveridge, Bull.M.C.Z. 95:119, 1944
Thrasops sp.	Schmidt, Bull.A.M.N.H. 49:1, 1923; Loveridge, Bull.M.C.Z. 95:119, 1944
Thrasops jacksonii jacksonii & j. schmidti diff.	Loveridge, Proc.Biol.Soc.Wash. 49:63, 1936
Trionychidae sp.	Gray, P.Z.S.Lond. 76, 1864
Trogonophidae fam. diff.	Gray, P.Z.S.Lond. 442, 1865
Trogonophis gen. diff.	Strauch, Bull.Ac.St.Petersb. 11:355, 1884
Tropiocolotes sp., subsp.	Leviton, Anderson, Occ.Pap.Cal.Ac.Sci. 96:1, 1972
Typhlops	
angolensis subsp.	Laurent, Bull.M.C.Z. 130:387, 1964
punctatus group sp.	Laurent, Bull.M.C.Z. 130:387, 1964
schlegelii subsp.	Loveridge, Bull.M.C.Z. 74:195, 1933
Typhlops, Leptotyphlops diff.	Angel, Paris 1933
Uriechis - see Aparallactus	
Uromastix sp.	Anderson, J.Lond. 1898; Pasteur, Bons, Trans.Inst.Cherifien 21:1, 1960
Varanus subgen. to subsp.	Mertens, Abh.Senck.Nat.Ges. 466:235, 1942; Smith, J.Bombay N.H.S. 35:615, 1932
miloticus miloticus & m. ornatus diff.	Loveridge, Bull.M.C.Z. 110:141, 1953; Dungar, Niger.Field. 32:170, 1967
Viperidae	Gray, Zool.Misc. 68, 1842, reprnt, SSAR, 1971
Xenocalamus sp.	Methuen, P.Z.S.Lond. 349, 1919; Broadley, Occ.Pap.N.M.Rhodesia 4:629, 1971
Xenopus sp.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908); Noble, Bull.A.M.N.H. 49:147, 1924; Arnoult, Lamotte, Bull.IFAN 30:270, 1968
laevis & mulleri diff.	Parker, P.Z.S.Lond. 897, 1930
Zonurus sp., subsp.	Roux, Zool.Jb. 25:403, 1907

AFARS and ISSAS

Hemidactylus sp.	Parker, P.Z.S.Lond. 335, 1932
Lygosoma sp.	Parker, P.Z.S.Lond. 335, 1932

ALGERIA

Amphibia subord. to sp.	Strauch, Mem.Ac.St.Petersb. 4:1, 1862; Doumergue, Amsterdam, 1901, reprnt 1972
Reptilia subord. to sp.	Strauch, Mem.Ac.St.Petersb. 4:1, 1862; Doumergue, Amsterdam, 1901, reprnt 1972

ANGOLA

Reptilia fam. to sp.	Monard, Arq.Mus.Boc.Lisb. 8:19, 1937
Serpentes fam. to sp.	Boulenger, P.Z.S.Lond. 193, 1915
Gerrhosauras sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919

Cabinda

Serpentes fam. to sp.	Boulenger, P.Z.S.Lond. 193, 1915
Gonionotrophis sp.	Loveridge, Bull.M.C.Z. 86:129, 1939

BELGIAN CONGO - See ZAIRE

BRITISH CENTRAL AFRICA - See MALAWI

BRITISH SOMALILAND - See SOMALI REPUBLIC

BURUNDI

Anura subord, to gen.	Nieden, Mitt.Zool.Mus.Berl. 7:345, 1915
Serpentes fam. to sp.	Laurent, An.Mus.Roy.Congo Terr. 48:1, 1956; deWitte, Mus.Roy.Afr.Cent. 104, 1962
Gastropholis sp.	Werner, Zool.Anz. 27:461, 1904

CABINDA - See ANGOLA CABINDA

CAMEROON

Amphibia fam. to subsp.	Perret, Zool.Jb. 93:289, 1966
Reptilia sp.	Werner, Verh.Zool.Bot.Wien 48:191, 1898
Anura fam. to sp.	Nieden, Mitt.Zool.Mus.Berl. 3:489, 1908
Anura, Gymnophiona diff.	Nieden, Mitt.Zool.Mus.Berl. 3:489, 1908
Gymnophiona gen.	Nieden, Mitt.Zool.Mus.Berl. 3:489, 1908
Gymnophiona, Anura diff.	Nieden, Mitt.Zool.Mus.Berl. 3:489, 1908
Serpentes fam.	Sternfeld, Mitt.Zool.Mus.Berl. 3:397, 1908
Agama agama agama & a. benueensis diff.	Monard, Mem.IFAN 1:123, 1951
Atractaspis sp., subsp.	Perret, Rev.Suisse Zool. 67:129, 1960
Boidae gen.	Sternfeld, Mitt.Zool.Mus.Berl. 3:397, 1908
Bufo sp.	Parker, P.Z.S.Lond. 135, 1936
Chamaeleo sp.	Perret, Rev. Suisse Zool. 64:79, 1957
Colubridae gen., sp.	Sternfeld, Mitt.Zool.Mus.Berl. 3:397, 1908
Dipsadoboa sp., subsp.	Perret, Rev.Suisse Zool. 67:129, 1960
Elapidae sp.	Sternfeld, Mitt.Zool.Mus.Berl. 3:397, 1908
Gekkonidae gen., sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Hymenochyrus sp., subsp.	Aroult, Lamotte, Bull.IFAN 36:270, 1968
Nectophryne sp.	Roux, P.Z.S.Lond. 58, 1906
Ptychadena sp.	Guibe, Lamotte, Bull.IFAN 20:1448, 1958
Typhlopidae sp.	Sternfeld, Mitt.Zool.Mus.Berl. 3:397, 1908
Viperidae gen., sp.	Sternfeld, Mitt.Zool.Mus.Berl. 3:397, 1908
Xenopus sp.	Arnoult, Lamotte, Bull.IFAN 30:270, 1968

CENTRAL AFRICA

May include area from Ethiopia and Somali Republic W. to Senegal and S. to Angola and Mozambique

Bufonidae (smaller toads)	Loveridge, Pap.Bost.Soc.N.H. 8:43, 1932
Calamelaps sp., subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Dasypeltis scaber subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Mioden sp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Rhamnophis aethiopissa subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Thrasops sp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Thrasops jacksonii subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Typhlops tettensis subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942

Grand Lakes Region (Zaire, Tanzania, Ruanda, Burundi)

Serpentes fam. to sp.	Laurent, An.Mus.Roy.Congo Belg.Terv. 48:1, 1956

CENTRAL AFRICAN REPUBLIC - See UBANGI-SHAIR

CHAD

Gonionotophis sp.	Loveridge, Bull.M.C.Z. 86:129, 1939

CONGO (REPUBLIC)

Gonionotophis sp.	Loveridge, Bull.M.C.Z. 86:129, 1939

CONGO (THE) - See ZAIRE

DAHOMEY

Crocodilia gen., sp.	Villiers, IFAN 15:1, 1958
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Boidae gen., sp.	Angel, Paris 1933
Colubridae gen., sp.	Angel, Paris 1933
Viperidae gen., sp.	Angel, Paris 1933

EAST AFRICA

Amphibia fam. to sp.	Loveridge, P.Z.S.Lond. 7, 1930
Lacertilia sp.	Parker, Bull.M.C.Z. 91:1, 1942
Serpentes fam. to sp.	Boulenger, P.Z.S.Lond. 611, 1915
Testudinata fam. to sp.	Loveridge, P.Z.S.Lond. 923, 1923
Agama colonorum & planiceps diff.	Loveridge, U.S.N.M.Bull. 151, 1929

Ancylocranium barkeri & somalicum diff.	Loveridge, Proc.Biol.Soc.Wash. 59:73, 1946
Boaedon sp.	Gunther, An.Mag.N.H. 1:322, 1885
Boodon - see Boaedon .	
Bufo sp.	Angel, et.al., Paris 1925
Bufonidae (smaller toads)	Loveridge, Occ.Pap.Bost.Soc.N.H. 8:43, 1932
Chamaeleo senegalensis senegalensis & s. laevigatus diff.	Loveridge, U.S.N.M.Bull. 151, 1929
Chamaesaura sp.	Boulenger, P.Z.S.Lond. 96, 1899
Chiromantis petersii, macrops, albescens & fasciatus diff.	Loveridge, U.S.N.M.Bull. 151, 1929
Dasypeltis medici medici & m. lamuensis diff.	(Gans, Breviora 79, 1957
Lacertidae gen.	Loveridge, P.Z.S.Lond. 133:29, 1959
Leptotyphlops scutifrons & conjuncta diff.	Loveridge, Bull.M.C.X. 74:195, 1933
Natrix olivacea subsp.	Loveridge, Bull.M.C.Z. 79:1, 1935
Nectophrynoides occidentalis, viviparo & tornier diff.	Guibe, Lamotte, Mem.IFAN 53:241, 1958
Pelusios nigricans nigricans & n. castaneous diff.	Loveridge, Bull.M.C.Z. 74:195, 1933 - see also Hewitt, An.Natal Mus. 6:461, 1931
Rana mutti & aberdariensis diff.	Loveridge, U.S.N.M.Bull. 151, 1929
Ramnophis, Thrasops diff.	Loveridge, U.S.N.M.Bull. 151, 1929
Xenopus laevis subsp.	Loveridge, Bull.M.C.Z. 74:195, 1933

EAST AFRICAN PROTECTORATE - See KENYA

EGYPT

Amphibia ord. to sp.	Marx, N.A.M.R.U.-3, 1968
Reptilia ord. to sp.	Marx, N.A.M.R.U.-3, 1968
Anura sp.	Al-Hussaini, Bull.Fouad U. 19:1, 1939
Lacertilia sp.	Anderson, London 1898
fam., sp.	Marx, U.S.N.Res.Rep.NM005, 1956
Serpentes fam., sp.	Marx, U.S.N. Res.Rep.NM005, 1956
Agama agama subsp., related sp.	Flower, P.Z.S.Lond. 735, 1933
Agama stellio subsp.	Daan, Beaufortia 14:109, 1967
Geckonidae - see Gekkonidae	
Gekkonidae gen., sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Mabuia - see Mabuya	
Mabuya sp.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908)
Zaminis sp.	Anderson, London 1898

Nubia

Eryx sp.	Boulenger, An.Mag.N.H. 9:74, 1892
Gongylophis sp.	Boulenger, An.Mag.N.H. 9:74, 1892

Sinai

Amphibia gen.	Schmidt, Marx, Field.Zool. 39:21, 1956 also N.A.M.R.U. 005 050 3938 undated
Reptilia gen.	Schmidt, Marx, Field.Zool. 39:21, 1956

ERITREA - See ETHIOPIA

ETHIOPIA

Amphisbaenidae gen., sp.,	Werner, Mitt.Nat.Mus.Hamb. 27:1, 1910
Eremias sp.	Boulenger, P.Z.S.Lond. 920, 1896
Gerrhosaurus sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Hemidactylus sp.	Parker, P.Z.S.Lond. 335, 1935
Philochortus sp.	Boulenger, P.Z.S.Lond. 145, 1917

FRENCH CONGO - See FRENCH EQUATORIAL AFRICA, CONGO REPUBLIC, UBANGI-SHAIR

FRENCH EQUATORIAL AFRICA - See CHAD, FRENCH CONGO, CONGO REPUBLIC, GABON, UBANGI-SHAIR (CENTRAL AFRICAN REPUBLIC

FRENCH GUINEA - See GUINEA

FRENCH SOMALILAND - See AFARS AND ISSAS

FRENCH WEST AFRICA - See DAHOMEY, GUINEA, IVORY COAST, MALI, MAURITANIA, NIGER, SENEGAL

GABON

Serpentes sp.	Knoepffler, Biol.Gabon. 4:183, 1968
Chamaeleo sp., subsp.	Knoepffler, Biol.Gabon. 3:245, 1967
Gonionotophis sp.	Loveridge, Bull.M.C.Z. 86:129, 1939

GERMAN EAST AFRICA - See TANZANIA, RUANDA AND URUNDI

GHANA

Serpentes gen., sp.	Hughes, Barry, Bull.IFAN 31:1004, 1969
with colubrid-type head shields sp.	Leeson, London 1950
Gekkonidae sp.	Booth, J.W.Afr.Sci.Assoc. 2:134, 1956
Philothamnus sp.	Leston, Hughes, Bull.IFAN 30:737, 1968

GOLD COAST - See GHANA

GUINEA

Crocodilia gen., sp.	Villiers, IFAN 15:1, 1958
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Boidae gen., sp.	Angel, Paris 1933
Colubridae gen., sp.	Angel, Paris 1933
Viperidae gen., sp.	Angel, Paris 1933

Mt. Nimba

Hyperolius sp.	Laurant, Mem.IFAN 53:275, 1958

ITALIAN SOMALILAND - See SOMALI REPUBLIC

IVORY COAST

Crocodilia gen., sp.	Villiers, IFAN 15:1, 1958
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Boidae gen., sp.	Angel, Paris 1933
Colubridae gen., sp.	Angel, Paris 1933
Viperidae gen., sp.	Angel, Paris 1933

Mt. Nimba Area

Hyperolius sp.	Laurent, Mem.IFAN 53:275, 1958

KENYA COLONY - See KENYA

KENYA

Amphibia fam. to sp.	Loveridge, P.Z.S.Lond. 7, 1930
Lacertilia gen., sp.	Loveridge, P.Z.S.Lond. 923, 1923
Arthroleptides sp.	Loveridge, Bull.M.C.Z. 79:1, 1935
Calamelaps sp., subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Chamaesaura sp.	Boulenger, P.Z.S.Lond. 96, 1899
Rhamnophis aethiopissa subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Rhamnophis batesii subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Thrasops sp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Thrasops jacksonii subsp.	Loveridge, Bull.M.C.S. 91:235, 1942

Nairobi District

Serpentes (common names) fam., sp.	Loveridge, E.Afr.N.H.S. 18:97, 1945

LIBERIA

Aparallactus lineatus, anomalus & niger diff.	Boulenger, P.Z.S.Lond. 267, 1919; Loveridge, Proc. NewEngl. Zool.Club 17:49, 1938 - after Boulenger op.cit.
Natrix anoscopus anoscopus & a. gendrii diff.	Loveridge, Proc.U.S.N.M. 91:113, 1941
Rana sp.	Loveridge, Proc.U.S.N.M. 91:113, 1941

Mt. Nimba Area

Hyperolius sp.	Laurent, Mem.IFAN 53:275, 1958

LIBYA

Serpentes fam.	Kramer, Schnurrenberger, Rev.SuisseZool. 70:453, 1963
Colubridae sp.	Kramer, Schnurrenberger, Rev. SuisseZool. 70:453, 1963
Viperidae sp.	Kramer, Schnurrenberger, Rev.SuisseZool. 70:453, 1963

MALAWI

Amphibia fam. to subsp.	Loveridge, Bull.M.C.Z. 110:325, 1953
sp.	Stewart, Albany 1967
Reptilia fam. to sibsp.	Loveridge, Bull.M.C.Z. 110:141, 1953
Serpentes fam., sp.	Sweeney, Zomba 1961
Chamaesaura sp.	Boulenger, P.Z.S.Lond. 722, 1894
Ptychadena sp.	Poynton, Senck.Biol. 45:193, 1964
Typhlops tettensis subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942

MALI

Crocodilia gen., sp.	Villiers, IFAN 15:1, 1958
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Boidae gen., sp.	Angel, Paris 1933
Colubridae gen., sp.	Angel, Paris 1933
Viperidae gen., sp.	Angel, Paris 1933

MAURITANIA

Crocodilia gen., sp.	Villiers, IFAN 15:1, 1958
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Boidae gen., sp.	Angel, Paris 1933
Colubridae gen., sp.	Angel, Paris 1933
Viperidae gen., sp.	Angel, Paris 1933

MOROCCO

Amphibia (adult larvae) ord., sp.	Pasteur, Bons, Trav.Cherifien 17:1, 1959
Reptilia ord. to subsp.	Bons, Girot, Trav.Cherifien 26:1, 1962
subcl. to subsp.	Doumergue, Amsterdam reprnt, 1972
Amphisbaenia sp.	Bons, St.Girons, Bull.Soc.Sci.Maroc. 43:117, 1963
Lacertilia gen.	Bons, Trav.Cherifien 18:1, 1959
Serpentes fam., sp.	Dollfus, Beaurieux, Var.Soc.Sci.Maroc. 4:1, 1928; St.Girons, Var.Soc.Sci. Maroc. 8:1, 1956
Acanthodactylus sp.	Bons, Trav.S-O Maroc. 18:1, 1959
Bufo (adult, tadpoles) sp.	Hoogmoed, Zool.Med. 47:49, 1972
Chalcides sp., subsp.	Werner, Sitz.Ak.Wien 140:271, 1931
sp.	Bons, Trav.Cherifien 18:1, 1959
Chalcides ocellatus subsp.	Bons, Sc,D.diss. 1967

MOZAMBIQUE

Dasypeltis scaber subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Melanoseps sp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Pelusios nigricans nigricans & n. casteneus diff.	Loveridge, Bull.M.C.Z. 74:195, 1933 - see also Siebenrock, Zool.Jb. 3:558, 1909
Typhlops tettensis subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942

NIGER

Crocodilia gen., sp.	Villiers, IFAN 15:1, 1958
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Boidae gen., sp.	Angel, Paris 1933
Colubridae gen., sp.	Angel, Paris 1933
Viperidae gen., sp.	Angel, Paris 1933

NIGERIA

Amphisbaenia sp.	Dungar, Niger.Field 33:167, 1968
Boaedon sp.	Dungar, Niger.Field 36:151, 1971
Boodon - see Boaedon	
Booedon - see Boaedon	
Chamaeleonidae sp.	Pasqual, Niger.Field 6:32, 1937; Dungar, Ibid. 32:53, 1967
Chamaeleontidae - see Chamaeleonidae	
Dibamidae sp.	Dungar, Niger.Field 38:54, 1973
Gekkonidae sp., subsp.	Dungar, Niger.Field 33:18, 1968
Gonionotophis sp.	Dungar, Niger.Field 36:54, 1971
Mehelya sp.	Dungar, Niger.Field 36:54, 1971
Philothamnus sp.	Dungar, Niger.Field 38:158, 1973
Scincidae sp.	Dungar, Niger.Field 38:54, 1973
Varanus niloticus niloticus & n. ornatus diff.	Dungar, Niger.Field 32:170, 1967

NORTH AFRICA

May include area from Morocco E to Egypt, SE to Ethiopion coast and Somali Republic northern coastal area; Barbary Coast

Amphibia fam. to sp.	Boulenger, Trans.Zool.Soc.Lond. 8:93, 1891
Reptilia fam to sp.	Ibid.
Anura fam., gen.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Caudata sp.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Lacertilia fam., gen.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Serpentes fam., gen.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895; P.Z.S.Lond. 299, 1919
sp.	Marinkelle, Lacerta no.2/3, 1962
Acanthodactylus sp., subsp.	Lataste, An.Mus.Genoa 22:476, 1885; Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Agama sp.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Amphisbaenidae gen.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Bufo sp.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Chalcides sp.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Clemmys, Emys, Testudo diff.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Emys, Clemmys, Testudo diff.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Eumeces schneiderii subsp.	Mertens, Senckenb. 27:53, 1946
Gekkonidae gen.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Lacerta subgen., sp.	Bedriaga, Abh.Senck.Nat.Ges. 14:17, 1886; Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Lytorhynchus sp.	Leviton, Anderson, Proc.Cal.Ac.Sci. 37:249, 1970
Psammodromus sp.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Testudo, Emys, Clemmys diff.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Tropicolotes	Guibe, Bull.Mus.Paris 38:337, 1966
Vipera sp.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895
Viperidae sp.	Schwarz, Marburg 1936
Zamens sp.	Boulenger, Trans.Zool.Soc.Lond. 13:93, 1895

NORTHEAST AFRICA

May include Egypt, Sinai, Sudan, E to N Kenya and Somali Republic

Lacertilia sp.	Parker, Bull.M.C.Z. 91:1, 1942
Serpentes fam. to sp.	Boulenger, P.Z.S.Lond. 641, 1915

NORTHERN RHODESIA -See ZAMBIA

MYASALAND - See MALAWI

PORTUGUESE CONGO - See ANGOLA, CABINDA

RHODESIA - SOUTHERN RHODESIA - See Also ZAMBIA (NORTHERN RHODESIA)

Serpentes fam., sp., subsp.	Broadley, Bull.M.C.Z. 120:1, 1959
Hildebrandtia (subgen. of Rana) sp.	Boulenger, Trans.Zool.Soc.Lond. 8:33, 1919

RUANDA - See RWANDA (REPUBLIC)

RUANDA - URUNDI - See RWANDA, See Also BURUNDI (REPUBLIC, RWANDA-BURUNDI

RWANDA

Anura subord., fam., gen.	Nieden, Mitt.Zool.Mus.Berl. 7:345, 1915
Serpentes fam. to sp.	Laurent, An.Mus.Cong.Terv. 48:1, 1956
fam., gen.	deWitte, Mus.Roy.Afr.Cent. 104, 1962
Gastropholis sp.	Werner, Zool.Anz. 27:461, 1904

SENEGAL

Crocodilia gen., sp.	Villiers, IFAN 15:1, 1958
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Boidae gen., sp.	Angel, Paris 1933
Colubridae gen., sp.	Angel, Paris 1933
Viperidae gen., sp.	Angel, Paris 1933

SOKOTRA (SOCOTRA) ISLANDS - See INDIAN OCEAN

SOMALIA - See SOMALI REPUBLIC

SOMALILAND - See SOMALI REPUBLIC

SOMALI REPUBLIC

Lacertilia sp.	Parker, Bull.M.C.Z. 91:1, 1942
Serpentes sp., subsp.	Parker, Zool.Verh. 6, 1949
Agamodon sp.	Gans, Laurent, Mus.Roy.Afr.Terv.Belg. 134:93, 1965
Boaedon sp.	Boulenger, An.Mus.Genoa 32:5, 1892
Boodon - see Boaedon	
Eremias sp.	Boulenger, P.Z.S.Lond. 920, 1896
Eremias erythrostica, brenneri & mucronata diff.	Boulenger, An.Mus.Genoa 32:5, 1892
Hemidactylus sp.	Parker, P.Z.S.Lond. 335, 1932
Lygosoma sp.	Parker, P.Z.S.Lond. 335, 1932
Naja melanoleuca sp., subsp.	Bruno, Doriana 4:1, 1968
Naja nigricollis & melanoleaca diff.	Bruno, Doriana 4:1, 1968
Philochortus sp.	Boulenger, P.Z.S.Lond. 145, 1917
Scincidae gen., sp.	Lanza, Monit.Zool.Ital. 2(Suppl):207, 1968
Typhlops cuneirostris subsp.	Gans, Laurent, Mus.Roy.Afr.Terv.Belg. 134, 1965

SOUTHERN HALF OF AFRICA

Ahaetulla	Gunther, An.Mag.N.H. 11:283, 1863

SOUTH AND SOUTHERN AFRICA

Amphibia fam. to sp.	Poynton, An.NatalMus. 17:1, 1964
Anura fam. to sp.	Boulenger, An.S.Afr.Mus. 5:455, 1910
larvae fam. to sp.	VanDijk, An.NatalMus. 18:231, 1966
larvae gen.	VanDijk, Newsl.Limnol.Soc.S.Africa 1:19, 1964 (not seen)
Lacertilia fam. to sp.	Boulenger, An.S.Afr.Mus. 5:455, 1910
fam. to subsp.	FitzSimons, Trans.Mus.Mem. 1, 1943
Serpentes fam. to sp.	Boulenger, An.S.Afr.Mus. 5:455, 1910
sp.	FitzSimons, CapeTown, 1919 (1920?)
sp., subsp.	FitzSimons, London, 1962; FitzSimons, An.Trans.Mus. 25:35, 1966
Testudinata (tortoises) gen., subgen.	Hewitt, An.NatalMus. 6:461, 1931
Acontias sp., subsp.	Broadley, Greer, Arnoldia 4:1, 1969
Afroedura karroica subsp.	Loveridge, Am.Mus.Nov. 1254, 1944
Afroedura of southern Africa and Oedura of Australia diff.	Loveridge, Am.Mus.Nov. 1254, 1944
Agama sp.	Boulenger, Trans.Roy.Soc.S.Afr. 9:229, 1921
Agama hispida, anchietae & atra diff.	Boulenger, Trans.Roy,Soc.S.Afr. 9:299, 1921
Bufo sp.	Angel, Paris 1925; VanDijk, An.NatalMus. 21:71, 1971
Bufo angusticeps group' sp.	Hewitt, An.S.Afr.Mus. 20:273, 1926
Gekkonidae sp.	Hewitt, An.Transvl.Mus. 2:77, 1910
Gerrhosauridae sp.	Hewitt, An. Transvl.Mus. 2:77, 1910
Lacertidae sp.	Hewitt, An.Transvl.Mus. 2:77, 1910
Leptodactylidae gen.	Lynch, U.Kans.Misc.Publ. 53, 1971
Lophosaura sp.	Power, P.Z.S.Lond. 209, 1932
Natrix olivacea tropical S. Afr. subsp.	Loveridge, Bull.M.C.Z. 79:1, 1935
Nucras sp.	Broadley, Arnoldia 5:1, 1972
Pachydactylus scutatus subsp.	Loveridge, Am.Mus.Nov. 1254, 1944
Pelusios sp., subsp.	Hewitt, An.NatalMus. 6:461, 1931

Pelusios nigricans nigricans & n. castaneous diff.	Loveridge, Bull.M.C.Z. 74:195, 1933 - see also Siebenrock, Zool.Jb.Syst. 3:558, 1909
Psammophis sp.	Roux, Zool.Jb. 25:733, 1907
Pteropus sp.	Haacke, Sci.Pap.Namib. 25, 1964
Ptychadena sp.	Poynton, An.NatalMus. 20:365, 1970; Stevens, Arnoldia 5:1, 1972
Scincidae sp.	Hewitt, An.Transvl.Mus. 2:77, 1910
gen.	Ibid.
Testudo sp.	Siebenrock, Sitz.Ak.Wien 113:307, 1904
Zonurus sp.	Roux, Zool.Jb. 25:403, 1907

Kruger National Park

Reptilia fam. to sp.	Pienaar, Koedoe 1, 1966

Transvaal Highlands

Anura sp. eggs	Balinsky, Zool.Af. 4:37, 1969

Zululand

Gerrhosaurus sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919

SOUTHEAST AFRICA

Lacertilia sp.	Parker, Bull.M.C.Z. 91:1, 1942
Chrysopelea boieii & capersis diff.	Smith, A., Mag.Zool.Bot. 1:141, 1837
Gerrhosaurus typicus, desjardini & chrysobronchus diff.	Smith, A., Mag.Zool.Bot. 1:141, 1837
Mehelya sp.	Loveridge, Bull.M.C.Z. 86:129, 1939
Pelusios nigricans nigricans & n. castaneus diff.	Loveridge, Bull.M.C.Z. 74:1, 1933 - see also Siebenrock, Zool.Jb.Syst. 3:558, 1909
Pleurotuchas - see Gerrhosaurus	

Southern Rhodesia - Rhodesia

Amphibia fam. to subsp.	Mertens, Abh.Senck.N.G. 490, 1955; Mertens, Abh.Senck.N.G. 529:1, 1971
Reptilia fam. to subsp.	Mertens, Abh.Senck.N.G. 490, 1955
Lacertilia fam. to subsp.	Mertens, Abh.Senck.N.G. 529, 1971
Serpentes fam. to subsp.	Mertens, Abh.Senck.N.G. 529, 1971
Testudinata fam. to subsp.	Mertens, Abh.Senck.N.G. 529, 1971
Gerrhosaurus sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Rhoptropus after R. boaltoni & barnardi diff.	Parker, Nov.Zool. 40:115, 1936

Damaraland

Pachydactylus sp., subsp.	Parker, Nov.Zool. 40:115, 1936

SUBSAHARAN AFRICA

Scincidae gen.	Greer, Bull.M.C.Z. 140:1, 1970

Sudan

Agama agama subsp., related sp.	Flower, P.Z.S.Lond. 735, 1933
Chamaeleo sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Eremias sp.	Schmidt, Bull.A.M.N.H 39:385, 1919
Gekkonidae sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Mabuia - see Mabuya	
Mabuya sp.	Werner, Sitz.Ak.Wien 116:1823, 1907 (1908)

Nubia

Eryx, sp.	Boulenger, An.Mag.N.H. 9:74, 1892
Gongylophis sp.	Boulenger, An.Mag.N.H. 9:74, 1892

TANGANYIKA, TANGANYIKA TERRITORY - See TANZANIA

TANZANIA

Amphibia fam. to sp.	Loveridge, P.Z.S.Lond 7,1930
Anura subord. to gen.	Nieden, Mitt.Zool.Mus.Berl. 7:345, 1915
Lacertilia fam. to sp.	Loveridge, P.Z.S.Lond. 841, 1923
Serpentes	Vesey, Fitzgerald, Prog.Trans.Rhodesia Sa.Assoc. 46:17, 1958
fam. to sp.	Laurent, Am.Mus.Roy.Congo.Terv. 48:1, 1956
Testudinata fam. to sp.	Loveridge, P.Z.S.Lond. 923, 1923
Amphisbaena newalaensis, ewerbecki, rondoensis & manguruwensis diff.	Loveridge, Breviora 163, 1962
Ancylocranium barkeri & somalicum diff.	Loveridge, Proc.Biol.Soc.Wash. 59:73, 1946
Ancylocranium barkeri newelae, b. barkeri & A. ionidesi diff.	Loveridge, Breviora 163, 1962
Calamelaps sp., subsp.	Loveridge, Bull.M.C.Z. 92:235, 1942
Chirindia sp., subsp.	Gans, Rhodes, An.Carneg.Mus. 39:1, 1967
Dasypeltis scaber subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Gastropholis sp.	Werner, Zool.Anz. 27:461, 1904
Melanoseps sp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Natrix olivacea subsp.	Loveridge, Bull.M.C.Z. 79:1, 1935
Nectophryne sp.	Roux, P.Z.S.Lond. 58, 1906
Nucras boulengerii subsp.	Loveridge, Bull.M.C.Z. 74:195, 1933
Phelsuma sp.	Loveridge, Bull.M.C.Z. 89:437, 1942
Phrynobatrachus pakenhami & acridoides diff.	Loveridge, Proc.Biol.Soc.Wash. 54:175, 1941
Thrasops sp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Thrasops jacksonii subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942
Typhlops tettensis subsp.	Loveridge, Bull.M.C.Z. 91:235, 1942

Pemba Island

Natrix olivacea subsp.	Loveridge, Bull.M.C.Z. 79:1, 1935
Phrynobatrachus pakenhami & acridoides diff.	Loveridge, Proc.Biol.Soc.Wash. 54:175, 1941

THE CONGO - See ZAIRE

TOGO

Serpentes gen., sp.	Sternfeld, Mitt.Zool.Mus.Berl. 4:207, 1908
Gerrhosaurus sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919

TROPICAL AFRICA

Mehelya sp.	Loveridge, Bull.M.C.Z. 86:129, 1939

TUNISIA

Amphibia subcl. to subsp.	Doumergue, Amsterdam 1901 reprnt, 1972
Reptilia subcl. to subsp.	Doumergue, Amsterdam 1901 reprnt, 1972

UBANGI - SHAIR

Gonionotophis sp.	Loveridge, Bull.M.C.Z. 86:129, 1939

UGANDA

Amphibia ord. to sp.	Loveridge, P.Z.S.Lond. 7, 1930
Lacertilia fam. to sp.	Loveridge, P.Z.S.Lond. 841, 1923
Testudinata fam. to sp.	Loveridge, P.Z.S.Lond. 923, 1923
Chamaesaura sp.	Boulenger, P.Z.S.Lond. 96, 1899
Rhamnophis, Thrasops diff.	Pittman, Uganda J. 4:41, 1936
Thrasops, Rhamnophis diff.	Pittman, Uganda J. 4:41, 1936

UPPER VOLTA

Naja sp.	Roman, Rev.Zool.Bot.Afr. 79:1, 1969

URUNDI - See BURUNDI

WEST AFRICA

Amphibia fam. to sp.	Perret, Zool.Jb.Syst. 98:289, 1966
Serpentes fam. to sp.	Boulenger, P.Z.S.Lond. 267, 1919
sp.	Villiers, IFAN 2:1, 1963; Knoepffler, Biol.Gabon. 4:183, 1968
Testudinata subord. to sp.	Villiers, IFAN 15:1, 1958
Ancylodactylus spinicollis, Cnemaspis africanus & occidentalis diff.	Grandison, Bull.IFAN 18:224, 1956
Boaedon sp.	Gunther, An.Mag.N.H. 1:322, 1885
Boodon - see Boaedon	
Cnemaspis africanus, C. occidentalis & Ancylodactylus spinicollis diff.	Grandison, Bull.IFAN 18:224, 1956
Geotrypetes & Uraeotyphlus of Orient diff.	Parker, An.Mag.N.H. 20:478, 1927
Gonionotophis sp.	Loveridge, Bull.M.C.Z. 86:129, 1939
Kassina sp.	Schiotz, Spol.Zool.Mus.Haun. 25:1, 1967
Kinixys sp.	Gray, P.Z.S.Lond. 192, 1863
Kinothorax - see Kinixys	
Lycophidian sp.	Parker, An.Mag.N.H. 12:544, 1933
Naja sp.	Roman, Rev.Zool.Bot.Afr. 79:1, 1969
Nectophrynoides occidentalis, vivipara & tornieri diff.	Guibe, Lamotte, Mem.IFAN 53:241, 1958
Rana tigrina occipitalis diff. from Asian R. tigrina subsp.	Boulenger, Rec.Ind.Mus. 20:1, 1920
Pelusios sp.	Gray, P.Z.S.Lond. 192, 1863
Tarentola mauritanica deserti, & m. mauritanica diff.	Pasteur, Girat, Bull.Sci.Nat.Maroc. 40:309, 1960
	See also Loveridge, Bull.M.C.Z. 98:1, 1947
Uraeotyphlus sp. of Orient & Geotrypetes sp. diff.	Parker, An.Mag.N.H. 20:478, 1927
Xenopus sp.	Arnoult, Lamotte, IFAN 30:270, 1968
Xenopus tropicalis & fraseri diff.	Guibe, Lamotte, Mem.IFAN 53:241, 1958

ZAIRE

Anura sp.	Noble, Bull.A.M.N.H. 49:147, 1924
Serpentes fam. to sp.	Boulenger, P.Z.S.Lond. 193, 1915; Laurent, An.Mus.Roy.CongoTerv. 48:1, 1956
fam., gen.	deWitte, Mus.Roy.Afr. 104, 1962
Testudinata gen.	Schmidt, Bull.A.M.N.H. 39:385, 1919
fam. to sp.	Laurent, An.Mus.Roy.CongoBelg. 48:1, 1956
Agamidae sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Anelytropidae sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Boulengerina sp.	Boulenger, An.Mag.N.H. 14:14, 1904
Chamaeleo sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Chlorophis sp.	Schmidt, Bull.A.M.N.H. 49:1, 1923
Gekkonidae gen., sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Gerrhosaurus sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Grayia sp.	Schmidt, Bull.A.M.N.H. 49:1, 1923
Hymenochyrus sp., subsp.	Arnoult, Lamotte, Bull.IFAN 30:270, 1968
Lacertidae gen.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Megalixalus sp., subsp.	Laurent, Rev.Zool.Bot.Afr. 39:119, 1941
Rhamnophis sp.	Schmidt, Bull.A.M.N.H. 49:1, 1923
Scincidae sp.	Schmidt, Bull.A.M.N.H. 39:385, 1919
Thrasops sp.	Schmidt, Bull.A.M.N.H. 49:1, 1923

Garamba National Park

Xenopus sp.	Inger, Expl.Nat.Pk.Garamba 52:1, 1968

Upemba National Park

Phrynobatrachus sp.	Schmidt, Inger, Inst.Parc.Nat.CongoBelg. 56:1959
Rana (Ptychadena) sp.	Schmidt, Inger, Inst.Parc.Nat.CongoBelg. 56, 1959

ZAMBIA

Amphibia fam. to sp.	Broadley, Puku.Occ.Pap.Zamb. 6:1, 1971
Reptilia fam. to sp.	Broadley, Puku.Occ.Pap.Zamb. 6:1, 1971
Serpentes fam. to sp.	Boulenger, P.Z.S.Lond. 193, 1915
sp.	Vesey, Fitzgerald, Proc.Trans.RhodesiaSci.Assoc. 46:17, 1958
Ptychadera sp.	Poynton, Senck.Biol. 45:193, 1964

ZANZIBAR - See TANZANIA

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