

A New Species of Grass Snake, *Natrix megalcephala*, from the Caucasus (Ophidia: Colubridae)[†]

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

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

Introduction

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

Methods

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

A comparative description of skulls in

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

Results

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

Nomenclature Remarks

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

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

[†] This publication combines material previously published in Russian by Orlov and Tuniyev (1986a) with additional information.

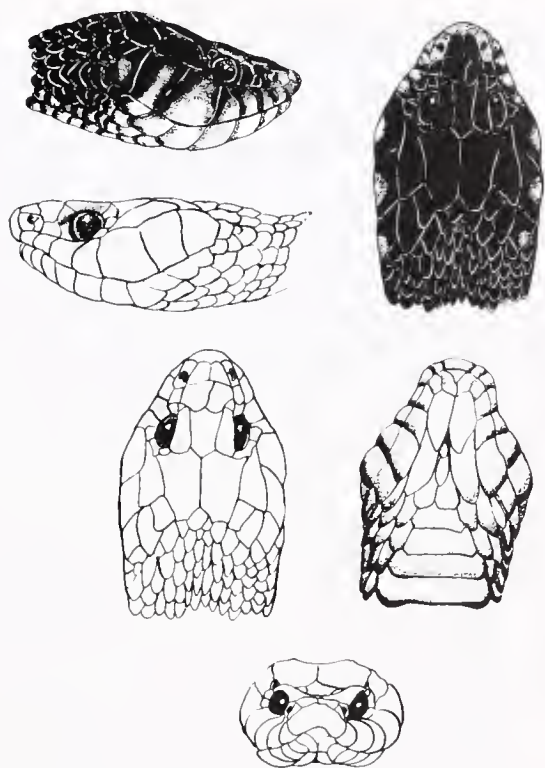


FIG. 1. Various views of the head of the holotype (ZIN 11846) of *Natrrix megaloccephala* from Pitsunda, Abkhazia, Georgia.



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

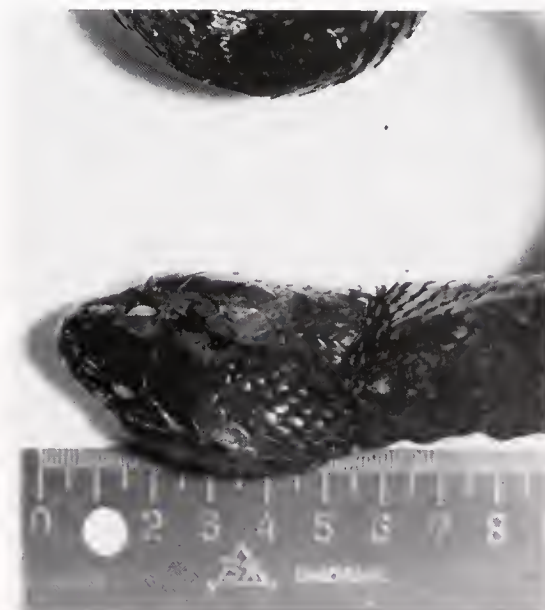


FIG. 2. The head of the holotype (ZIN 11846) of *Natrrix megaloccephala* from Pitsunda, Abkhazia, Georgia.



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

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

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

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

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

Natrix megalcephala
Orlov and Tuniyev, 1986

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

Description of holotypes.—SVL 960

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

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

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

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

TABLE I. Morphological characters of *Natrix megalcephala*.

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

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

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

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

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

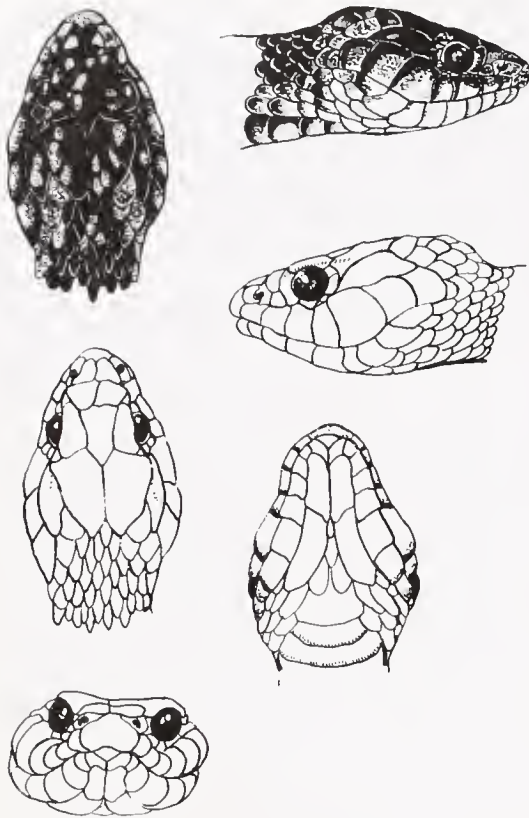


FIG. 5. Various views of the head of *Natrix megalcephala* from Lagodekhi, Georgia.

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

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

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



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

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

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

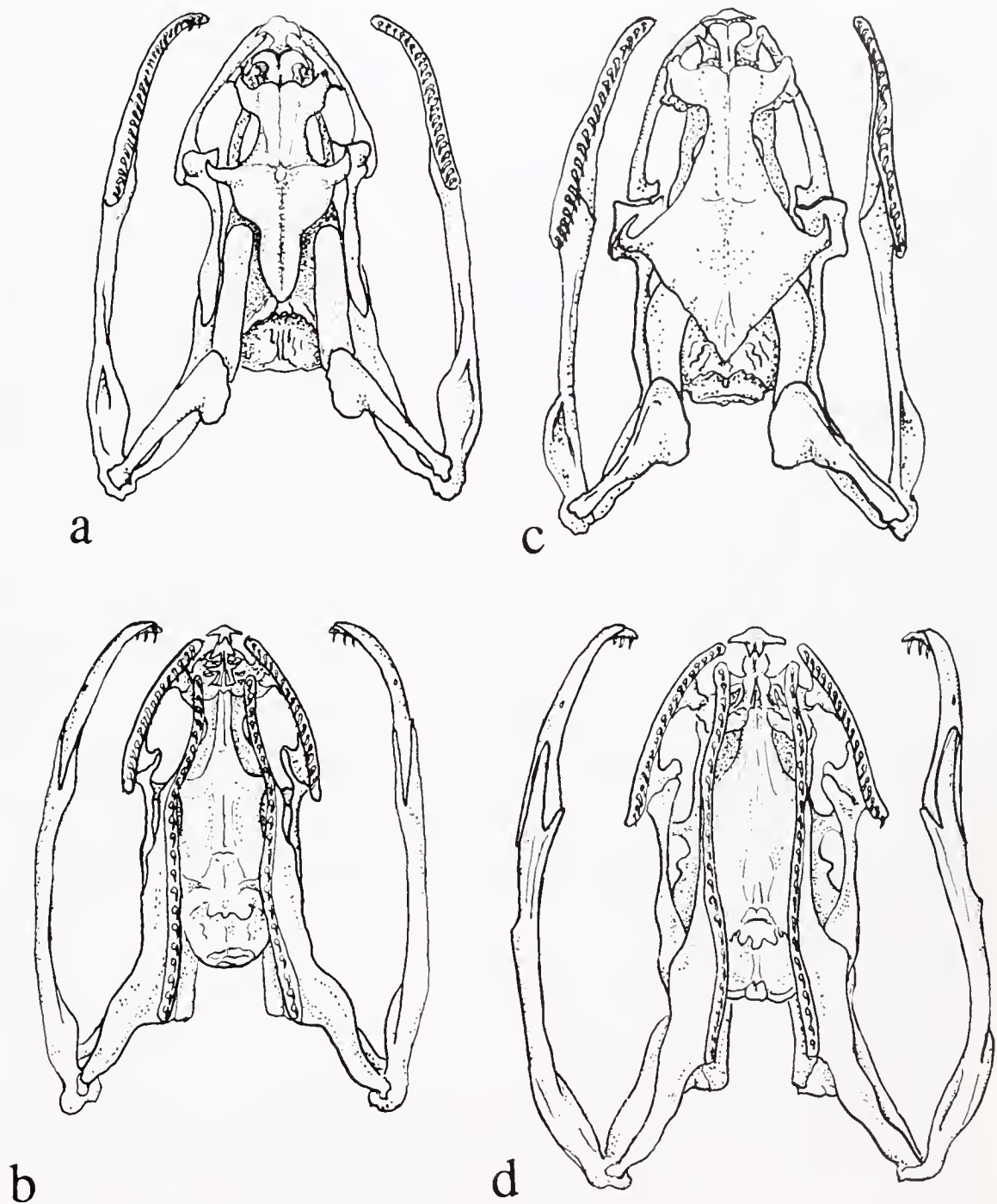


FIG. 7. Skulls of *Natrrix natrix scutata* (a, b) and *Natrrix megalcephala* (c, d).

encountered.

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

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

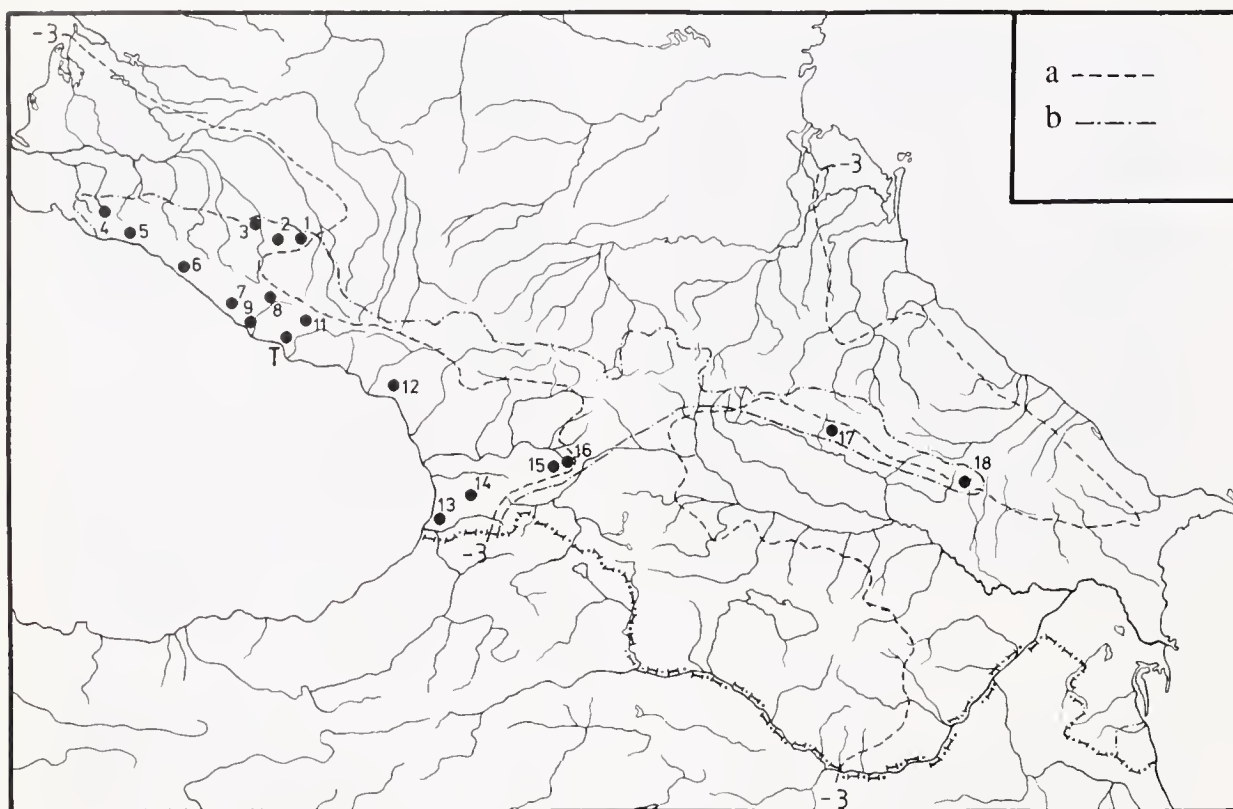


FIG. 8. Distribution of *Natrrix megalcephala*. Russia, Krasnodarsky Territory: 1- mouth of the Urushten River; 2- Kisha Cordon, Caucasian Reserve; 3- Stanitsa (a small settlement in the country side) of Khamyshki; 4- Tuapse; 5- Lazorevskoye; 6- Sergei-Pole; 7- Sochi; 8- Malaya Khosta River; 9- Yew-box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

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

Breeding.—A female *N. megalcephala*,

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

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

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

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

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

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

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

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

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

Shedding.—We observed snakes

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

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

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

Discussion

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

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

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

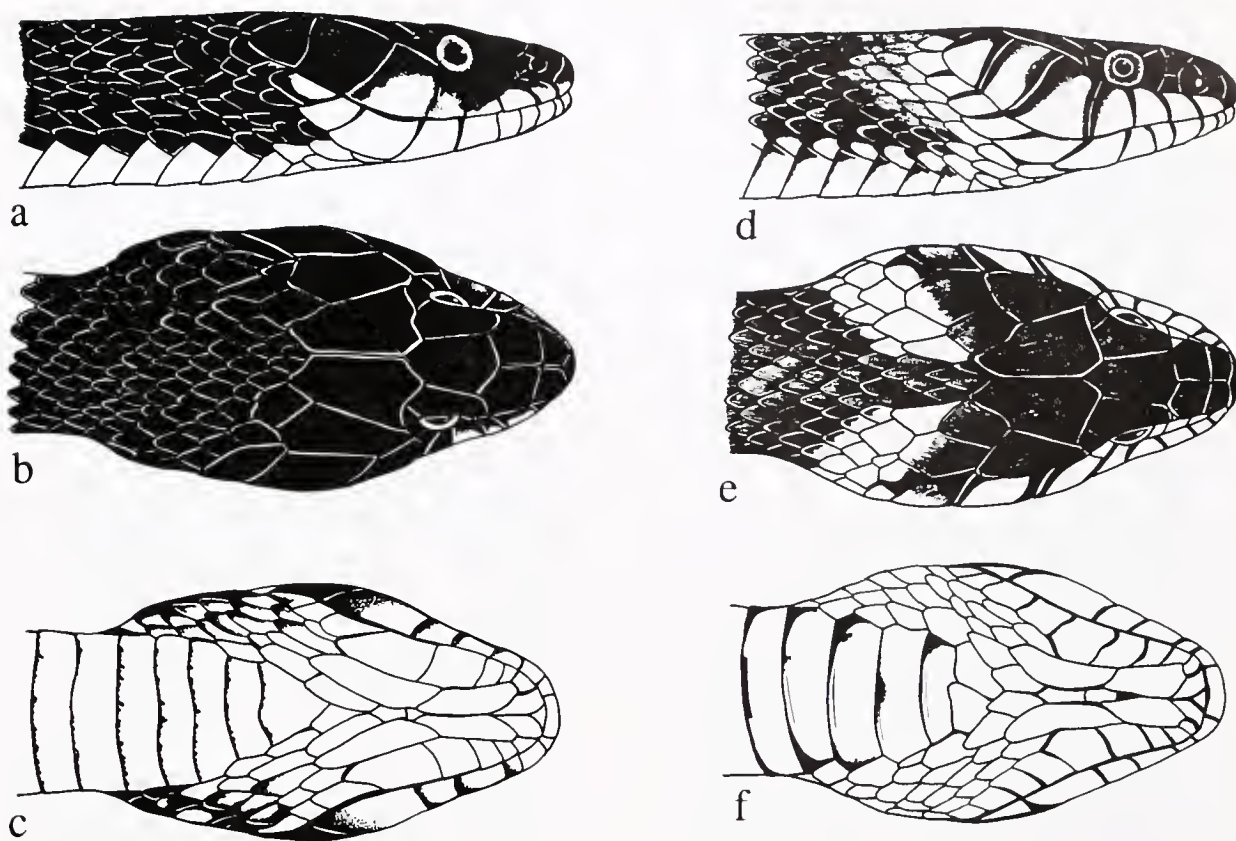


FIG. 9. The heads of *Natrix megalcephala* (a, b, c) and *Natrix natrix scutata* (d, e, f) from sympatric populations at Stanitsa of Khamyshki, Krasnodarsky Territory, Russia.

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

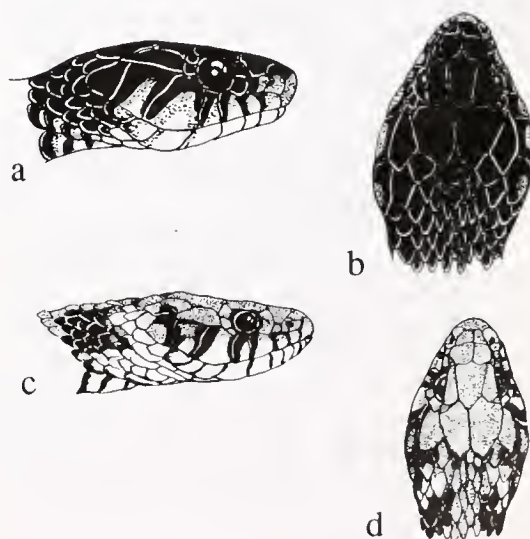


FIG. 10. The heads of *Natrix megalcephala* (a, b) and *Natrix natrix scutata* (c, d) from sympatric populations in the vicinity of Pitsunda, Abkhazia, Georgia, the type locality for *Natrix megalcephala*.

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

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

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

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

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

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

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