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**Systematics and Evolution of the Species Group *Coluber jugularis*
Linnaeus, 1758 – *Coluber caspius* Gmelin, 1789 (Reptilia, Serpentes)**

**Thesis submitted for the Degree “Doctor of Philosophy”
By Hermann ZINNER**

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SUMMARY

The two species *C. jugularis* and *C. caspius* and their subspecies are distributed from the eastern Mediterranean to central Iran. Because of their apparent adult polychromism but similar juvenile forms up to now their systematical status was not clear.

In the course of this work numerous collection trips were made in nearly all areas of distribution. On the basis of private collections and material from various museums the systematics of this species-group was revised.

All known forms were separated into two species with three subspecies each. The Separation into two species is based on the statistical evaluation of pholidotical counts

and ecological and ethological differences. The new subspecies were described. The revised and described forms are:

Coluber jugularis jugularis Linnaeus 1758

Coluber jugularis asianus Böttger 1880

Coluber jugularis cypriacus ssp. nov.

Coluber caspius caspius Gmelin 1789

Coluber caspius schmidtii Nikolski 1909

Coluber caspius eiselti ssp. nov.

Keys for live and preserved specimens were worked out, the distribution of the two species mentioned above and of *Coluber gemonensis* Laurenti and literature on the climatic and geologic changes in the area of distribution served as a basis for a hypothetical time scheme of the phylogenetic development within the species group.

From a supposedly common ancestor *C. gemonensis* was split off on the Balkan peninsula as a result of the development of colder climate. In southern Turkey, Lebanon and Israel *C. jugularis* evolved in the late pliocene, then isolated from the common ancestor, which already then presumably was very similar to *C. caspius*.

The climatic scintillations of the pleistocene and the Separation of Mediterranean islands from the mainland brought forth the six subspecies of *C. jugularis* and *C. caspius*.

C. caspius eiselti, which during the pleistocene connected the two species as a transitional form, remained after the last ice age isolated on the Island of Rhodes.

INTRODUCTION

In the year 1758 Linnaeus described *Coluber jugularis* in his 10-th edition of Systema Naturae as follows: Ater, jugulo sanguinolento, habitat in Aegypto. He also gives measures and a scale count in this description and determines his specimen as a male.

This specimen reached Sweden together with the collection of Hasselquist who died a few years before, in Smyrna. ANDERSSON (1898) states that neither this nor a similar species was ever found in Egypt. He declares also that Linnaeus' scale count is erroneous giving his own scale count and that of Mr. Smitt, who was at that time working for the Royal Museum in Sweden. All three counts differ from each other.

A vast number of species and genera of species identical or closely related to *C. jugularis* were described by many authors (see list of Synonyms in BOULENGER 1895 and MERTENS & WEBMUTH 1960). In all these publications Linnaeus' Type Specimen was disregarded or just used as reference without closer investigation. Even in most recent times, RAI repeated without hesitation the Linnean Terra Typica and drew even from this description the conclusion that the Saharo-Arabian area might be the evolution center of the whole species group (1965 and pers. comm.).

The Situation of most of the European collections in the last decades showed mainly determinations according to localities or according to superficial similarities to other specimens which were already determined before by other scientists.

As in all forms of the Rassenkreis the juveniles differ in color pattern and proportion from the adults. Descriptions were made of new species on the basis of juvenile specimens, NIKOLSKII (1909), BOETTGER (1880).

Most of the recent authors who dealt in their publications with the species group *C. caspius - jugularis* unhesitatingly copied the original descriptions or what they thought to be the original descriptions. Some recent authors assume GMELIN (1789) to be the author of *C. caspius*. SCHREIBER (1912), BOULENGER (1895) and others assume IWAN (1769) to be the author. Not one has sufficiently substantiated his assumption. There was never a Type Specimen as a basis of Gmelin's description, yet even Russian authors such as NIKOLSKII (1916) and TERENCEV & CHERNOV (1949) did not bother about the original description of IWAN (1769). Had they checked the original literature of Iwan and Gmelin they would have discovered that Iwan was only the private name of I. Lepechin who described *C. caspius* for the first time in his book on voyages in Russia and gave, even for modern taxonomy, an astonishingly exact description. Gmelin merely translated Lepechin's description and even translated it with some mistakes.

Several authors, NIKOLSKII (1916), BOETTGER (1880), SCHREIBER (1912) and others, discussed in their publications the problem whether or not *C. viridiflavus*, *C. gemonensis*, *C. schmidtii*, *C. caspius*, *C. jugularis* etc. were good species or just subspecies of one species.

While working on ecological studies of *C. caspius* and *C. jugularis*. I found myself confronted with all the systematic problems described above.

The necessity arose to rearrange the systematics and taxonomy of the group, in spite of the insufficiency of purely morphological taxonomy.

Preliminary field studies showed that some of the forms differ in behavior as well as niche selection. The zoogeographical distribution of all the species and subspecies mentioned above on mainland and islands presented a good basis for thought about the phylogenetical development.

The aim of this thesis is to describe the systematic relationships among all forms of the *C. caspius - jugularis* group on the basis of morphological features as well as ethology and ecology, to describe two new subspecies: and attempt to reconstruct the evolution of the entire group on the basis of our knowledge about geological and climatic changes in its area of distribution and the recent pattern of distribution on mainland and islands.

MATERIAL AND METHODS

As a basis for taxonomical investigations, about 600 specimens of snakes supposedly belonging to the Rassenkreis *C. caspius - jugularis* were examined. Part of the material was examined in the collections, and part was sent to me in Jerusalem for further study.

The greater part of the material stems from the collections of the Natural History Museum, Vienna; the Natural History Museum, Basel; the Senckenberg Museum, Frankfurt; the Natural History Museum, Istanbul; the Zoological Department of the Aegean University in Izmir; American University, Beirut; the Zoological Department of

the University, Teheran; and the Zoological Department of the Hebrew University of Jerusalem.

Altogether 62 specimens were collected by me in various places of the distribution area, and preserved. These specimens are part of my own reptile collection.

Some of the existing Type Specimens were photographed by me and photographs of the rest were supplied by the Natural History Museum, Stockholm and the Senckenberg Museum, Frankfurt.

For pholidotical investigations, a selection of 164 fully grown undamaged specimens with complete tails was made from the total number of available specimens.

As nearly all the material investigated was preserved, it was not possible to work on the population genetics of this group.

Altogether 52 specimens were kept alive for periods of from two months to five years. Attempts were made to breed them but not even specimens belonging to the same subspecies mated. Since in nature even one generation lasts for several years, breeding experiments would have required far more time than was available within the scope of this work.

As not all forms were available as live specimens, no cytogenetical investigations were made. A few tests showed that Colubrids are extremely conservative in their karyotypes and hardly show any specific differences even in more distantly related species (GORMAN 1970, pers. comm.).

Eighteen collecting trips were made in all countries within the distribution area with the exception of Russia and Rumania. About 180 specimens were collected alive and in some areas e.g. Yugoslavia, Greece and Israel, they were marked and released. Seventeen of the marked specimens were collected again, most of them within a few months, but two of them only after two years, and all of the recollected specimens served as a basis for Information about territorial behavior. All habitats were photographed, some of them during different seasons, and ethological observations were carried out in the field. Altogether 15 months were spent investigating the habitat.

Microclimatic observations were made in most of the areas. These observations were made partly, and with limited accuracy, using minimum-maximum thermometers and "Lufft" - hygrometers and partly using a "Yellowsprings" - telethermometer.

List of Material (Preserved Specimens) used for Systematic Investigations and Statistical Evaluations

No.	Coll.	No.	Species	V.	SC.	Squ.	Locality	
1	NMW	15192	<i>C. schmidtii</i>	199	107	19	Sultanabad	Iran
2	IZM	131/69	<i>j. jugularis</i>	208	114	19	Viransehir	Turkey
3	IZM	161/69:1	<i>j. jugularis</i>	202	109	19	Viransehir	Turkey
4	NMW	18618:1	<i>c. eiselti</i>	197	95	19	Lindos	Rhodes

5	IZM	185/69:1	c. schmidtii	198	92	19	Van	Turkey
6	NMW	19506	g. gemonensis	170	70	19	Dukati	Albania
7	NMW	19507:4	v. viridiflavus	199	97	19	Mamsiade	Sardinia
8	NMW	15181:4	c. caspius	197	109	19		Romania
9	IZM	159/69	c. schmidtii	207		19	Viransehir	Turkey
10	NMW	18618:2	c. eiselti	191		19	Pefki, Lindos	Rhodes
11	NMW	15180:2	c. caspius	202	101	19	Krim	USSR
12	NMW	18618:3	c. eiselti	194	110	19	Lindos	Rhodes
13	NMW	15181:3	c. caspius	195	99	19	Rustschuk	Bulgaria
14	NMW	15186:3	j. cypriacus	?		19		Cyprus
15	NMW	15186 :1	j. cypriacus	204	113	19		Cyprus
16	NMW	15186:2	j. cypriacus	203	112	19		Cyprus
17	NMW	15186 :6	j. cypriacus	202	104	19		Cyprus
18	NMW	15186 :7	j. cypriacus	202	100	19		Cyprus
19	NMW	15186:4	j. cypriacus	197	97	19		Cyprus
20	IZM	193/69	j. jugularis	203	108	19	Diyarbakir	Turkey
21	IZM	161/69:2	j. jugularis	203	117	19	Viransehir	Turkey
22	NMW	15181:1	c. caspius	194	93	19	Budapest	Hungary
23	IZM	1	c. caspius	202		19	Izmir	Turkey
24	HZC	31	j. asianus	208	121	19	En Hashofet	Israel
25	HZC	32	c. caspius	199	109	19	Kavalla	Greece
26	HZC	33	j. asianus	208	122	19	Gaza	Israel
27	HZC	34	c. schmidtii	197	107	19	Homs	Syria
28	HZC	35	c. caspius				Erzincan	Turkey
29	HZC	51	g. gemonensis	172	95	19	Zadar	Yugoslavia
30	HZC	21	j. cypriacus				Limassol	Cyprus
31	HZC	22	j. jugularis	201	107	19	Ephesus	Turkey
32	HZC	36	j. asianus	206	120	19		Israel
33	HZC	37	c. caspius	209	103	19	Kavalla	Greece
34	IZM	2	c. caspius	205	110	19	Izmir	Turkey
35	IZM	3	c. caspius	202	112	19	Izmir	Turkey
36	IZM	4	c. caspius	219	102	19	Izmir	Turkey

37	HZC	23	j. jugularis	207	105	19	Ephesus	Turkey
38	HZC	38	j. asianus	208	120	19	Jerusalem	Israel
39	NMW	15189:1	c. schmidtii	202	97	19	Sultanabad	Iran
40	IZM	129/69	j. jugularis	203	105	19	Urfa	Turkey
41	NMW	15189:2	c. schmidtii	206	103	19	Sultanabad	Iran
42	NMW	15181:2	c. caspius	203	98	19	Budapest	Hungary
43	IZM	164/69	c. schmidtii	196		19	Akcakkale	Turkey
44	NMW	15186:5	j. cypriacus	210	87	19		Cyprus
45	NMW	15185 :2	j. cypriacus	204	102	19	Platraes	Cyprus
46	NMW	15180:3	c. caspius	198		19	Krim	USSR
47	IZM	194/69	j. jugularis	201		19	Birecick	Turkey
48	IZM	185/69:2	c. schmidtii	207	84	19	Van Gölü	Turkey
49	NMW	15186:8	j. cypriacus	205	106	19		Cyprus
50	NMW	15180:6	c. caspius	206	105	19	Odessa	USSR
51	NMW	18619	j. jugularis	193	106	19	Jermuk	Turkey
52	IST		j. jugularis	207	117	19	Diyarbakir	Turkey
53	NMW	18701:1	c. caspius	193	98	19	Slivno	Yugoslavia
54	NMW	18701:2	c. caspius	200	111	19	Kupinova	Yugoslavia
55	NMW	18701:3	c. caspius	193	102	19	Plovdiv	Bulgaria
56	NMW	15191	c. caspius	187	102	19	Aksehir	Turkey
57	NMW	15180:2	c. caspius	199	108	19	Dobrukscha	Romania
58	NMW	18702	c. caspius	199	101	19	Istanbul	Turkey
59	NMW	18718:1	c. caspius	196	105	19	Skopelevo	Bulgaria
60	NMW	18717:2	c. caspius	196	89	19	Tresca	Yugoslavia
61	NMW	15179:1	c. caspius	202	101	19	Corfu	Greece
62	NMW	15179:6	c. caspius	205	93		Budapest	Hungary
63	NMW	15179:5	c. caspius	197	104		Fehertemplon	Hungary
64	NMW	18716:1	c. caspius	197	100		Crna Zemlia	USSR
65	NMW	18716:2	c. caspius	206	99		Crna Zemlia	USSR
66	NMW	18621	c. caspius	202	101			Hungary
67	NMW	7269:1	j. jugularis	204	101		Adana	Turkey
68	SMF	11198	jugularis ??	202	114		Aleppo	Syria

69	SMF	60218	c. eiselti	189	118		Lindos	Rhodes
70	SMF	53076	c. caspius	204	104		Ancara	Turkey
71	SMF	18178	c. caspius	194	109		Sinope	Turkey
72	SMF	60217	c. caspius	192	100		Karpathos	Greece
73	SMF	18189	j. asianus	207	109		Jerusalem	Israel
74	SMF	18177	c. caspius	207	98		Krim	USSR
75	SMF	45302	jugularis	205	88		Ararat	Turkey
76	SMF	18179	c. caspius	203	109		Chios	Greece
77	SMF	36655	c. caspius	196	106		Sebastopol	USSR
78	NMB	12941	j. jugularis	203	102		Mardin	Turkey
79	NMB	15401	c. caspius	199	105		Othiys-mt.	Greece
80	NMB	15193	c. caspius	202	108		Vardar	Yugoslavia
81	UTA	8713	j. asianus	209	110	19	Ayanot	Israel
82	UTA	8628	j. asianus	207	97	19	Kvuzat	Israel
83	UTA	8712	j. asianus	206	95	19	Avish-Gaeh	Israel
84	UTA	8714	j. asianus	213	105	19	Aylet Hashchar	Israel
85	UTA	8581	j. asianus	193	108	19	Bar-Ilan Univ.	Israel
86	UTA	8526	j. asianus	202	117	19	Yavney	Israel
87	UTA	8626	j. asianus	212	113	19	Bukatah- Golan	Israel
88	UTA	3069	j. asianus	210		19	Abu-Cabir	Israel
89	UTA	6712	j. asianus	206	97	19	Mique	Israel
90	UTA	6561	j. asianus	221	123	19	Abu-Cabir	Israel
91	UTA	3222	j. asianus	201	101	19	Beary	Israel
92	UTA	7097	j. asianus	195	115	19	Netania	Israel
93	UTA	7459	j. asianus	211		19	Yakum	Israel
94	UTA	2248	j. asianus	205		19	Saad	Israel
95	UTA	1886	j. asianus	206	121	19	T.A. surroundings	Israel
96	UTA	1713	j. asianus	198	120	19	Rishon-Le- Zion	Israel
97	UTA	2266	j. asianus	208	116	19	Botanical garden	Israel
98	UTA	2267	j. asianus	202	113	19	Neveh- Monosson	Israel
99	UTA	3318	j. asianus	199	132	19	Lavah	Israel

100	UTA	2550	j. asianus	214	68	19	Jaffa	Israel
101	UTA	3875	j. asianus	208		19	Saad	Israel
102	UTA	3831	j. asianus	208	120	19	Hulata	Israel
103	UTA	1412	j. asianus	209	106	19	Hagoshrim	Israel
105	Literature		j. asianus	205	109		Jerusalem	Israel
106	Literature		j. asianus	211	115		Jerusalem	Israel
107	Literature		j. jugularis	202	105		Halicornassos	Turkey
108	Literature		j. cypriacus	203	131			Cyprus
109	Literature		j. cypriacus	205	112			Cyprus
110	Literature		j. cypriacus	204	113			Cyprus
111	Literature		j. cypriacus	201	111			Cyprus
112	Literature		j. cypriacus	211	105			Cyprus
113	Literature		j. cypriacus	206	103			Cyprus
114	Literature		j. cypriacus	207	113			Cyprus
115	Literature		j. asianus	212	107			Israel
116	Literature		j. asianus	205	105		Merom	Israel
117	Literature		j. asianus	214	125		Merom	Israel
118	Literature		j. asianus	209	115		Merom	Israel
119	Literature		j. asianus	204	119		Galilea	Israel
120	Literature		j. asianus	209	122		Galilea	Israel
121	Literature		c. caspius	187	96		Anatolia	Turkey
122	Literature		c. caspius	197	100		Anatolia	Turkey
123	Literature		c. schmidtii	204	85		Kurdistan	Turkey
124	Literature		c. schmidtii	206	84		Kurdistan	Turkey
125	Literature		c. schmidtii	196	86		Kurdistan	Turkey
126	Literature		c. schmidtii	201	82		Kurdistan	Turkey
127	Literature		c. schmidtii	188	91		Kurdistan	Turkey

SEPARATION OF *COLUBER JUGULARIS* AND *COLUBER CASPIUS* INTO TWO SPECIES ON BASIS OF PHOLIDOTICAL STATISTICS. JUVENILE AND ADULT COLORATION. SYMPATRY AND BIOTOPE SELECTION

All forms, having been described under various taxa, which are lined up in my list of Synonyms, belong to one big species-group (Artenkreis, RENSCH, 1929). This fact was responsible for a lot of confusion in systematic literature, ANDERSSON (1898), NIKOLSKI (1916), SCHREIBER (1912), BOULENGER (1893), WERNER (1928) and WETTSTEIN (1953).

In the first half of the Century some authors included *C. caspius* and *C. jugularis* into *C. gemonensis*. (NIKOLSKI 1916, SCHREIBER 1912.) Other authors dealt with *C. gemonensis* being an own species and included *C. caspius* into the species *C. jugularis*.

The basic error for the mixing of *C. jugularis* and *C. caspius* was the opinion that Melanotic Forms occur in all populations. This opinion was held by NIKOLSKI (1916), TARENT'EV and CHERNOV (1949) and previously even by BODENHEIMER (1935).

During my investigations I found out: there are no melanotic species in *C. caspius* populations (one black specimen of *C. caspius* mentioned by WETTSTEIN (1953) from Greece, is not available, as Wettstein never used Collection Numbers; a dark Transitional Form between *C. caspius* and *C. jugularis* exists on the Island of Rhodes, which morphologically and pholidotically resembles *C. caspius*; all adult *C. jugularis* are dorsally black. With the exception of *C. c. eiselti* from Rhodes all juvenile *C. caspius* have uniformly light ventral surfaces and all juvenile *C. jugularis* show a spotted pattern on the ventral.

Second Key to the Species of *Coluber caspius* and *Coluber jugularis* For determination of live adult specimens of more than 1500 mm in length.

- 1 Dorsum black.....2
Dorsum other than black..... 3
- 2 Upper side of head clouded or spotted ventrum orange to brickred,
black blotches from throat to subcaudal region.....***Coluber caspius eiselti***
Upper side of head uniform black.4
- 3 Dorsum greyish brown to olivaceous, broad light longitudinal streak on
dorsalscutes ventrum white to yellow, unspotted.....***Coluber caspius caspius***
Dorsum orange to bright brickred, light streak on dorsal scutes
faint or absent, ventrum yellow to orange unspotted.... ***Coluber caspius schmidtii***
- 4 Ventrums uniform black or greyish black, gular region and labials white
.....***Coluber jugularis asianus***
Ventrums and sides of neck bloodred, densely spotted or clouded
with black, narrow red longitudinal streak on dorsal scutes, gular
region and labials yellow.....***Coluber jugularis jugularis***
Ventrums from second to fourth fifth dark grey to black with occasional
red spots, first and last fifth spotted or clouded with black on purplish
back-ground, narrow red streak on dorsal scutes,
gular region yellow.....***Coluber jugularis cypriacus***

Scale counts in both species show significant differences as well for sexual dimorphism, as also indicating two different species.

In both species ventral and subcaudal scale counts show increases in number of scales from the north to the south of distribution and from mountain dwelling populations to those inhabiting coastal regions.

For adult *C. caspius* and *C. jugularis* including all subspecies I worked out a Key to determine adult specimens alive and, as some of the colors fade in the preservatives, also a Key to determine preserved specimens.

First Key to the Species of *Coluber caspius* and *Coluber jugularis*

For determination of adult specimens of more than 1500 mm in length which were preserved for more than one year

- 1 Dorsum black..... 2
Dorsum other than black..... 3
- 2 Upper side of head clouded or spotted ventrum yellow to ochraceous, black blotches from throat to subcaudal region..... *Coluber caspius eiselti*
Upper side of head uniform black..... 4
- 3 Dorsum grey to greyish brown, sometimes olivaceous, light broad longitudinal streak on dorsal scutes, ventrum pale, unspotted.....*Coluber caspius caspius*
Dorsum light brown to reddish brown, light streak on dorsal scutes faint or absent, ventrum yellow to ochraceous, unspotted.....*Coluber caspius schmidtii*
- 4 Ventrums uniform black or greyish black, gular region and labials light.....*Coluber jugularis asianus*
Ventrums densely spotted or clouded blackish on light background, narrow light streak on dorsal scutes, gular region and labials light..*Coluber jugularis jugularis*
Ventrums from second to fourth fifth uniform black to dark grey, first and last fifth spotted or clouded, narrow light streak on dorsal scutes, gular region light.....*Coluber jugularis cypriacus*

Statistical Evaluation of Ventral and Subcaudal Scale Counts in Adult Specimens of *C. jugularis* and *C. caspius* from Various Museums, Own Collection and Literature:

Sex	Species	Ventrals*	P(t)	Subcaudals*	P(t)
♂	jugularis	205,6 ± 4,5(37)	-	115,0 ± 7,0(37)	-
♂	caspius	195,9 ± 4,9(27)	0,001	104,7 ± 6,2(27)	0,001
♀	jugularis	207,5 ± 3,2(21)	-	102,8 ± 7,1(21)	-
♀	caspius	203,0 ± 3,8(20)	0,001	95,0 ± 7,6(20)	0,001
♀+♂	jugularis	205,0 ± 4,5(58)		110,6 ± 9,1(58)	
♀+♂	caspius	199,9 ± 5,6(47)	0,001	100,6 ± 8,3(47)	0,001

Sex	Species	Ventrals and Subcaudals*	P(t)
♂	jugularis	318,6 ± 9,4(37)	-
♂	caspius jugularis	300,6 ± 9,4(27)	0,001
♀	caspius	310,1 ± 8,8(21)	-
♀		297,6 ± 9,4(20)	0,001

*Mean ± Standard error (number of Specimens).

The graphical evaluation of the same counts shows clearly the split into two species and the sexual dimorphism of both species. (See graphs 1, 2, 3, 4).

During polydotal investigations of *Coluber jugularis* and *caspius* another significant characteristic turned up. The two species and their sub-species differ from each other in the proportions of their lateral scales. The most significant differences are found in the second lateral scale row on both sides, at around midbody.

It is difficult to define the term "midbody". Usually in systematics of snakes the number of scale rows is given at "midbody". In the case of *Coluber jugularis* and *caspius* I found 19 scale rows without exception, but usually not at midbody but at the beginning of the second third of the distance from snout to cloaca. At "midbody" there are usually 15-17 scale rows; the application of DOWLING'S (1951) Method in *C. caspius* and *C. jugularis* did not bring helpful or significant results.

The scales of the second lateral row on both sides in *C. jugularis* and *C. caspius* between the area of 19 scale rows and "midbody" show surprisingly constant proportions. In areas in southwestern Turkey where *C. jugularis* and *C. caspius* are found sympatrically, these scales are much broader and shorter in *C. caspius* than in *C. jugularis* (see Figs. 9, 10). These differences can only be seen in fully grown specimens. This is due to the fact that fully grown *C. caspius* of the same length as *C. jugularis* are always much bulkier. The widest scales I found in *C. caspius eiselti* on Rhodes.

Within *Coluber jugularis* the nominate race shows the narrowest and longest scales, the scales of *C. jugularis cypriacus* being a little shorter and broader and *C. jugularis asianus* showing the shortest and broadest scales, this subspecies also being the bulkiest of the three.

Coluber caspius shows a cline from the broadest scales in the southwest (*C. caspius eiselti*) still broad and short scales in the western area of distribution of *C. caspius caspius* becoming gradually narrower to *C. caspius schmidtii* and showing the narrowest and longest scales in the southernmost populations of *C. caspius schmidtii* in southern Iran, central Iraq and Syria.

In southwestern Turkey a broad-scaled *caspius* lives sympatrically with a narrow-scaled *jugularis*. In Syria and Lebanon a broad-scaled *jugularis* meets a narrow-scaled *C. caspius*.

These differences in scale proportions give another basis for Separation into two species.

The two species differ in the shape of the head, but this can be seen only in fully adult specimens. The heads of adult *C. jugularis* (see Figs. 11, 12, 15) are more elongated than those of *C. caspius* (see Figs. 22, 23, 24) and show a distinct edge on both dorsolateral sides, running through the lateral parts of the internarals, prefrontals, supraoculars, the anterior quarter of the parietals and the upper half of the upper preoculars. This edge is absent or only weakly developed in *C. caspius*.

Pholidotical variability is found in a few shields on the dorsal side of the heads of both species. The figures 11, 12, 15, 22, 23, 24, show the shape of shields in about 90% of the population, supraoculars meeting prefrontals. In about 10% of the specimens of both species the upper preoculars are elongated dorsally, touch the frontal and separate prefrontals from supraoculars.

As mentioned above, *Coluber jugularis* and *Coluber caspius* live sympatrically in southwestern Turkey. In southeastern Anatolia and northern Kurdistan the nominate race of *C. jugularis* was found sympatrically with *C. caspius schmidtii*. *Coluber caspius* tends to drier habitats, *Coluber jugularis* tends to moister climates. Up to now no transitional form between the two species has been found in areas of sympatry.

Specimens of *Coluber caspius* from areas of sympatry always show highly aggressive behavior; all specimens of *Coluber jugularis* from southwestern Turkey show gentle behavior, hardly ever attempting to bite when caught.

On the basis of all the facts mentioned above I do consider *Coluber jugularis* and *Coluber caspius* to be two different species.

List of Synonyms for *C. caspius* and *C. jugularis* up to the year 1900

Coluber	jugularis	Linn.	1758
"	"	Georgi	1800
"	sp.	Lepechin	1769
"	caspius	Gmelin	1789
"	Viridiflavus	Lacep.	1789
"	"	Daud.	1803
"	"	Desmarest	1826
"	"	Bonap.	1833
"	"	Schleg.	1837
"	"	De Betta	1857
"	vulgaris	Bonnat	1790
"	communis	Donnd.	1798
"	Sardus	Suckow	1798
"	luteostriatus	Gmel.	1799
"	petalarius	Georgi	1883
"	atrovirens	Shaw	1802
"	personatus	Daud.	1803
"	"	Lesson	1841
"	atrovirens	Metaxa	1823
"	trabalis	Pall.	1811
"	trabalis	Rathke	1837

"	"	Nordm.	1840
"	glaucoides	Millet	1828
"	griseo-coerulescens	Dwigubski	1832
Coluber	acontistes	Pall.	1811
"	thermalis	Pall.	1811
"	erythrogaster	Fischer	1832
Natrix	gemonensis	Laur.	1768
Bothriophis	erythrogaster	Eichw.	1837
Haemorrhois	Trabalis	Bonap.	1841
Coelopeltis	erythrogastra	Eichw.	1837
Zamenis	viridiflavus	Dum. u. Bibr.	1854
"	"	Viaud-Grandm.	1868
"	"	Fatio	1872
"	"	De Betta	1874
"	"	Schreib.	1875
"	"	Jan	1876
"	"	Lataste	1876
"	"	Leydig	1883
"	"	R. Martin	1892
"	trabalis	Dum. u. Bibr.	1873
"	atrovirens	Günth.	1858
"	caspicus	Jan	1867
"	gemonensis	Bedr.	1882
"	"	Boettg.	1888
"	"	Camerano	1891
"	caspicus	Blanf.	1876
"	viridiflavus var. Carbonarius	Bonap.	1839
Tyria	atrovirens	Cope	1862
"	Asiana	Boettg.	1880
Bascanium	anthicum	Cope	1862

COLUBER JUGULARIS JUGULARIS LINNAEUS 1758

Description and Terra Typica

Coluber jugularis Linnaeus 1758 Linn. Syst. Nat. XIII.

The following description is accepted as being the valid description of *Coluber jugularis*. As the Type Specimen (see Fig. 11), collected by Hasselquist, which is still in the collection of the Mus. Ad. Frid. Rigis. Kat. 1900: pp 28, does not exactly resemble in colour live specimens of the same species, there were always doubts about its identity.

LINNAEUS (1758) gives his original description as follows:

"297; *Coluber jugularis*, 195-102, ♂, Habitat in AEGypto, Hasselquist, niger, jugulo sanguinolento".

In the Type Specimen there are no signs which might be called "jugulo sanguinolento". There is in fact no red colour at all on this specimen. The length of the Type Specimen is given by Anderson as 1415 mm (total; tail 370 mm).

The type Specimen has, according to the scale count of C. Edelstam (personal communication) 203 ventrals, 104 subcaudals and 19 scale rows at midbody.

There are slight differences in the scale counts of LINNAEUS (1758), ANDERSSON (1898) and EDELSTAM (1970, personal communication). This is due to a damaged part in the ventral surface and to the missing tail tip. According to my experience with missing tail tips in this species, which heal completely when damaged in early age, at least five or six subcaudal scale pairs are missing in the Type Specimen. As the Type Specimen is male, the proportion of 203 ventrals to 104 caudals is very improbable.

Fullgrown specimens of *Coluber jugularis jugularis* are dorsally always black; in most specimens a narrow longitudinal red streak runs through every scale (see Fig. 9). In a few specimens all dorsal scales are completely black. The ventral surface of adult specimens is spotted to clouded black on a purplish background; labials and gulars are yellow to orange (see Figs. 15, 19).

Young specimens show between four and six rows of dark brown to black blotches on the back on a greyish brown to greyish orange background (see Fig. 14). The ventral surface of young specimens is white to yellow and all ventral and sub-caudal shields from about the fifth shield are spotted densely brown to dark grey (see Fig. 5). Juvenile specimens of about 600-700 mm in length start to become darker and show small reddish spots on the ventral surface. When reaching a length of 1200 mm the adult coloration is fully developed.

In its western distribution in southwestern and southern Turkey the ventral Spots and dots of adult specimens are clearly developed and clearly visible on a red background. In eastern specimens the blotches tend to enlarge and form dark clouded areas so that only very little red is left at midbody.

Unfortunately there is not enough fresh material available from the whole area of distribution, but from the few specimens I have seen until now I deduce that there is a cline in ventral coloration of adults from the westernmost area of distribution to the easternmost, the darkest specimens being in the east.

The Terra Typica given by Linnaeus is surely wrong (see Discussion of this chapter). The only area where Hasselquist collected, and a snake fitting Linnaeus' description can be found, is in southwestern Turkey in the surroundings of Selcuk and Ephesus. Terra Typica Restricta; moist biotopes in southwestern Turkey, areas around Selcuk and Ephesus.

Ecology and Ethology

As all other preserved specimens of the nominate race lack information about habitat and behaviour, I rely in my descriptions only upon the seven specimens which I collected and another eight which I observed in the field. Nearly all of Turkey is inhabited by *C. caspius*, an euryoecic form inhabiting anything from Mediterranean shrub to open desert steppe areas. *C. caspius* usually avoids forrests and swamps. From Selcuk in the southwest along the whole southern Turkish coast, to central Kurdistan and probably to Transcaucasia, *C. jugularis jugularis* is found in scattered populations within the distribution of *C. caspius*. However it is only very superficially sympatric because of its ecological linkage to water. *C. jugularis* is rather stenoecic and is only found near swamps, along permanently water-fering rivers and around ponds and lakes (see Fig. 17). In summer when water is scarce in the surroundings, the biotope of *C. j. jugularis* is penetrated by *C. caspius* who seeks the water to drink. In spring, during the mating season, the two forms are separated by niche selection

(see Fig. 16), no transitional forms were ever found, and this is one of the reasons why the two forms have to be treated as different species.

In contrast to *C. caspius*, which is mainly a ground dweller, *C. jugularis* is usually found in and on bushes, on trees, walls, and gives in behaviour more the Impression of an *Elaphe* than a *Coluber*. It seems not usually to be an active hunter but rather ambushes birds, rodents and lizards. As, in captivity, it sometimes also feeds on frogs, it may easily be that also preys on anures in nature.

During the spring and autumn it can be found active throughout the day, in Summer it switches to crepuscular activity.

When caught *C. j. jugularis* rarely bites, but always shows a much more gentle behaviour than the ferocious *C. caspius*. After a few weeks in captivity it is possible to handle *C.j. jugularis* without being bitten. It moves slowly compared to other Colubers and differs in all these features completely from *C. caspius*.

As only a few specimens were observed and collected by me in the field nothing is known to me about mating behaviour and reproduction of *C. j. jugularis*.

Discussion

As mentioned in the introduction, the Linnean type, stems from the collection of Hasselquist, who was sent out like many of Linne's students to collect mainly plants, but animals as well. He collected in Egypt, Palestine, Syria and Turkey and died in Smyrna in the year 1752.

His collections were sent some years after his death to Sweden and described by Linnaeus then. His Animal Collection contained among others, one big black snake, which probably was found by Linnaeus together with other specimens labeled as originating in Egypt. This specimen was described by LINNE (1758) as *Coluber jugularis*.

In fact, the only black snake occurring in Egypt is *Walterinnesia aegyptia* Lataste, the Black Desert Cobra.

ANDERSON (1898) and FLOWER (1933) however, indicate that they saw big snakes which might have been identical with the Linnean type occasionally on sale in Egypt. They further indicate that these specimens might have been brought from Palestine or Syria. But the form occurring in these two countries, *C. jugularis asianus*, is completely black and does never show anything which might be described as "jugulo sanguinolento".

Also the Type Specimen does not show any signs of the described blood red coloration. This discrepancy might be one of the reasons why most later authors described the various forms of *C. caspius* and *C. jugularis* as other species and subspecies, but hardly ever dealt with the nominate race of *C. jugularis*.

During the first years I checked specimens in various collections and collected in the field, I never came across a specimen which might fit in color Linnaeus's description.

In the years 1965 to 1968;, I collected in Southwestern and Southern Turkey, where a big black *Coluber* with a blood red ventral surface intermingled with black Spots, occurs together with the widely distributed *C. caspius caspius*, which is light brown to light olive. This sympatric occurrence was known and misunderstood and led among other descriptions to the remark of NIKOLSKI (1916) "Melanotic forms are occurring in all subspecies". No author paid particular attention to the blood red belly of these specimens.

TERENT'EV and CHERNOV (1949) mention in their Key to Amphibians and Reptiles (p. 239) *Coluber jugularis jugularis* as being black with "somewhat lighter abdomen, red throat and supralabial scutes", without further explanation. They give no locality and just state that these subspecies is not found in the USSR.

This description would fit somehow the Linnean description. It seems to me to be a "heresay description", a translation of the original description just to define a hypothetical nominate race.

C. jugularis jugularis was sometimes mixed up with *C. schmidtii* and juvenile specimens from Southern Central Turkey determined as belonging to *C. schmidtii* (*Coluber caspius schmidtii*) MÜLLER (1939). As the original description of *schmidtii*, NIKOLSKI (1909) describes a juvenile specimen and Nikolski suggests the possibility of occurrence of melanotic specimens also in this form, dark unidentifiable juveniles were sometimes identified as belonging to *schmidtii* (Labels in various Museums). As *C. jugularis jugularis* has on every dorsal scale a narrow red streak and a red belly, freshly collected adult specimens sometimes were identified in Museum Collections as partly melanotic forms of *C. jugularis schmidtii*.

Müller discusses extensively the possibility of identifying of juveniles by the number of rows of dark spots dorsally and laterally situated. He gives six rows as typical for *C. jugularis schmidtii* and four rows as typically as *C. jugularis caspius*. Müller did not realize the significance of spotted and unspotted ventrum.

The high variability in the juvenile patterns with irregular, intermingled rows of dorsal spots and blotches gives in my opinion no basis for identification. The only method of identification of a juvenile in Turkey, Persia and Transcaucasia, is according to the color of the ventral surface which in all subspecies in *C. caspius* in these areas is always uniform white, yellow or pink, and is always spotted or clouded black in *C. jugularis*. This method of identification fits for all areas where two or more forms are found sympatric.

South of Smyrna in the swamps of Selcuk and Ephesos, I collected several specimens of this black snake and preserved them. After a few months in alcohol the red color started to fade while the back remained unchanged. After a few years of preservation the only red left was on the throat and sides of the neck and on the ventral surface of the tail. Thus I had, for a short period of time, specimens which exactly matched the Linnean description.

In order to ascertain in which locality the Type Specimen was collected» I checked the occurrence of the nominate race In all areas where Hasselquist collected. In Egypt it definitely does not occur. No specimen of the population of *Coluber jugularis* in the areas of Lebanon and Israel show any sign of red coloration. The only place where red-bellied black snakes (fitting the Linnaean description after a short period of preservation) could be found and also where Hasselquist collected, is the area around

Smyrna. According to BASHOGLU (1968, 1970, personal communication) red bellied snakes are not known to him from the area of Smyrna and north of Smyrna. As *Coluber jugularis jugularis* was found by me and is commonly known, in moist biotopes around Selcuk and Ephesus south of Smyrna this has to be the area where the Type Specimen was collected.

COLUBER JUGULARIS ASIANUS BOETTGER 1880

Description and Terra Typica

Zamenis viridiflavus Latr. 1802 var. *asiana*

Jahresber. des Senck. Nat. Ges. 1879/80.

Boettger did not actually describe this subspecies but only stated the differences between it and another subspecies *Zamensis viridiflavus* var. *trabalis* Pall. His original description reads as follows.

"Meine neue Varietaet *asiana*, zu der ich saemmtliche nicht schwarz gefaerbte Stuecke aus Syrien ziehe, zeichnet sich vor var. *trabalis* Pall., mit der sie oberseits die meiste Aehnlichkeit hat, durch constant schwarz und gelb gewuerfelte Unterseite und durch die trotz des relativ kuerzeren Schwanzes bedeutendere Anzahl von Subcaudalen (108-115) aus."

"My new variety *asiana*, in which I include all specimens from Syria which are not black, shows closest similarity dorsally to var. *trabalis* Pall. but differs from this form in its constantly black and yellow chequered ventral side and greater number of subcaudal scales (108-115 instead of 87-107) even if the tail is relatively shorter".

The var. *trabalis* Pall. is actually a synonym of *Coluber caspius*. It has to be noted here that the last sentence of Boettger's description indicates already two of the most important differences between *Coluber caspius* and *Coluber jugularis*. Boettger included all forms of *Coluber caspius* and *Coluber jugularis* in *Zamensis viridiflavus* and believed that the black specimens he collected in Syria and Palestine belonged to *Zamenis viridiflavus carbonaria* Fitz.

Of course there is no connection between *Coluber viridiflavus carbonaria* and *Coluber jugularis asianus*.

Boettger described as *Z. viridiflavus* var. *asiana* a series of six snakes from Jerusalem and Haifa, in his collection.

As mentioned above, Boettger determined adult specimens that he had encountered in Palestine as belonging to *Z. viridiflavus carbonarius*. As the juvenile *carbonarius* change to black when they are still quite small, the rather large greyish and brown specimens seemed to him to be adults of another variety.

Even BODENHEMER (1955) still believed that two different forms of the Syrian Black Snake occur sympatrically in Israel.

In fact there is one homogenous population in all Mediterranean areas from northern Lebanon south to Beersheba in Israel. All adult specimens are black with dark grey ventral surfaces (see Fig. 21) and whitish gulars and labials, hardly showing any Variation (see Figs. 13, 15).

All juveniles and half-grown specimens of *C. jugularis asianus* throughout its range resemble the description of Boettger. The fact that Boettger described juveniles is already mentioned by SCHREIBER (1912).

As within the Type-series Böttger did not specify any Holotype, a specimen was selected by MERTENS (1967) as Lectotype. This specimen, SMF 18189, was collected according to Böttger in Jerusalem.

Terra Typica: Surroundings of Jerusalem, Israel (Palestine, Syria) being the most euryoecic of the three subspecies.

Ecology and Ethology

Coluber jugularis asianus inhabits very similar biotopes as does *Coluber caspius*. Open Mediterranean scrub and flat steppe areas as well as dry mountain slopes up to about 2000 meters above sea level and areas of fixed coastal sand dunes are inhabited.

The distribution of *C. j. asianus* reaches from northern Lebanon to north and west of Beersheba in Israel. It seems to be limited by more than 250 mm of rain per annum and was up to now never found south or east of the 250 precipitation line.

There might be an area between southern Turkey and northern Lebanon where transitional forms between *C. j. jugularis* and *C. j. asianus* do exist, but no material is known to me from the Syrian Mediterranean coast. In the north east of its distribution it is bordered by the Anti-Lebanon Mountains, in the Syrian Plain only *C. caspius schmidtii* was found up to now. In the south it is found on the Golan Heights and all over northern and central Israel, being bordered in the east by the Yarmuk river and the lower Jordan Valley. It might occur in the north-westernmost areas of the Kingdom of Jordan, but no specimens from there are known to me.

C. j. asianus feeds on any vertebrate ha can subdue and swallow and is in spring and autumn a day-active hunter. In summer its activity is more crepuscular.

This subspecies is a typical culture-follower in agriculture areas and reaches enormous size in areas of high food density. Especially in chicken yards where it feeds on mice, rats and chicks it reaches a length of more than seven feet.

In its southwesternmost area of distribution, between Beer Sheba and Gaza, *C. jugularis asianus* seems to be still in the process of establishing a new form. Adult specimens from this area show the highest numbers of ventrals and subcaudals (V + Sc up to 340) and differences in ventral coloration (see Fig. 20).

As there is a cline towards higher numbers from North to South in all subspecies of *C. jugularis*, as well as from high elevations to seashore, this fact does not indicate a new form. But as there was hardly any variability in ventral coloration found in the whole north and center of distribution of *C. jugularis asianus*, the big white areas on every ventral shield, which I found in each of the seven adult specimens known to me from the Gaza area, seem to me significant.

More material has to be collected and further investigations will show, whether a subspecific rank can be applied to this border-population.

***COLUBER JUGULARIS CYPRIACUS* ssp. nov.**

Description and Terra Typica

Holotype; NMW 15186:3 (Natural History Museum, Vienna)

Total length 158 cm, tail 41,5 cm, female Ventrals 205, anals 1/1, subcaudals 101/101, 19 scale rows before midbody. Labials 8, temporals 2+2

Collector: Unknown

Locality: Cyprus

Paratypes: NMW 15186: 1, 2, 4, 5, 6, 7

The name of this subspecies indicates that this form exists only on the Island of Cyprus. The Type Specimen (see Fig. 12) is an adult female of black dorsal coloration, the head also being black and only the supralabials, preoculars and postoculars showing light spots. The lower jaw is light yellow and the borders between the infralabials are dark. The gulars are mottled black on a light yellow surface; the first two ventrals are nearly without spots, and the other ventrals are almost black showing a fine irregular pattern of tiny white dots and lines. Single light blotches are visible on a few ventrals at irregular distances. These light blotches continue onto the subcaudals which are dark grey to black and become gradually lighter towards the tail.

According to fully grown specimens collected by me alive on Cyprus all light spots and lines on the holotype were bloodred in life except the supra - and infra-labials and the gulars, which were yellow in life.

The Type Specimen does not show light narrow longitudinal streaks on the dorsal scutes.

The bodies of the Holotype and the Paratypes are very slender; this applies also to all specimens I saw and collected in Cyprus. Pholidotically the holotype and the paratypes resemble *Coluber jugularis jugularis*. All specimens show remarkably small heads (which might be due to age).

This subspecies differs from *jugularis jugularis* by the constantly larger area of black as compared to the red, on the ventral side and by the fact that red narrow streaks on its dorsal scutes are usually absent. All adult specimens appear to be completely black dorsally and most of the ventral surface is mottled dark grey with a few dispersed bright bloodred blotches (see Fig. 18), a feature which was not observed in *Coluber jugularis jugularis*. It differs consistently from *Coluber jugularis asianus* which never shows any red coloration ventrally.

In times when Cyprus was still connected to the mainland (see chapter on phylogenetic development) this subspecies developed as a transitional form between *C. jugularis jugularis* and *C. jugularis asianus*, as it occurs exclusively on the island of Cyprus, I consider it to be a subspecies of *C. jugularis*.

Juvenile specimens (see Fig. 7) show the identical shape, pholidosis and color pattern of juvenile *C. jugularis jugularis*, always showing traces of reddish and orange dots on dorsal and ventral sides. All juvenile specimens show yellowish ventral sides with a few orange and many dark grey to brown dots.

Measurements and Scale Counts of the Paratypes

Total length (cm)		Tail	Ventrals	Subcaudals	Squami
15186:1	104	23	207	98	19
15186:2	138.5	38	191	112	19
15186:4	125	35	218	113	19
15186:5	98	23.5	195	90	19
15186:6	64	17	213	101	19
15186:7	37	9	206	112	19

Terra Typica: Open Mediterranean biotopes and cultivated areas, Cyprus.

Ecology and Ethology

As in the nominate race not too much is known about the ecology of this form.

I personally collected and observed the species a few times in areas of irrigation and along rivers between Larnaca and Limassol.

According to information I received from local people in Cyprus, where nearly everyone knows the only large black snake of the Island, it is less stenooecic than the nominate race, being also found in drier areas. It sometimes bites viciously when caught but settles down very soon in captivity and after a short time behaves in captivity like the nominate race.

It inhabits nearly all biotopes in Cyprus where there are rocky slopes, stone walls, river beds, or ponds and even penetrates cities like Limassol, where it is found in parks and gardens.

According to the late entomologist A. Mavromoustakis (personal communication) who collected many specimens for the zoo in Limassol, it avoids wide flat areas with sparse vegetation, which are usually inhabited by *Malpolon monspessulanus*.

Not much is known about territorial behavior of *C. jugularis cypriacus*. Mavromoustakis stated that large old specimens were seen sometimes for years in the same place, a statement which fits for nearly all of the big Colubrids.

In captivity it feeds on lizards, birds and small mammals, constricting its prey only when the prey bites. Usually it presses its prey into a corner with one loop of its body and swallows it alive.

In this subspecies a remarkable observation has been made. A young specimen in typical juvenile coloration was caught by me in 1965 near Limassol in Cyprus. Shortly after its arrival in Jerusalem it escaped within the animal room and was found only nearly a year later. It fed in the meantime probably only on a few gekkoes which were always free in the animal room. After recapturing the specimen it was fed, due to my absence, only rarely and within six years only grew from about 85 cm to 115 cm. It can be estimated that the specimen was only about 1½ years old when caught in Cyprus. Due to lack of food it retained its juvenile coloration and only in the year 1969/70 when it was fed more frequently, did it start to change into the adult color pattern.

The dorsal spots grew and met each other and within three molts of about a duration of half a year, the whole dorsal and lateral sides were of a brownish black, just leaving a light streak on the median line of every scute. The originally spotted ventral surface changed to a dark clouded pattern and single orange to red spots appeared on the sides of the throat and the labials as well as on the subcaudal scales.

In late summer 1971, the red spots expanded and started to meet each other in the shape of blurred blotches on the throat.

Under optimum conditions in nature or captivity it can be estimated that *Coluber jugularis* and *Coluber caspius* both reach adulthood within three years, losing their juvenile color patterns at an age of about two years.

Due to lack of food a young specimen has remained in its juvenile stage (in this case up to six years) till it meets more favorable conditions inducing the change to adulthood within a short period of time.

In a natural population of Colubrids the following events might have taken place at the beginning of an Ice Age. A slow change of climate produces unfavorable conditions for the population of snakes by expanding the hibernation time and by reducing the food availability. The phylogenetic development of this form might be influenced within many generations as follows: all juveniles would remain small and would not lose, or hardly lose their juvenile color pattern. Lower embryonal temperatures may reduce the number of somites and in due course the number of ventral and subcaudal scales. At least part of the population would even under these conditions develop ripe gonads in a certain number of years and the new form would start to reproduce, being smaller in size and retaining the juvenile color pattern. This would lead to what we might call a "neotenic" species of snakes. Such a change towards small adults with juvenile color patterns may have led towards the speciation of *Coluber gemonensis* Laurenti.

COLUBER CASPIUS CASPIUS GMELIN 1789

Description and Terra Typica
Coluber caspius Gmelin 1789.
Linn. Syst. Nat. XIII, 1: 1112.

The following description is commonly accepted as being the valid description of *Coluber caspius*. As can be seen, there are a few words, especially concerning coloration (*oculi globosi*, *dilutius fusci*, *marginē nigrarum*) which were translated wrongly.

Even if Gmelin's description is a mere translation of Lepechin's work (in Russian) and Lepechin described *Coluber caspius* after 1758, he did not give this species a binominal taxon, and therefore Gmelin has to be considered the author of *Coluber caspius*. *Coluber caspius*, 198 Scutis - 100 Scutellis - 298.

C. Lepechin it. I.P. 317. t. 21

Habitat ad littora maris Caspii in dumeti et depressioribus pratis, irritatus hominem violenter petens, quem alias metuui et sibilando se prodens, capite erecto prorepens, ultra 5 pedes longus, supra alternatim flavo - et fusco - fasciatus, subtus flavus. Oculi globosi, dilutius fuscis, maxillae dentium minorum acutorum ordinibus binis armatae, dorsum et latera squamarum medio flavarum, margine nigrarum, ordinibus 18 tecta.

As all *Coluber caspius* investigated by me had 19 scale rows, the given (even) number of 18 scale rows by both authors must be based on counting error.

To show the differences between the two descriptions, I am giving here a correct translation from the Russian Original.

Coluber sp. Lepechin I. 1769.

Voy. en Russie, i. p. 513 - 514, Pl. XXI.

A frightening Species of snake, it forces us to take care at night in the field. The inhabitants of Krassno Jar call this snake the Yellow Belly. It is true that they (the snakes) fear men, but if angered, they are extraordinarily aggressive. After they quiet down, they lift their head about one Arshin, about 630 mm, and betray their presence by hissing.

We killed one of this species, it was five Parisian Feet long, and this specimen was not especially large. On the jaws we found two rows of sharp but small teeth.

The lower surface of this snake is yellow to light yellow; its back and sides are covered with 18 rows of scales, the center of each yellow, the sides dark, because of that it looks like light and dark longitudinal stripes.

The eyes - with round pupil - are of dark skyblue coloration. The ventrum has 198 shields, the tail from the cloaca to its end is covered with two rows of scales and every row has 100 scales (a).

(a)*Coluber*, inferne totus flavus, superne lineis flavis fuscis que alternatim positae, distinctus, scutis abdominalibus CXCVIII, squamis subcaudali in una serie C.

Lepechin gives his description in the chapter on his travels in the Jaikian Steppes. The only town or village he mentions in this context is Krassno Jar. I was not able to find out where this Krassno Jar was exactly situated.

As *Coluber caspius* (see Fig. 22) occurs in all the areas north of the Caspian Sea and also in the Jaikian Steppes, the Terra Typica as stated by GMELIN, (1789) and MERTENS, (1967) can be considered valid.

Terra Typica: Jaikian Steppes (lower reaches of the Ural River), shores of the Caspian Sea.

Ecology and Ethology

During the years 1958 to 1969 about 120 specimens of *C. caspius caspius* were observed and/or collected by me in the habitat. All together more than a year was spent in its habitat within 18 observation and collection trips covering all seasons of the year.

Throughout its range of distribution *C. caspius caspius* hibernates between December and March. The first warm spring days let it emerge from crevices between rocks, in stone walls or in rodent burrows. By moving boulders and, digging in mouse holes a few solitary specimens were collected in torpid. state, no hibernating aggregation was ever found.

Immediately after emerging from hibernation, adult specimens show territorial behaviour for a few weeks until the mating season, and after the mating season throughout the summer.

In uninhabited areas of low food-density, the size of territories vary in diameter from 50-500 meters. In inhabited areas, agricultural areas and other areas of high food density, the size of the territory is reduced, and the territories overlap. In some places of extremely high food densities like on and around fields in Makedonia (Yugoslavia and Greece), places were found with territories smaller than 20 meters in diameter.

We have to differentiate between Home Range (Sleeping Niche) and Hunting Range (Working Niche). Observations were made for a duration of several years in the months of April to June (a time of highest activity for *C. caspius caspius*). In a densely populated area near Edessa (northern Greece) on stone walls and dams bordering peach plantations in the morning every 6 - 15 meters a *C. caspius caspius* was observed basking on the sun.

These specimens were rarely more than about 5 meters away from the entrances of their holes. In the evening, however, when the foraging started they left their Home Range and wandered in irregular way-patterns through plantations and surrounding areas for food.

According to my observation *C. caspius caspius* feeds, as an adult, on any vertebrate, besides fish, it can obtain. During times other than the mating season it feeds as well on members of its own species when it can overwhelm and swallow them. Young specimens feed on small lizards and mice, and in the stomachs of a few young specimens, remains of crickets and myriopods were found. This wide range of food variety, not being specialized to a certain type of food, is one of the sources of the enormous success of this polyoecic species and the power of survival in different climates and biotopes. *C. caspius caspius* is a vivid example of Cope's "Law of the Unspecialized" (1884).

As mentioned in the chapter about phylogenetic development, *C. caspius* is the most widely distributed and seems to be the form closest to the common ancestor of the whole group. Even on small Islands like Khasos, which are separated from the mainland for hundreds of thousands of years it does not differ significantly from the mainland population. Only the Island of Rhodes shows an exception.

Although, *C. caspius caspius* in the north of its area of its distribution is limited to the warmer areas around and along big rivers and streams, it is found in the south

(Turkey) in levels up to more than 2000 meters. Specimens from the North and from high altitudes differ from those from the south and low altitudes only by the lower number of vertebrae, a feature which can be found in all subspecies of the species and also in *C. jugularis*.

Due to their size, strength and speed, full grown specimens have hardly any enemies. Half-grown and young specimens are protected by their cryptic color and dorsal pattern. Throughout the area of distribution full grown specimens of *C. caspius caspius* exceed all other species of snakes in their environment, perhaps not in weight, but in length, speed and fighting technique. This species is also the most aggressive snake within its range of distribution, attacking and biting viciously any intruder, even when Man is concerned. Specimens kept for years in captivity hardly ever lose their viciousness, and captive *C. caspius caspius*, are usually recognizable by their bleeding snouts and their smashed or missing rostral shields. After many years in captivity they still strike ferociously against the glass, when aroused by the slightest movement from the outside.

Natural enemies of half-grown and young specimens are mainly Storks (*Ciconia ciconia*), the Snake Eagle (*Circaetus gallicus*), the Hedgehog (*Erinaceus europaeus*), the Marbled Polecat (*Vormela peregusna*), crows and ravens.

C. caspius caspius inhabits mainly steppe areas (see Fig. 27) or open Mediterranean bush and shrub country. In some areas it is found in facultative commensalism with man, and in this case can be found in a various range of artificial and natural biotopes.

It usually only avoids swamps, dense forests and areas with extremely high humidity throughout the year.

Marking of specimens in Makedonia showed that adult specimens lived in the same places for several years. As the rate of recapture of marked specimens was extremely low, only vague estimations of age can be made. The maximum age of *C. caspius caspius* in nature may be something between 10-15 years. Adulthood is reached depending on food density in two to four years. Specimens less than 1000 mm in length were not observed showing mating display. Mating takes place dependent on the climate between the end of March and the end of May. An average of 6-12 eggs are laid about 1½ to 2 months after mating and hatch after another 6 weeks.

C. caspius caspius was never observed by me mating in captivity and even females caught after the mating season did not lay eggs. Only in two cases were highly pregnant females caught, and eggs were laid in captivity. From these two cases and three batches of eggs found by chance in nature, the above information was drawn.

Discussion

Because of its enormous range of distribution from Hungary to southern USSR and Persia, the species *Coluber caspius* was described by many authors under synonyms (see reference lists: BOULENGER (1893), MERTENS and WERMUTH (1960).

In the eastern part of its distribution area, it does not occur together with similar forms thus the descriptions remained for a long time valid and were not mixed up with other

species. In the east (handwritten corrected to "west") where it occurs sympatric with *Coluber gemonensis* and meets *Coluber viridiflavus carbonarius* it was considered by various authors alternatively as being a good species or a subspecies of one of the two other species mentioned above. Still, SCHREIBER (1912), who did a lot of field work and collected many specimens by himself, stated, that in his opinion *C. caspius* might easily be a good species, but except differences in adult color patterns and size he could not find any signs enabling him to split caspius as a species from *C. gemonensis*.

He deals with the sympatric occurrence of the two forms. He reports one case from the island of Corfu which might have been a transitional form (p. 720), without mentioning in which collection this specimen might be found. But it apparently had never occurred to Schreiber to count the ventral and subcaudal scales. The two species, *gemonensis* and *caspius* differ clearly in number of ventral scales.

Later on WETTSTEIN (1953) deals with this group, splits it clearly into subspecies of *C. jugularis* and gives correct information about sympatric and allopatric occurrence of these forms. Already WERNER (1903) reports on specimens of *C. caspius* from Turkey, reaching three meters in length, and states that *C. caspius asianus* (*Zamenis viridiflavus asianus*, BOETTGER 1880) is based on a description of juvenile specimens. WETTSTEIN (1953) states, that "*asiana*" has to be the phylogenetic ancestor, not knowing, that BOETTGER'S (1880) description fits only juveniles.

NIKOLSKI (1916) gives a description of all forms of this species known to him and mixes all possible color patterns of *C. jugularis* and various subspecies of *C. caspius* without any clear definition. His statement: "Melanotic forms occur in all races" probably influenced many of the later authors in believing that the statement might be true, without investigating the possibility of sympatry or differences between juvenile and adult.

In fact Melanotic forms do not occur in all races but there is only one partially melanotic subspecies (*C. c. eiselti*) within the species. No melanotic specimen was ever found by me within the nominate race *C. caspius caspius* which ranges from central Hungary to northern Caspian Shores and to eastern Anatolia.

WETTSTEIN (1953) mentions one melanotic specimen of *C. caspius* from southern Greece but does not give any reference as to Collection or Number.

Slight color variations are found in the nominate race throughout its range. The ventral coloration may range from a whitish-yellowish to a deep orange, but the ventral surface is always without any black blotches or spots. The dorsal coloration varies from a pale yellowish grey to olive brown. Certain color combinations are typical for certain areas but not distinct or uniform enough to rectify a subspecific split.

Red-headed forms were described by WETTSTEIN (1957) from the Aegean Islands, Karpathos and Khasos and were collected by me in Makedonia (see Fig. 25) as well as transitional forms to *C. c. schmidtii* in Anatolia (see Fig. 26). Red or orange headed specimen can be found as a local variation in fairly big numbers, as well as solitarily within brown or grey headed populations.

In southwestern Turkey, *C. c. caspius* hardly shows any variability. It is always easily distinguished from *C. jugularis* occurring in the same areas.

COLUBER CASPIUS SCHMIDTII NIKOLSKI 1909

Description and Terra Typica

As the specis taxon *erythrogaster* FISCHER (1832) is unfortunately preoccupied by *Natrix (Coluber) erythrogaster* Gatesby 1771, this Subspecies has to be called *C. c. schmidtii* NIKOLSKI (1909).

Mitt. Kaukas. Mus. Tiflis, 4: 303.

2. *Coluber schmidtii* species nova.

Materia:

Pag. Deirusty ad fl. Bolgar-cai, Mugan merid. 27.III. 1907.

leg. Schmidt et Schelkovnikov,

6 ex. in salsis Adzi, Mugan centr. 29. III. 1907

leg. Schmidt et Schelkovnikov.

2 ex. Tiflis, hortus botanicus. leg. W. Klippert.

Coluber C. quadrivirgato Boie valde similis, sed sutura inter sc. internasalia quam sutura inter sc. praefrontalia paulo brevior (apud *C. quadrivirgatum* valde brevior), scutis inframaxillaribus posterioribus inter se attingentibus (apud *C. quadrivirgatum* una squama oblonga inter se disjuncta); scuto post-oculari superiore quam postoculare inferius valde majore (apud *C. quadrivirgatum* non majus); sc. frontalis longitudine quani sc. parietalis longitudo non minore, vel vix minore (apud *C. quadrivirgatum* valde minor), squamis corporis laevibus, differt.

Coluber oculi diametro longitudinali $1\frac{1}{3}$ in rostri longitudine; sc. rostralis latitudine valde quam ejusdem scuti altitudo majore, partis ejusdem scuti superioris, supra visae, longitudine $2\frac{1}{2}$ in distantia ejusdem scuti a scuto frontali; scuti internasalia latitudine quam ejusdem scuti longitudo majore; scuti internasalis longitudine quam sc. praefrontalis longitudo vix minore; sc. frontalis longitudine in $1\frac{1}{2}$ - $2\frac{2}{3}$ quam ejusdem scuti a rostri apice valde majore et quam scuti parietalis longitudo non minore, vel vix minore; scuti frenalis longitudine quam ejusdem scuti altitudo paulo majore, vel non majore, vel vix minore; scuto praeoculari unico, sub scuto praeoculari scuto suboculari posito; scutis postocularibus duobus; sc. postoculari superiore valde quam sc. postoculare inferius majore; sc. temporalibus 2 + 3; sc. supralabialibus 8; sc. supralabialibus quarto quintoque oculum attingentibus; 5 scutis infralabialibus scutum inframaxillare antierius attingentibus; sc. inframaxillaris anterioris longitudine quam sc. inframaxillaris posterioris longitudo non majore, vel vix majore; sc. inframaxillaribus posterioribus inter se attingentibus; squamis corporis laevibus, in 19 series longitudinales dispositis; scutis abdominalibus 196-200, in ventri lateribus angulum distinctum formantibus; scuto anali diviso, scutis sub-caudalibus 90-93; corpore supra griseo, maculis nigris parvis in 6 series longitudinales dispositis, ornato; capite supra griseo, maculis nigris oblongis ornato; scutis supralabialibus albis, marginibus eorum scutorum posterioribus nigris; ventro albo, immiaculato; angulis scutorum ventralium vix flavescentibus, cauda subtus flavescente.

Longitudo totalis: 390 mm, caudae longitudo 87 mm.

Habitat in Transcaucasia orientale in deserto Mugan et prope urbem Tiflis.

Typus: in Museo Caucasico.

Nikolski described as his Type Specimen a juvenile of 380 mm in length and this description fits nearly any juvenile of any race of *C. caspius*. As the Type Specimen (it is not known to me whether it still exists) is at the moment inaccessible for me, I can just refer to its description.

Reaching from Transcaucasia in the north over large areas of Persia to central Syria in the south, a subspecies of *C. caspius* occurs, differing from the nominate race due to its bright red to brown coloration. This form was described first by FISCHER (1832) as *C. erythrogaster*, then by EICHWALD (1837) as *Bothriophis erythrogaster* and later again by EICHWALD (1841) as *Coelopeltis erythrogaster*.

SCHREIBER (1912) does apparently not worry about *erythrogaster* being a valid subspecies. Probably because of lack of material he mixes *caspius* and *erythrogaster* as being one polychrome subspecies. Schreiber did not give his subspecies names but lists the Synonyms and gives in this case the description (p. 714) as follows: "Supra griseo - fuscescens vel fuscus...., subtus flavescens vel aurantiacus", so in this way leaving all possibilities open. In the text, Schreiber does not mention *erythrogaster* again.

Unfortunately, the name *erythrogaster* is preoccupied by *Natrix erythrogaster*, which was originally described by GATESBY (1771) as *C. erythrogaster*. This fact makes a rather good description of adults invalid, the later description by Nikolski, where there are doubts about the identity of the type specimen, valid.

Terent'ev and Chernov mention *C. schmidtii* NIKOLSKI (1909) but describe adult specimens as being "Red, brown, or cherry-red color with lighter scale edges and red tinges on abdomen" as *C. jugularis erythrogaster*, FISCHBACHER (1832).

Both authors state on p. 240 that *C. jugularis erythrogaster* FISCHER (1832) is found in Azerbaidzhan without caring about the correct name of the author or a preoccupation of the taxon.

One of the first (besides MERTENS 1960) to find out about the preoccupation of the taxon *erythrogaster* is RAI (1965) who uses for this subspecies the taxon *C. jugularis schmidtii*.

Until a further examination of the type specimen might reveal its true identity the name *C. caspius schmidtii* NIKOLSKI (1909) has to be used as valid. Even if Nikolski also writes about black specimens being found in the surroundings of Tiflis, his type specimen must have been a juvenile of *C. caspius*, as Nikolski states in the description an immaculate white ventrum.

If we accept Nikolski's description as the valid one the Terra Typica of this subspecies must be Deirutschy (Bolgar Tschai), Saltsteppe Adshi, Eschaktschi, Tiflis. The habitat given by Nikolski in his original description refers to the general distribution of this subspecies.

It proved to be very difficult to identify preserved specimens (see Fig. 24) in museum collections as *C. caspius schmidtii*. The bright red coloration of live adult specimens fades in alcohol or formalin within a few months. After a few years all specimens of this subspecies are dorsally of pale brown coloration with pale yellow ventral sides.

Most taxonomists do not accept determinations according to locality. In this case the only possibility to determine specimens which are preserved for decades in museums is according to the locality of collection.

The red color of *C. caspius schmidtii* is still under examination. Usually specimen are preserved already during collection trips and the preserving medium is changed

several times until the specimen reaches its final place in the museum collection. Discolored preservatives are usually replaced by fresh ones.

One adult specimen of bright red coloration was collected by me in 1966, near Homs in Syria and preserved in about 1,200 cc of colorless alcohol which was not replaced later. The specimen now (1972) is of a pale ochraceous brown, the preservative is bright orange, which proves that the red coloration is of chemical origin. Unfortunately no live adult specimen can be acquired at the moment for further investigation.

Ecology and Ethology

C. caspius schmidtii inhabits dry mediterranean Biotopes from Transcaucasia over northern and western Iran, southeastern Turkey, northern Iraq and northern and western Syria. It is frequently found in dryer Biotopes than the nominate race, reaching in Iran and Syria the 200 mm Precipitation line.

In areas of reddish soil this subspecies blends perfectly in the background and is not easily seen. Its red dorsal coloration indicates a development as a result of predative selection-pressure on more sematic morphs over a long period of time. *C. caspius caspius*, living in areas of denser vegetation, shows greyish-green to brown dorsal coloration. In the border area between *C. c. caspius* and *C. c. schmidtii* in eastern Anatolia transitional forms are found (see Fig. 26). In most areas of *C. c. schmidtii* reddish soil coloration prevails over the sparse vegetation.

Nevertheless, *C. c. schmidtii* is also found on greyish and other soils in southeastern Anatolia (Van-Gölü). It occurs sympatrically with *C. j. jugularis*, according to NIKOLSKI (1916) also in the surroundings of Tiflis.

C. c. schmidtii is a fast, aggressive snake and resembles the nominate race in its behavior. It is like the nominate race quite euryoecic within Mediterranean and steppe-biotopes (RAI, 1968, pers. comm.).

Nothing is known to me about territorial and reproductive behavior of *C. c. schmidtii*.

***COLUBER CASPIUS EISELTI* ssp. nov.**

Description and Terra Typica

Holotype: NMW 18618: 1 (Natural History Museum, Vienna)

Total length 182 cm, tail 52 cm; male

Ventrals 186, anals 1/1, subcaudals 94/94 (perhaps 4 - 5 subcaudal pairs missing), 19 scale rows just before midbody (17 at midbody).

Labials 8, temporals 2 + 3 (right) 2 + 2 (left)

Collector: K. Bilek

Locality: Pefki (Lindos) Island of Rhodes

Paratypes; NMW 18618:2, 18618:3

Both paratypes are from the same locality as the holotype and were collected by K. Bilek.

The name of this subspecies is dedicated to Dr. J. Eiselt, Curator of Herpetology, Natural History Museum, Vienna, who devoted many years of hard work to the systematics and zoogeography of Egean and Turkish reptiles.

The Type Specimen (see Fig. 23) is a fully adult male of blackish brown dorsal coloration, the head being lighter in colour and every scale on the dorsal surface of the head and neck being mottled irregularly with dark brown. The dorsal scales also show an irregular pattern of blackish brown on a somewhat lighter surface. The ventral side is light yellow, (it was orange in life, K. Bilek, personal communication) and strongly mottled with black dots and blotches in an irregular pattern. The dots are fewer on the last 20 ventrals and absent on the ventral surfaces of the head and throat. The first ventromedian dot appears on the fifth ventral.

Pholidotically, both the Holotype and the Paratypes resemble *Coluber caspius caspius*; no significant difference could be detected from adult specimens of *Coluber caspius caspius*. This subspecies differs from *caspius caspius* and *caspius schmidtii* by its constantly dark to black adult coloration of the dorsum and its mottled ventrum. WETTSTEIN (1953) stated, that adult females from Rhodes tend to be dark brown, adult males to be black dorsally. The Holotype, a shows the coloration typical for a female as described by Wettstein. In these features it differs completely from specimens of *Coluber caspius caspius* found on the adjacent islands of Karpathos and Khasos and from specimens of *C. caspius* found on the mainland.

To my knowledge this form was found up to now only in Rhodes and lives thus isolated from all other populations of *Coluber caspius*. According to the zoogeographical distribution of the whole species it might be that specimens of this subspecies or similar to it might be found in the extreme southwest of Turkey on the peninsulas near Halicarnassos.

One Paratype (18618:5) is a juvenile male (see Fig. 8), total length 52 cm, tail 14 cm, ventrals 196, subcaudals 117/117. It shows dorsally the typical pattern of a juvenile *Coluber caspius* - black on greyish brown background – but has a conspicuous pattern of black dots on its ventral shields.

It is not possible to determine this subspecies according to a juvenile specimen without locality. As this subspecies was probably once a transitional form in the phylogenetic development of *Coluber caspius* and *Coluber jugularis*, and was later isolated, it is the only subspecies of *Coluber caspius* which shows a juvenile ventral color pattern similar to *Coluber jugularis*.

Terra Typica: Open pine-wood and dry Mediterranean biotopes near Pefki (Lindos), Island of Rhodes.

Ecology and Ethology

According to Dr. J. Eiselt and K. Bilek (personal communication) and various travellers who saw big black snakes on Rhodes, *Coluber caspius eiselti* inhabits rocky steppe areas and open pine forests all over the Island of Rhodes (see Fig. 28).

Although there is no proof available to me, it probably feeds on small reptiles, rodents and birds, like the nominate race.

It moves extremely fast and bites ferociously when cornered or captured. In this behavior it is identical to *Coluber caspius caspius* and differs from *Coluber jugularis jugularis*.

Up to now nothing is known about the mating behavior and reproduction of this species.

PHYLOGENETIC DEVELOPMENT AND EVOLUTION IN THE *COLUBER CASPIUS JUGULARIS* GROUP, INCLUDING EVOLUTIONARY PROBLEMS OF THE CLOSELY RELATED SPECIES *C. GEMONENSIS* LAUR. 1768, *C. VIRIDIFLAVUS* LATR. 1802

Part I: Basic facts and background for a hypothetical time scheme of the successive developments within the different species.

Whilst compiling literature and material for studies on the evolution of the Rassenkreis *C. caspius -jugularis*, it became apparent that the phylogenetic development of the species mentioned above is directly connected with the development of a few other species of the genus *Coluber*, i.e. *C. gemonensis*, *C. viridiflavus* and probably also *C. hippocrepis*.

Noting the morphological similarities and the nearly identical color-patterns of all juvenile forms, I concluded. that all the species mentioned above had one common ancestor.

Taking into consideration the recent distribution of all these species, reaching from western north Africa all over the northern Mediterranean lands eastwards to Iran, the hypothesis that during a period of warm steppe climate in this area the common ancestor existed in the pliocene period seems reasonable.

Teeth and vertebrae from the pliocene period were found in central Europe (Austria, Hungary) and from the pleistocene period in Israel. According to my comparisons with recent material (*C. c. capius*) and the findings of BACHMEIER (Pers. comm.), many of the vertebrae belong to a large (about 2 m) Colubrid very similar or even morphologically identical to *C. caspius*.

From the beginning of the Ice Ages, the whole population of the ancestral form was separated by cold and mountainous regions into well divided areas, at various times. Some of these areas were repopulated, after the snakes became extinct in several places, in keeping with climatic changes, especially glaciation of certain areas.

It is, of course, very difficult to relate the findings of paleontologists (VAUFREY, 1929) and geologists (BUTZER, 1966; SCHMIDT, 1960; PAPP, 1947; DALY, 1934; FLINT, 1948; BLANC, 1942; and many others) to an absolute timing.

A few authors (WETTSTEIN, 1953; LA GRECA and SACCHI, 1957) have already tried to date the development and intrusion of various animals on a few Mediterranean Islands, but their efforts were concentrated on Islands which were separated from the mainland as late as after the last Ice Age, or like WETTSTEIN based on PAPP, they came to some wrong conclusions because at their time they did not have enough material from Turkey.

In order to build up a hypothetical scheme from the development of the species and subspecies of the genus *Coluber* in the northern Mediterranean, we have to take into

consideration that the genus *Coluber* is not so uniform as a systematic genus should be. It consists of many palearctic and nearctic species which according to the laws of modern taxonomy belong probably to several genera. All these species were brought together according to morphological similarities to the genotype, but are in fact to be divided into several groups. For the present work, only one group, which I shall arbitrarily call the *Coluber caspius* group, was chosen.

In this group I include the species *caspius jugularis*, *gemonensis* and *viridiflavus* on the basis of morphological and ecological similarities and very similar juvenile color patterns.

In order to give more exact statements about the evolutionary development of this group, it has to be divided, and for this purpose the terms *Artenkreis* and *Rassenkreis* (RENSCH, 1929) can be used. It seems inappropriate in this case to use the term "superspecies" proposed by MAYR (1953) for any of the forms. For the ancestral form and also the now-existing *C. jugularis*, the term "prospecies" (BIRULA, 1910) can be used.

Let us now compile the distribution of the species worked on. The recent distribution of all the species and subspecies of the *Rassenkreis C. caspius - jugularis* extends from Dalmatia in the west to northern Iran in the east, and from central European Russia in the north to Israel in the south. In this area of about 4000 kilometers in diameter, three races of *C. caspius* and three races of *C. jugularis* developed.

The third species, *C. gemonensis*, does not split into any races or subspecies. It is distributed from Istria, southwards along the Adriatic coast of Yugoslavia and Albania, all over western and southern Greece, a few western Aegean islands and Crete. With the exception of Corfu, it vicariates with *C. caspius* on the islands.

The fourth species, *C. viridiflavus*, is found in its nominate race all over Italy and the melanotic subspecies *C. viridiflavus carbonarius* inhabits northern and north-eastern Italy as well as the north-western parts of Yugoslavia and the Dalmatian coast.

Not enough material has been gathered for accurate data about this species to be obtained and because of its distribution on Corsica and Malta which does not fit very well into the sequence of geological events, it might even have been distributed to these places with the aid of man.

My scheme of evolution of the species worked on is based on their recent distribution according to literature, my own collection and material from various museums, the rather well known geological changes which occurred within the area of distribution, and the spreading of the different forms on the Mediterranean islands.

Dating the Separation of most Islands in the Mediterranean from the mainland involves a lot of difficulties. Only very little absolute timing was done by geologists. Most of the work done in this field is the result of a combination of data gathered from zoology, botany, paleobotany, archaeology, paleontology, geology and geography.

Among the paleontologists, it was VAUFREY (1929) who dated the immigration of elephants to Mediterranean Islands and came to his conclusions mainly on paleontological and geological grounds. The large Islands in the central and eastern Mediterranean Sea, such as the Cyclades and Southern Sporades, should have had

their last connections with the mainland during the plio-pleistocene transition, if not again in the Mindel Ice Age (BUTZER, 1966; SCHMIDT, 1960; and others).

As quite a large number of authors have written about the geology of the Mediterranean and the development of its Islands, it seems proper to refer here to the reference lists of BUTZER (1966), PAPP (1947), OEKONOMIDIS (1934), PFANNENSTIEL (1944), WOLDSTEDT (1958) and AVNIMELECH (1961).

A few facts in the development of the shape of the Mediterranean Sea up to now, seem most important. There was a land bridge between Spain and Morocco during the time of the Romanum (Mindel-Pluvial). At the same time, Sicily and Malta were connected with Italy but there was surely no connection between Sicily and North Africa. Corsica and Sardinia were one island. Crete, which was already disconnected in the late Pliocene, was very probably reconnected to Greece during the Mindel-Pluvial, although there was no connection between Crete and the Karpathos - Khasos complex, which might have been reconnected with Rhodes and the Turkish mainland or with the Cyclades (WETTSTEIN, 1953, based on PAPP, 1947).

Several authors (VAUFREY, 1929; BUTZER, 1966; SCHMIDT, 1960; and others) dealt with the development of Cyprus as an island. The information about the date of eventual dis- and reconnections of Cyprus from and to the mainland, does not give too many clues. From the geological point of view, the existence of a landbridge between Cyprus and the nearest mainland (Antiochia, Turkey) after the Pliocene cannot be proved. The immigration of elephants is dated by VAUFREY to some time during the early Pleistocene.

The recent fauna of Cyprus points very much to a later landbridge. If we take into consideration that there are still tectonic movements in the north-eastern Mediterranean and that the Anatolian plateau, is still lifting. I suppose it might easily have happened that the areas between the northeasternmost tip of Cyprus and Antiochia were lifted up again for a certain time, or even several times, and were exposed at least once during the Mindel-Pluvial.

The presence of *C. jugularis* in Cyprus, indicates a connection with the mainland at the time of, or after, the Romanum, a time when the hedgehog *Hemiechinus auritus* might also have immigrated.

As the subspecies of *C. jugularis* which is found on Cyprus is very closely related to the nominal race in southern Turkey (but sufficiently different to indicate that it could not have been brought to Cyprus with the aid of man) and the nominate race is only found on the Turkish mainland and not on the Aegean Islands, it seems possible that a Mindel landbridge to Cyprus could have existed.

If the speciation process of *C. jugularis* had already started in the late Pliocene, a later reconnection of Cyprus to the mainland cannot be proved.

The development of all the species and subspecies worked on, to their present stage, can be shown by means of the much more accurate knowledge of the geological and climatic development of the last 40 000 years. It is mainly the work of BÜDEL (1949, 1950) with its maps of the Würm-Klimate and the accumulated information of WOLDSTEDT (1954, 1958) which give a picture of the Mediterranean areas, Europe and Asia, at the time of the last Ice Age.

It was only after the receding of cold climate towards the end of the Würm Ice Age that *C. caspius* and *C. jugularis* reached some areas of their recent distribution which they were not able to inhabit before. The highlands of Anatolia and Caucasia, central

and northern Greece and the mountainous parts of Italy were surely not inhabited by Colubers at the climax of the Würm Ice Age.

By superimposing the climatic map of the Würm Ice Age (BÜDEL, 1949, 1950 and WOLDSTEDT, 1958) upon a zoogeographical map, showing the recent population of *C. caspius*, *C. jugularis* and *C. gemonensis*, it can be demonstrated that all those species and their subspecies were clearly separated from each other by climatic barriers or by the sea at the time of the last Ice Age (Fig. 32).

Two points of information are gained by this superimposition. Firstly the separation of the species and subspecies mentioned above during the Würm period and secondly, if there are recent populations of any of the species and subspecies in the areas which were too cold for a thermophile snake at the time of Würm, they must have migrated to these areas within the last 20 000 years.

Using all the Information available to me, it was possible to draw a picture of the phylogenetic development of the species group, the accuracy of which seems highly probable to me (Fig. 29).

Part II: The succession within the phylogenetic development of the different species and subspecies of the *C. caspius* group from the Pliocene to the present

At the time of the late Pliocene period one can estimate that there was a rather warm, dry, steppe climate in the whole Mediterranean area including, of course, drier and damper areas.

There are quite a lot of different opinions about the absolute timing of the Plio-Pleistocene boundary because the methods of determining this time are very difficult and do not give the same results. The absolute timings given vary from about 600 000 to 2 000 000 years ago (MILANKOVITCH, 1930, 1938, 1941; ZEUNER, 1946, 1959; FLINT, 1948; BLANC, 1942; CARRINGTON, 1962; WOLDSTEDT, 1954, 1958; and others).

A time of about 650 000 years ago seems most probable if we do not take into consideration the fact that there might have been slight increasing fluctuations in the climate for a million years previous to the first Ice Age. This might already have strongly influenced speciation in the affected areas. Many modern authors now refer to a time of 600 000 to 650 000 years ago, but the future with new and better methods might one day present the possibility of exact absolute timing.

My basis for the scheme which follows is the presumed presence of a common ancestor of the four species worked on, living all over the northern Mediterranean.

At the Plio-Pleistocene boundary, Cyprus was already disconnected from the mainland, but could have been reconnected during the Romanum. Crete was already an island but was also reconnected to Greece in the Mindel-Pluvial. The Aegean Sea existed in the north of its present area; there was an Aegean mainland between Greece and Anatolia. Anatolia was lifting the Aral Lake at the time of the Plio-Pleistocene transition and the Caspian Sea and Black Sea were connected.

In the central Mediterranean the Adria existed only in its southernmost part. Sicily and Malta were connected to Italy, but there was no connection between Sicily and North Africa. The islands around Elba were connected or reconnected in the Pluvials to

Italy; Corsica and Sardinia were one Island and the Iberian Peninsula was, at least in the Romanum, connected to Morocco but did not seem to have a connection within the Plio-Pleistocene transition.

The population of the ancestral form, reaching probably from northern Iran to the Iberian Peninsula, could have been rather uniform but there is also a possibility that there were subspecific changes from the east to the west. If there was a fairly uniform climate within this area for a long period, it is not very probable that a number of forms of an unspecialized species would develop, especially when we see that the recent population of *C. caspius* hardly shows any variation between Hungary and the northern Caspian region (COPE, 1884, Law of the Unspecialized).

Only drastic changes in the biotope and climate, which increase the selection pressure in some areas, could have caused the many different forms which we find today.

When the Günz Ice Age or the fluctuations of climate in the late Pliocene cooled the northern Mediterranean and west Asia in a southerly direction, it can be estimated that the whole population of the ancestor form was divided into several separated areas by uninhabitable regions (see Figs. 31, 32, 33).

One area, which stayed rather warm and later was not very much influenced by the Ice Ages, stretched from northern Iran to central Syria, and from there southwards to Israel and westwards to Cyprus and southernmost Turkey with the possible barrier of the Amanus Mountains in the Lebanon. Another area which stayed warm enough to be inhabited by thermophile Colubers was southern Greece and Crete. Central and western Greece was throughout the Ice Ages one of the coldest biotopes in which a form of the common ancestor remained and developed further.

The Aegean mainland and the areas of Thracia, northwestern Turkey and southwestern Russia were also at no time in the Pleistocene too cold for Colubrids.

Southern Italy and Sicily presented space for a third population and the Iberian Peninsula for a fourth.

In the Günz – Mindel - inter-pluvial all forms which developed or remained during the time of separation were able to spread and very probably met again. They were separated again in the north of the whole distribution area by the Mindel- pluvial, during which period the most drastic changes occurred in the Mediterranean areas.

Anatolia, which was lifted at that time to nearly its present level, separated a northwestern population in the area of the northern Aegean Sea and on many islands in the Aegean (*C. caspius caspius*) from a southern population west and southwest of the area of Taurus and Antiochia, a form (*C. jugularis*) which was able at that time to reach Cyprus if it did not speciate already at the time of an earlier landbridge. I suppose that the developing *C. jugularis* was still connected with *C. caspius* in the areas of southwestern Turkey in the west and the Lebanon in the south.

Again, all Mesopotamia and parts of northwestern Iran were probably not very much influenced. Of course fluctuations in drier and more humid climates occurred. This Mesopotamian population (*C. c. schmidtii*) was separated by the high Lebanon from the southeastern Mediterranean coast where still another form (*C. j. asianus*) which was connected with *C. j. jugularis* in the north of its distribution, could exist.

Southwestern Greece and Crete were reconnected and gave space for a population isolated from the northern Aegean area and the northern Adriatic area (*C. gemonensis* see Figs. 34, 35, 36).

WETTSTEIN (1957) based on PAPP (1947) in his theories on the reptile populations on Aegean islands, wrote about invading species and times when certain species reached certain areas. Because it can be assumed that the islands Karpathos and Kasos were probably isolated for a longer time from Rhodes than from Greece, WETTSTEIN gave an hypothesis of intrusion from the west; that *Coluber caspius* invaded the islands mentioned above from Greece, were cut off later and then Crete was invaded by *Coluber gemonensis*. WETTSTEIN does not explain why *C. caspius* ceased to exist in central and southern Greece and on the large island Euboea.

Taking into consideration that the population of Karpathos - Kasos does not differ significantly from any *C. caspius* on the mainland but was isolated from the mainland for a longer time than most of the Aegean Islands, there is a strong possibility that this population descends directly from the common ancestor species and did not change significantly.

In my opinion there was no further connection between Greece and Karpathos-Kasos in the Pleistocene, these two islands being already inhabited by *Coluber caspius* from the time in the Pliocene when they were still connected to Turkey. As a basis for this statement I take the absence of *C. caspius* in Crete and southern Greece.

The Cyclades were probably inhabited by *C. caspius* from the same period as Karpathos-Kasos and the eastern Sporades.

C. caspius is unspecialized and successful and it might easily have survived on the Aegean Islands with almost no phylogenetic changes, from the end of the Pliocene until now. The mountainous complex Greece-Crete was probably affected far more severely by the beginning of the Ice Ages and so was Anatolia. This would also explain the occurrence of *C. caspius* on the Cyclades but not on Euboea. The population of *C. caspius* in western Greece (Theban, Tempe-valley, Volos a.s.o.) is a most recent, i.e. after Würm Ice Age, invasion from the areas of Macedonia and Thracia.

The Apennine Mountains separated the Italian population (*C. viridiflavus*) into a northeastern (carbonarius) and a southwestern (*viridiflavus*) part. Southern Spain was connected to North Africa giving the form which existed there the possibility of reaching North Africa.

During the time of the Riss Ice Age, most of the larger islands and the islands a greater distance from shore were already disconnected and all the forms established during the Mindel and post-Mindel time were again able to spread on, the mainland and meet, but all the mainland forms were separated completely, once more, during the last, the Würm, Ice Age.

It was only during and after the last Ice Age that all the species and subspecies reached their present distribution and large areas were only populated after the Würm-pluvial in the last 20 000 to 50 000 years (see Figs. 36, 37, 38).

To begin in the east, the red subspecies of *C. caspius schmidtii* developed in the large area between northern Iran and Syria, showing mainly red soil. Its distribution area during Würm was not connected to the Lebanese and Palestinian coasts, where the black form *C. jugularis asianus* developed.

I assume that some time in the late Pliocene a large portion of the ancestor population was isolated from the main contingent. That portion reached from southwestern Turkey across southern Turkey and Cyprus, which was then connected with the mainland in the area of Antiochia, southwards to Lebanon and Israel.

The only remaining connection with the main population, which must already at that time have been very close or even identical to *Coluber caspius* as it is today, was situated in southwestern Turkey in the area where the Island Rhodes was later formed.

All the coastal regions in the western Mediterranean as well as the area Antiochia-Cyprus must have remained rather warm and moist throughout the Pleistocene as is indicated by the presence of various thermophile plants and animals living until now in these areas (e.g. *Liquidambar* and *Chamaeleo*). I did not find any clues to the absolute timing for the start of the speciation process of this population towards *Coluber jugularis*. It may be that changes had already occurred earlier in the Pliocene when the speciating population was still connected to the ancestor population at all its mainland borders.

The speciation process continued into the Pleistocene, but must already have reached a very advanced stage when Cyprus was disconnected from the mainland.

From the transitional *C. caspius eiselti* in the extreme southwest of Turkey *C. jugularis jugularis* developed in southern Turkey forming the subspecies *C. jugularis cypriacus* on Cyprus and *C. jugularis asianus* in Lebanon and Israel, as new species isolated from the ancestor form. *C. jugularis* shows a cline from almost black in the northwest to black in the southeast and nowhere up to now were intermediate forms found between the two species *C. jugularis* and *C. caspius* in areas where both occur sympatrically.

After the Würm Ice Age, the intermediate form between the two species *jugularis* and *caspius*, *C. caspius eiselti*, was disconnected from the mainland on the newly formed Island of Rhodes. It is unknown to me whether *C. caspius eiselti* still exists on the Turkish mainland where the population of *C. j. jugularis* expanded northwards after the last Ice Age and where *C. c. caspius* intruded southwards into the area previously occupied by *C. j. jugularis*. All specimens collected or examined by me and originating in southwestern Turkey, are either *C. c. caspius* or *C. j. jugularis*. Still the possibility exists that *C. c. eiselti* may be found on some of the peninsulas of the southwestern Turkish coast.

Even if this form is similar in coloration to *C. jugularis*, morphologically and ecologically it is closer to *C. caspius* and is therefore included by me in this species. *C. gemonensis* on Crete, the Greek mainland, the Yugoslavian Adriatic coast and the Yugoslavian Adriatic Islands, must have reached its present form very early, probably already at the beginning of the Pleistocene, because it hardly shows any variation or differences on Crete, the mainland, and the Islands which separated only within the last 10 000 years.

The nominate race of *C. caspius* which only had the chance to reach southern European Russia after the Wurm Ice Age, emigrated to Bulgaria, Rumania, Hungary and Yugoslavia and reached the Dalmatian Adriatic coast only quite recently. Its distribution northwestwards follows mainly the warmest areas within the countries mentioned above and its present distribution is mainly along big rivers and in the deepest levels of flat or hilly country (see Fig. 37). It must have reached Albania and the Adriatic coast after Wurm, but before the Separation of the coastal islands (one of which, Corfu, is now inhabited by *C. caspius* and *C. gemonensis*) i.e. about 10 000 to 20 000 years ago.

In Italy another species was formed, *C. viridiflavus*, and its separation into two populations enabled the development of the nominate race in the south and of *C. viridiflavus carbonarius* in the north.

On Monte Cristo, which has probably been separated since the Romanum, a dwarf form of *C. viridiflavus* evolved.

Even now, speciation in the *Coluber caspius* group continues. According to my own collections, *C. caspius asianus* in southern Israel not only shows a tendency to shift its border of distribution southwards, but also a new form with different ventral coloration is developing (see Fig. 20).

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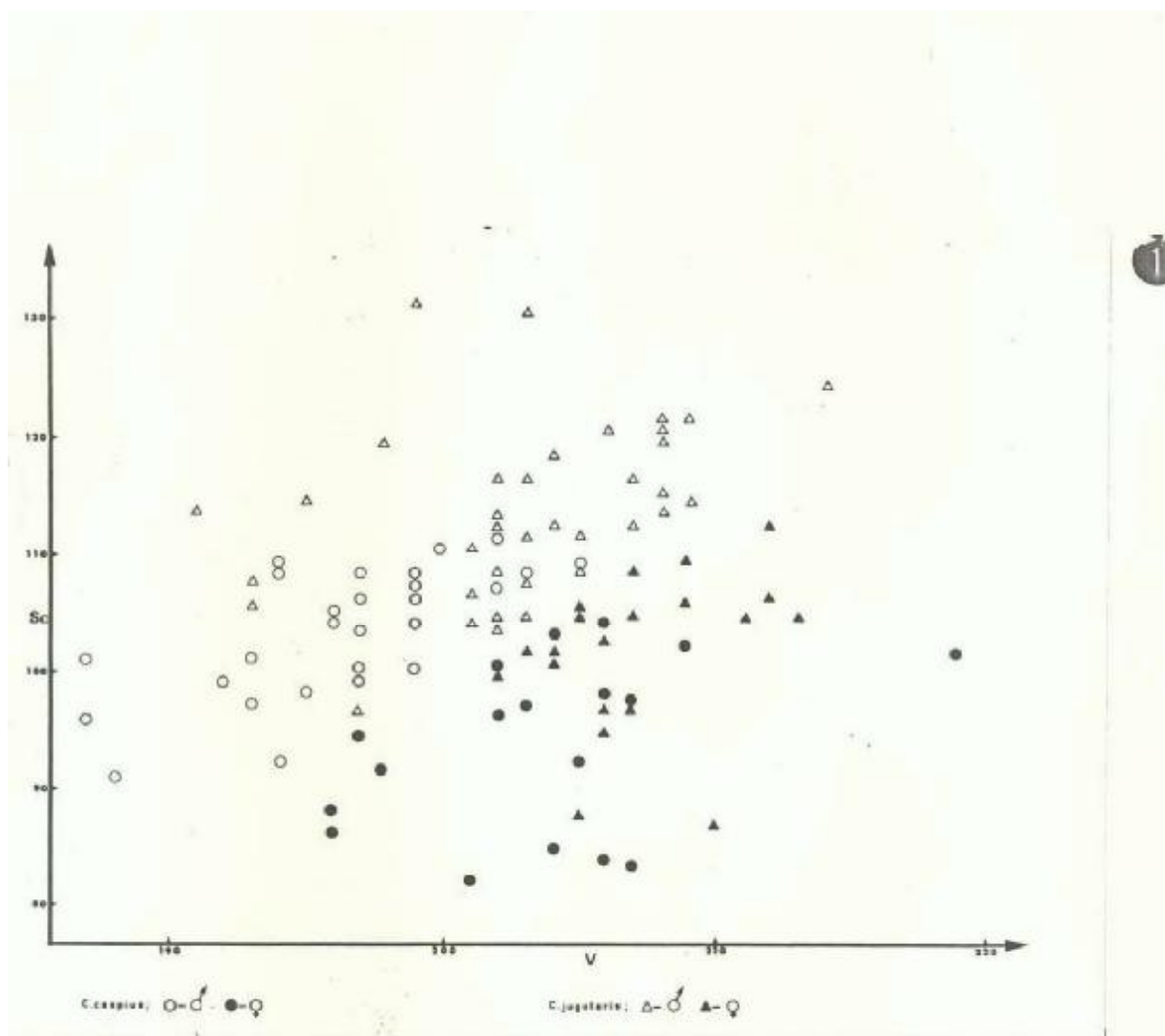


Fig. 1: Distribution and range of males and females of *C. jugularis* and *C. caspius* according to ventrals and subcaudals, 115 specimens.

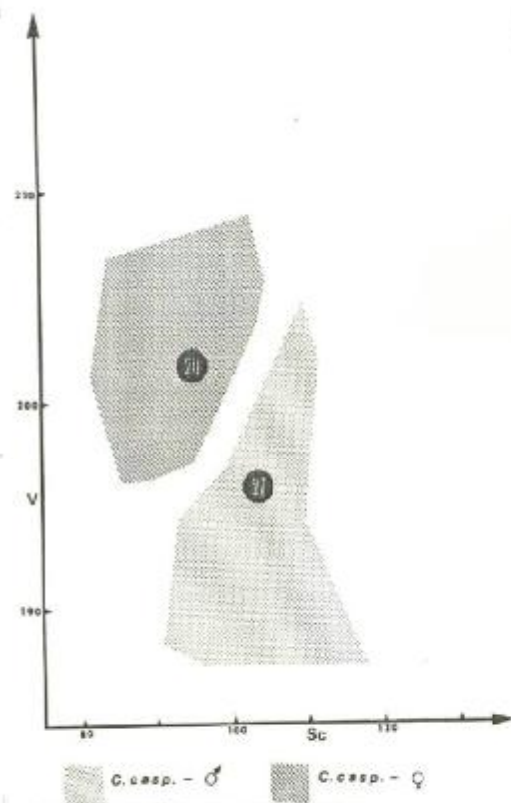


Fig. 3: Range of *C. oasius*. Black circles give number of specimens, placed on mean.

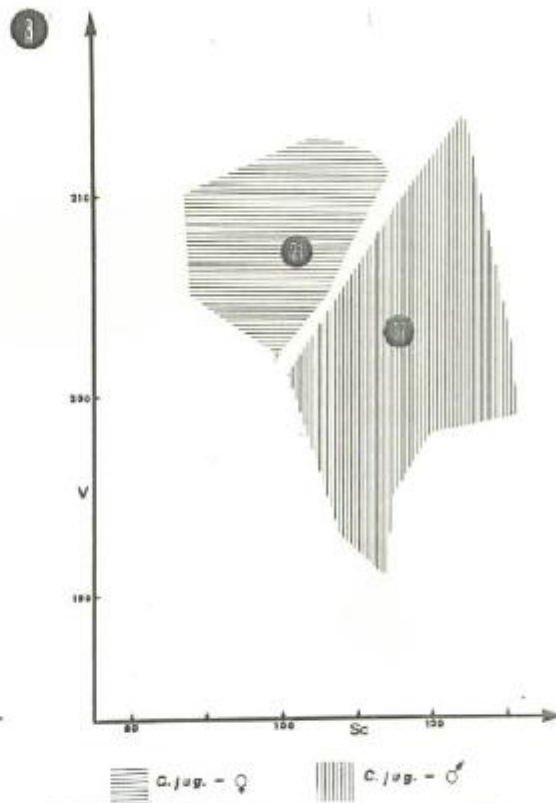


Fig. 2: Range of *C. jugularis*. Black circles give number of specimens, placed on mean.

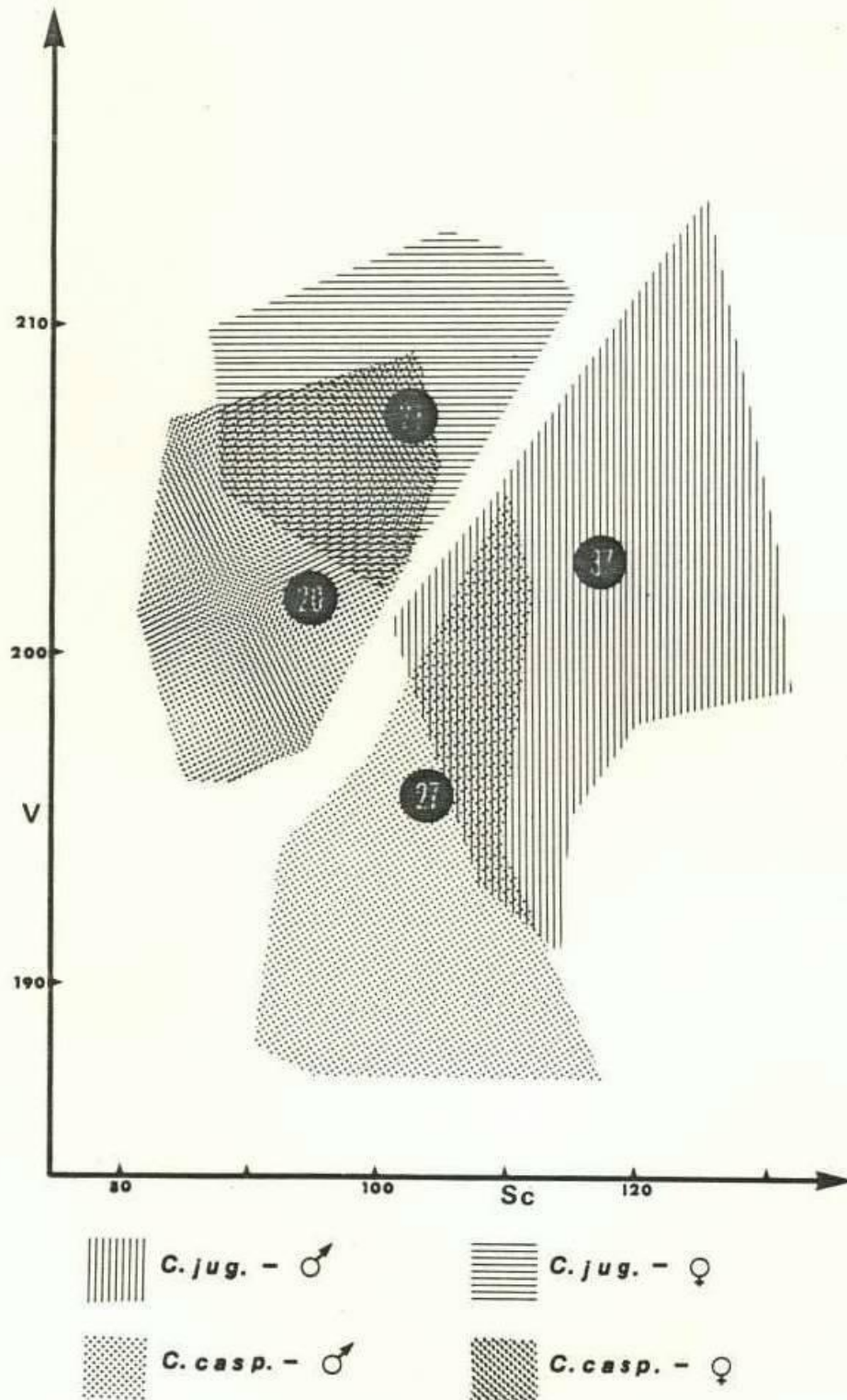
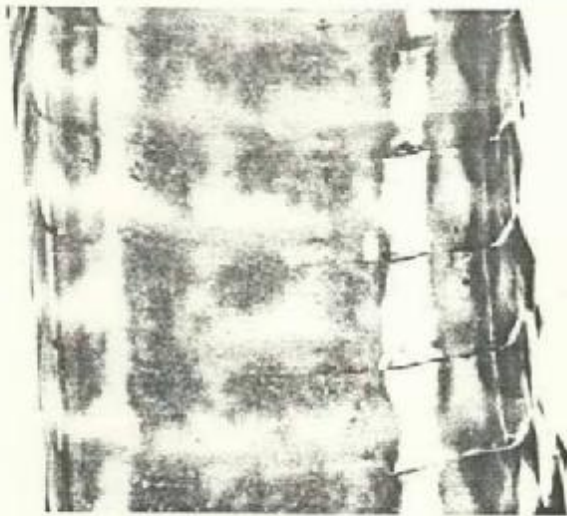


Fig. 4: Superimposition of *C. jugularis* and *C. caspius*.



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Fig. 5: Typical ventral pattern of juvenile C. jugularis in all sub-species. Specimen of C. j.asianus from Beit Guvrin, Israel.



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Fig. 6: Typical ventral pattern of juvenile C. c. caspius and schmidtii.
C. c. caspius from Izmir, Turkey.

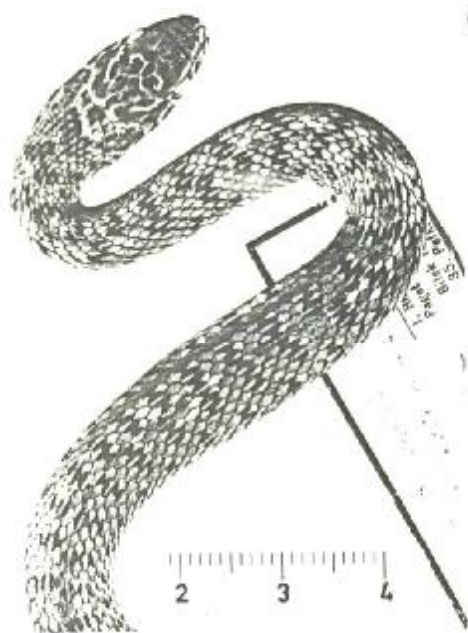


Fig. 6: Juvenile specimen of *C. aspidus sigulii* from Perki, Rhodes.

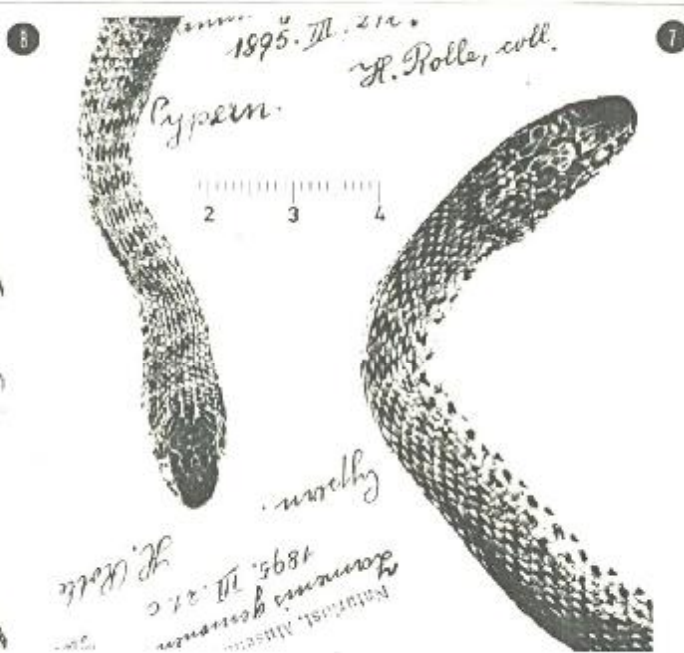
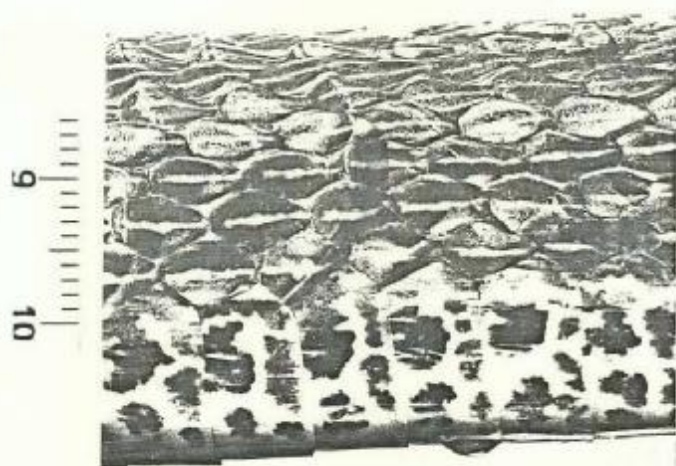


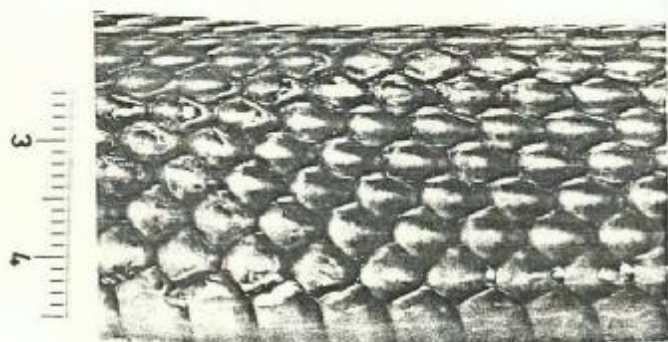
Fig. 7: Juvenile specimens of *B. jaculatoria eximius* from Cyprus.



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Fig. 9: Distribution of melanophores on lateral scales of C. jugularis
jugularis, one enlarged scales from the second row at midbody.
Specimen from Ephesus, Turkey.



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Fig. 10: Distribution of melanophores on lateral scales of C. caspius
caspius, one enlarged scale from the second row at midbody.
Specimen from Izmir, Turkey.

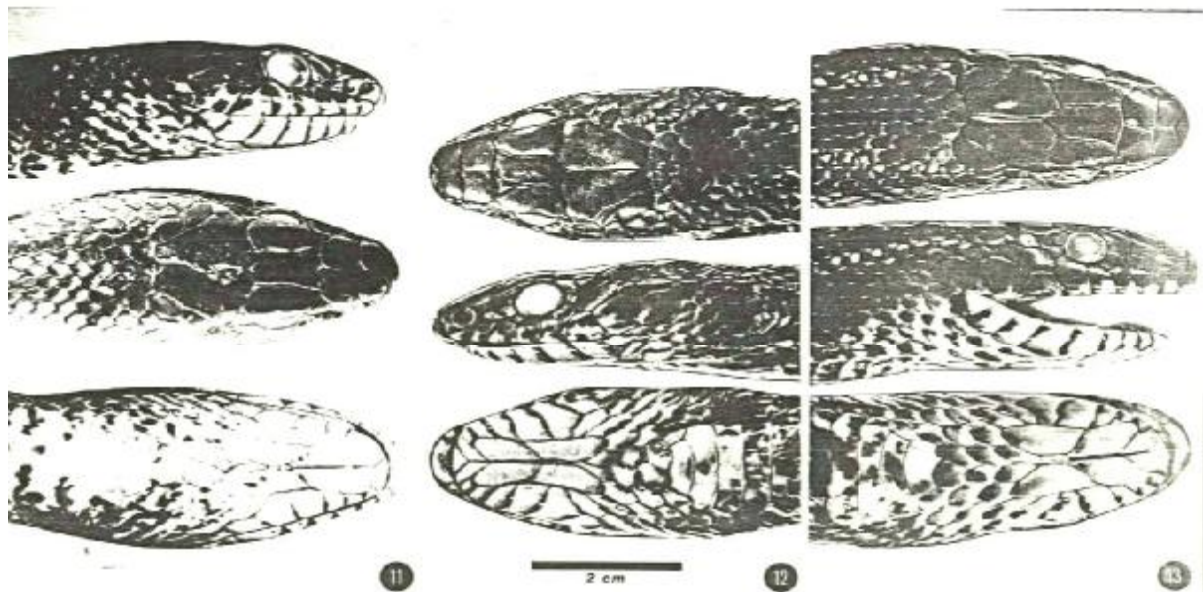


Fig. 11: The Linnean type of *Coluber*
variegatus at Stockholm.

Fig. 12: Holotype of *C. variegatus*
(Nat. Hist. Mus. Vienna).

Fig. 13: Adult *C. variegatus*
from Atlit, Israel.

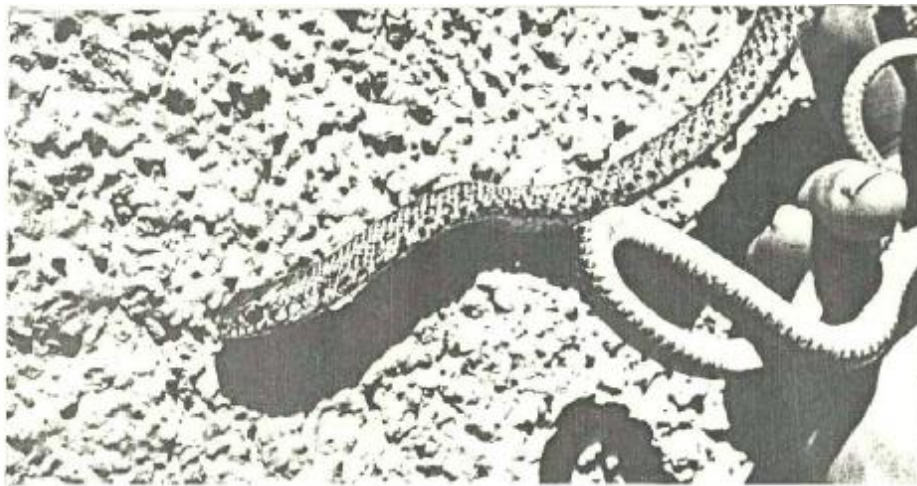


Fig. 14: Juvenile C. j. jugularis from Ephesus, Turkey.

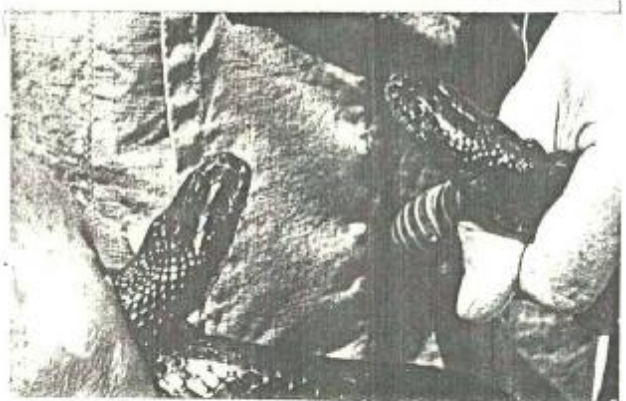
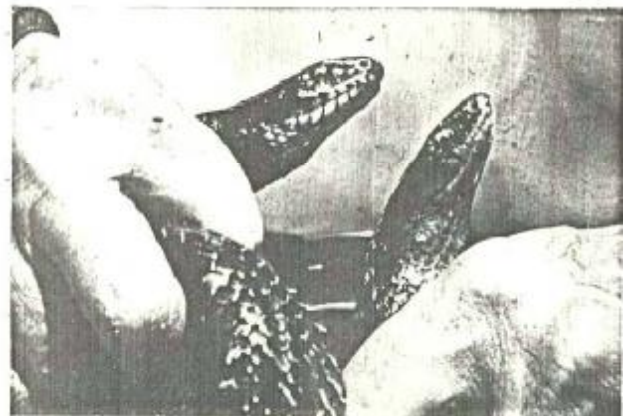


Fig. 15: Adult specimens of C. j. jugularis from Selçuk, Turkey (red ventrum) and C. j. asiaticus from Israel (dark grey ventrum).



Fig. 14: Juvenile *E. A. jugularis* from Ephesus, Turkey.

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Fig. 15: Adult specimens of *E. A. jugularis* from Balçuk, Turkey (red ventrum) and *E. A. anisus* from Israel (dark grey ventrum).



Fig. 16: Typical locality of sympatric occurrence of C. caspius and C. jugularis at Kusadasi, Turkey.



Fig. 17: Typical Biotope of C. j. jugularis at Ephesus, Turkey.

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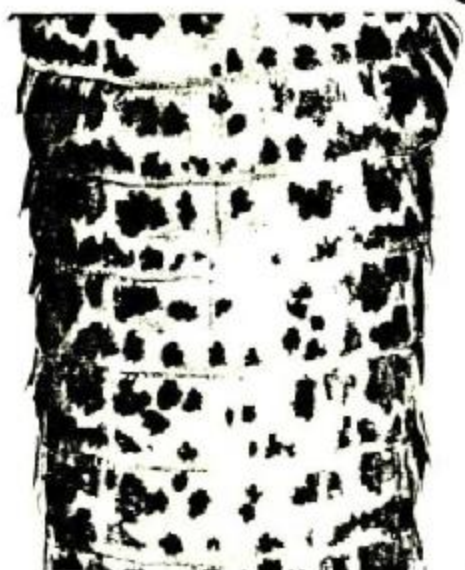


Fig. 19:
Ventral pattern of adult C. i. jugularis
from Ephesus, Turkey.

18

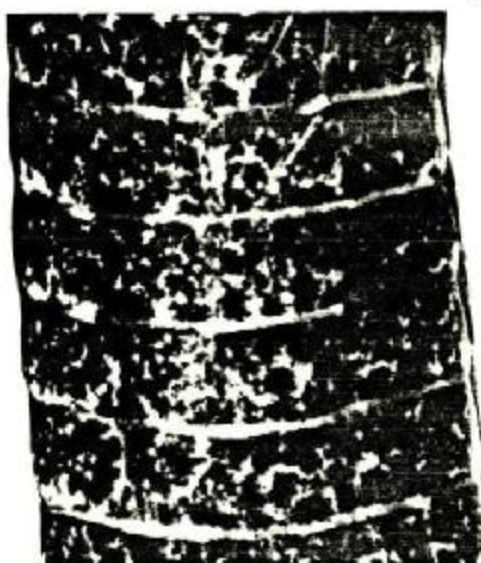


Fig. 18:
Typical ventral pattern of adult
C. i. curriacus.

21

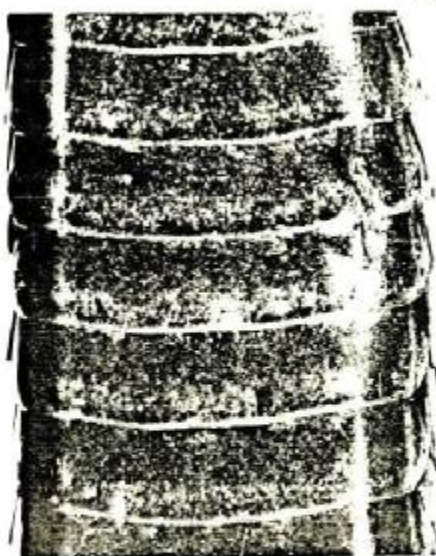


Fig. 21:
Typical ventral pattern of adult C. i. arisus.

20



Fig. 20:
Ventral pattern of adult C. i. arisus
from Gaza, Israel.

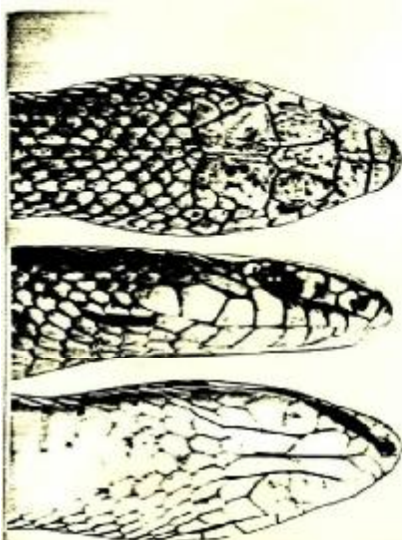


Fig. 22: Adult *C. caspius caspius* from Cavalla, Greece.

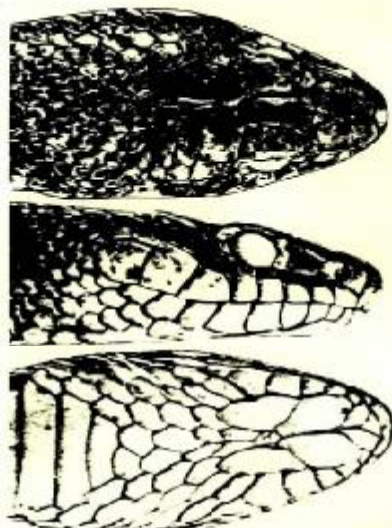


Fig. 23: Holotype of *C. n. nisselti* from Rhodes (Nat Hist. Mus. Vienna).

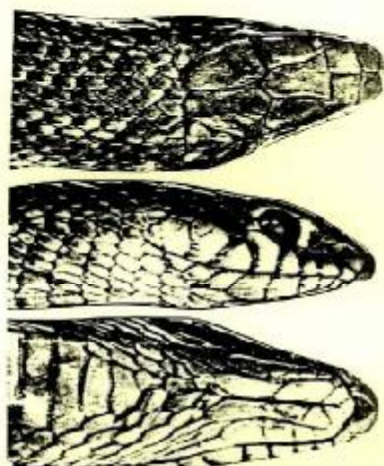


Fig. 24: Adult *C. c. schmidtii* from Kurdistan.



25

Fig. 25: Adult C. c. caspius, red headed phase at Stepance, Yugoslavia.



26



Fig. 26: Adult C. c. caspius from Eastern Anatolia, transition to C. c. schmidtii.

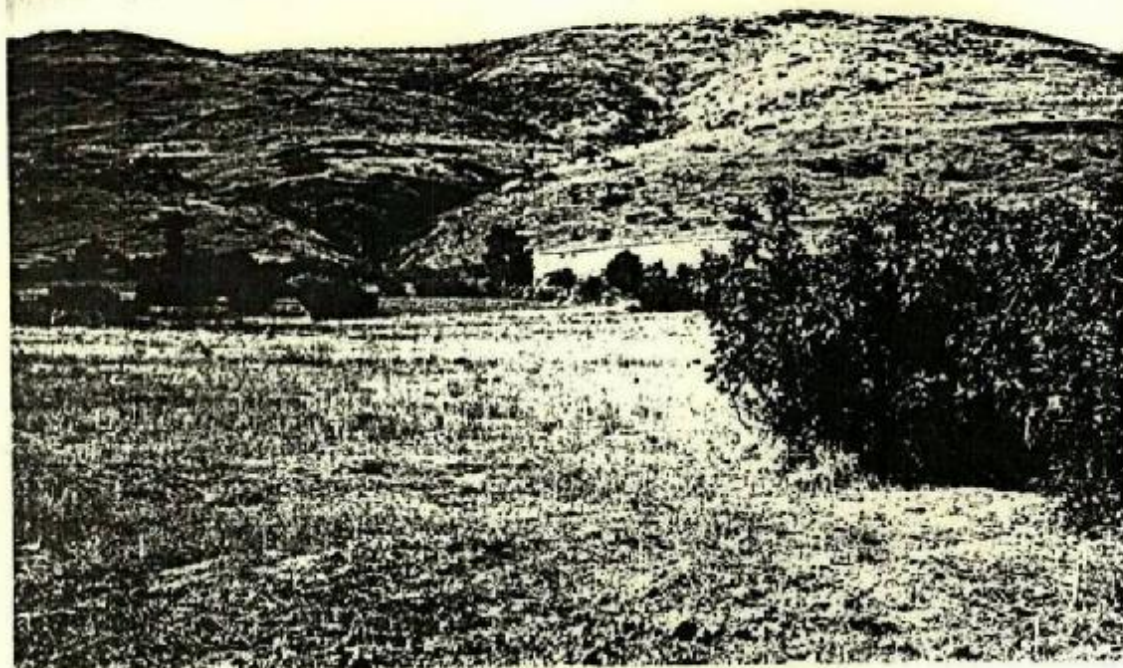


Fig. 27: Typical Biotope of *C. c. caspius* at Volvi, Greece.



Fig. 28: Typical Biotope of *C. c. eiselti* on Rhodes
(photomicrograph by Bilek).

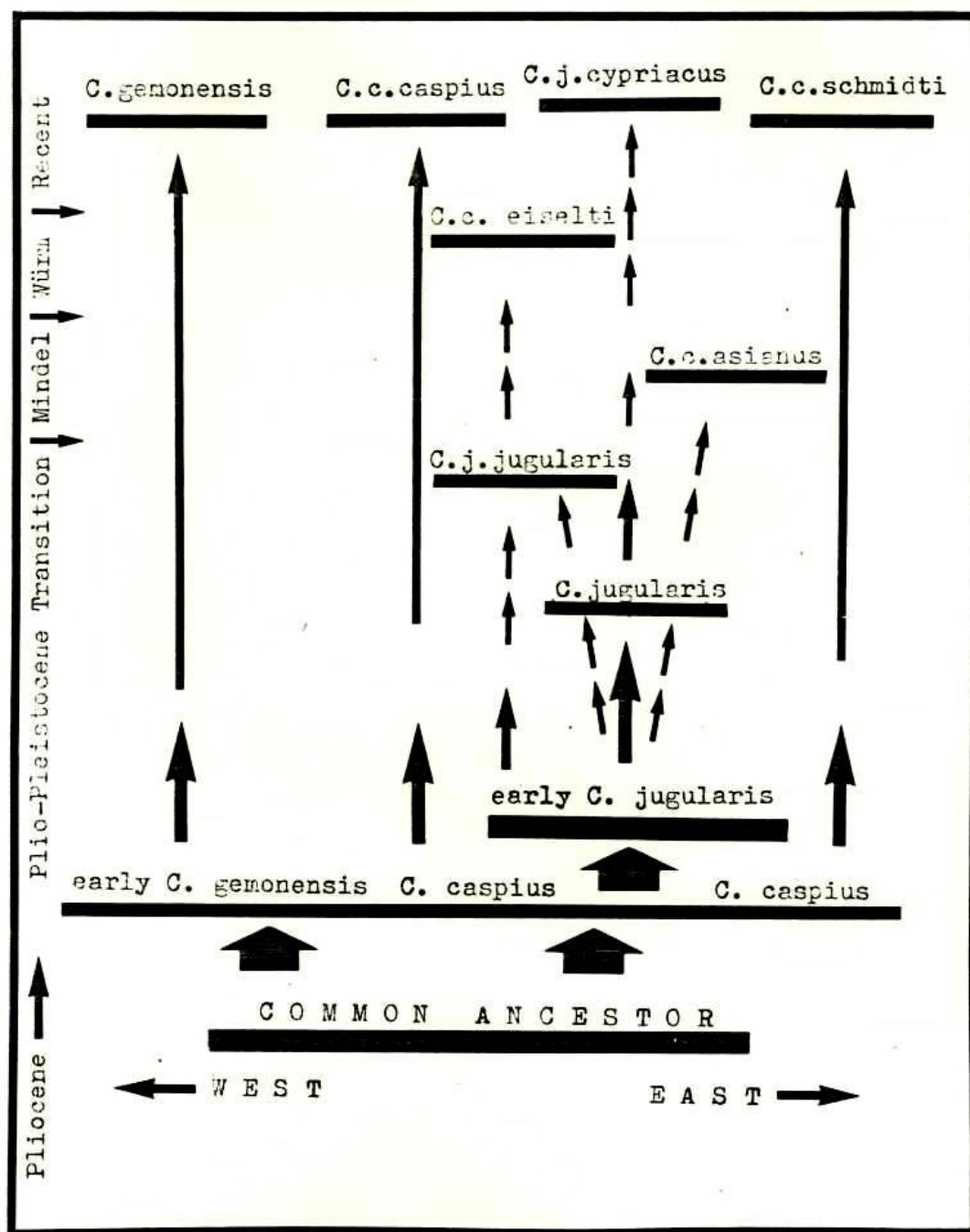


Fig. 29: Hypothetical scheme of the evolution of *C. jugularis*, *C. caspius* and *C. gemonensis*.

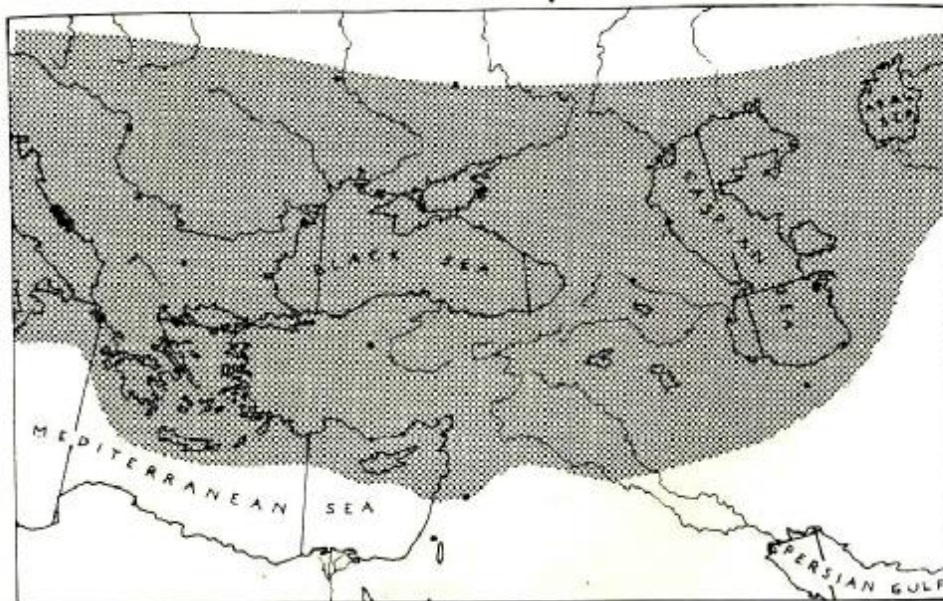


Fig. 30: Distribution of the assumed common ancestor in the early Pliocene.

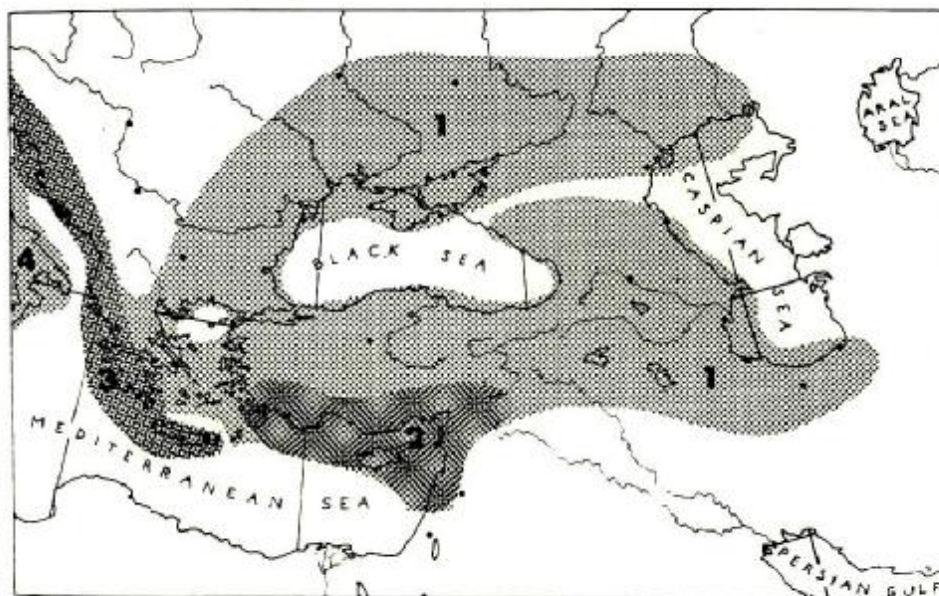


Fig. 31: Beginning of speciation in the late Pliocene. 1: Early caspius split into two populations by the connection between Black Sea and Caspian Sea. 2: Early jugularis develops at a time, when Cyprus is still connected to the mainland. 3: Early gemonensis speciates in western Greece, Crete might have been reached only during Mindel-Pluvial. 4: Early viridiflavus develops in southern Italy.

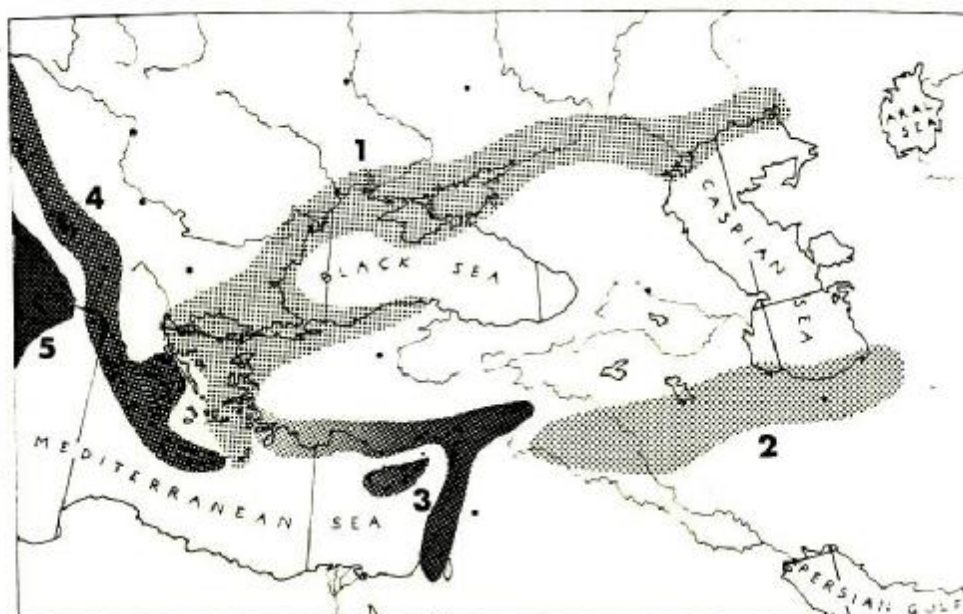


Fig. 32: Reduction of populations as result of climatic changes in the early Pleistocene. First subspecific development. 1: caspius caspius, 2: caspius schmidtii, 3: jugularis, still connected with caspius in the west, 4: cypricus already disconnected. 4: gemonensis, 5: viridiflavus.

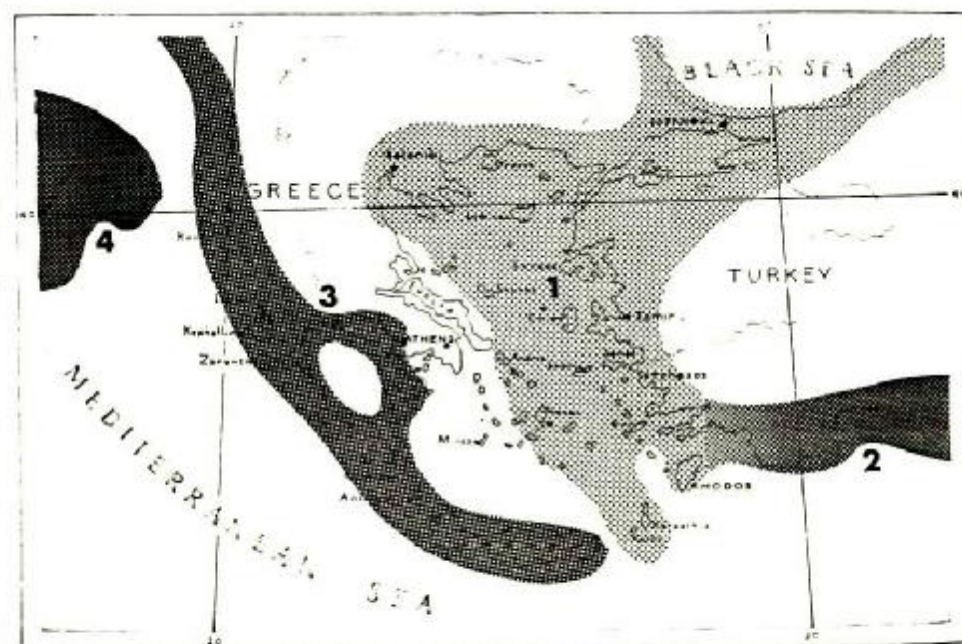


Fig. 33: Situation in the Aegean Area in the early Pleistocene. 1: caspius caspius still connected with the speciating jugularis in the area of southwestern Turkey (2) 3: gemonensis, 4: viridiflavus.

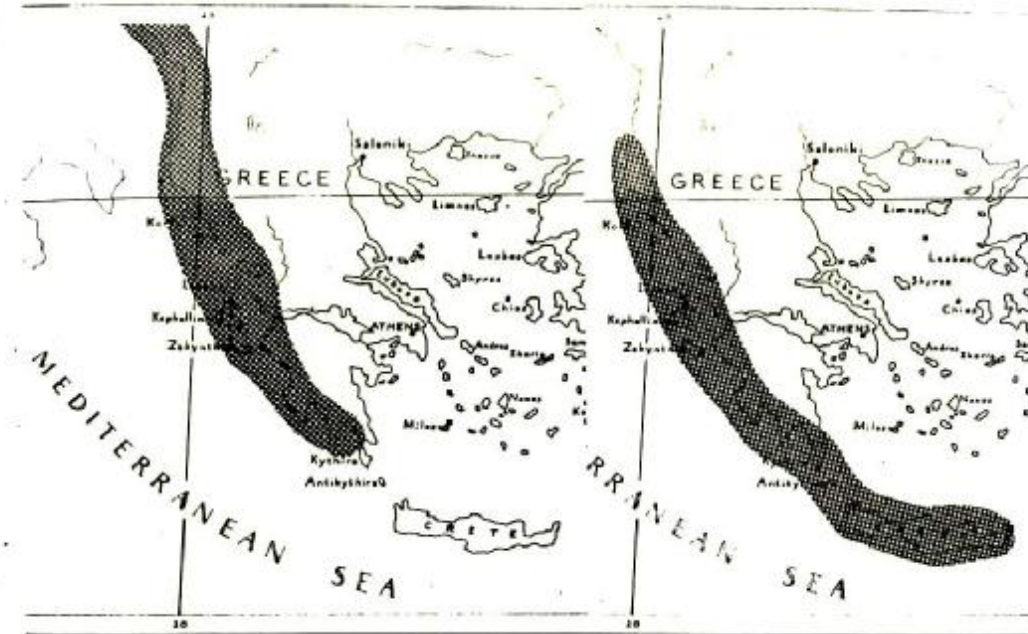


Fig. 34: Speciation of *C. gemonensis* in the eastern Adriatic Area in the late Pliocene (Crete not connected with Greece).



Fig. 35: Shifting of the whole Population southwards due to glaciation at the beginning of the Ice Ages, Crete is reached and invaded in the Mindel Pluvial.



Fig. 36: Recent Distribution of *C. gemonensis* as result of Post-Würm population shifting.

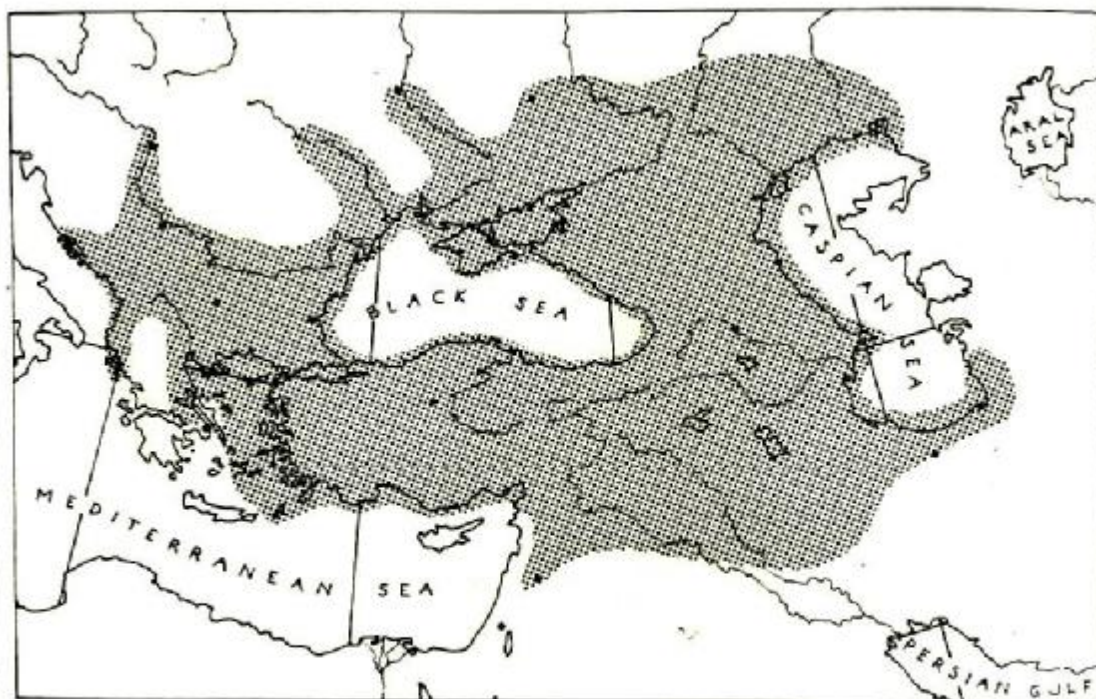


Fig. 37: Recent distribution of Coluber caspius.

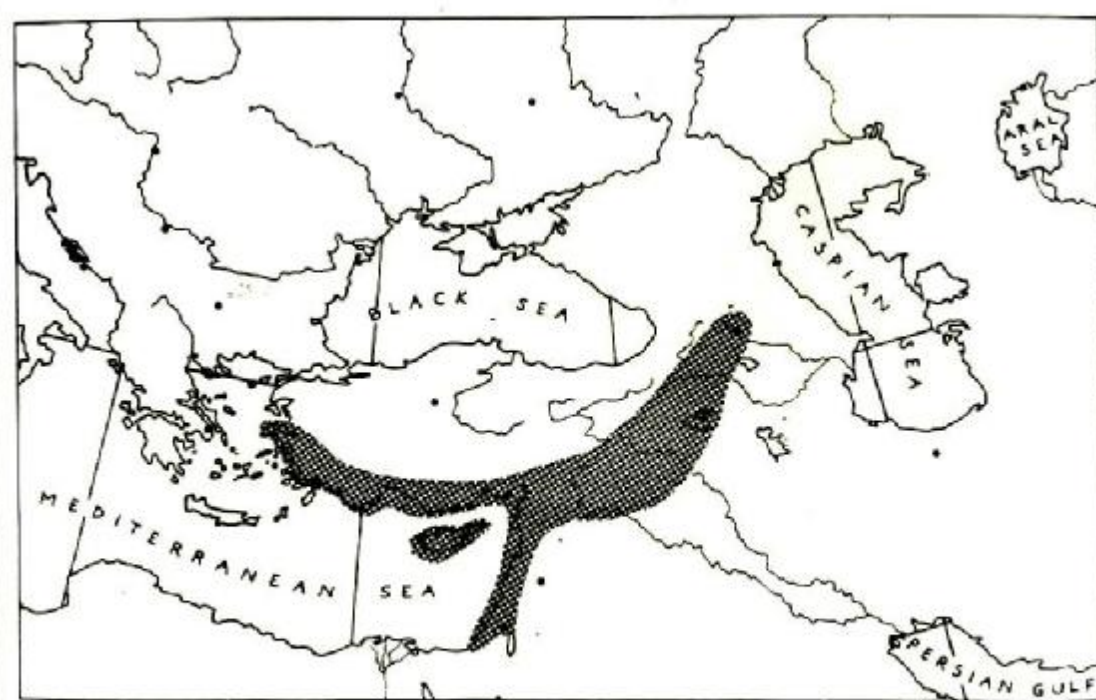


Fig. 38: Recent distribution of Coluber jugularis.

