

The **distribution** and ecology of the amphibians of Georgia and the **Caucasus**: a biogeographical analysis

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Verbreitung und Ökologie der Amphibien in Georgien und im Kaukasus: eine biogeographische Analyse

Die Republik Georgien liegt im westlich-zentralen Gebiet der Kaukasus-Landenge zwischen dem Schwarzen und dem Kaspischen Meer. 13 Amphibienarten kommen in Georgien vor: *Triturus karelinii*, *T. vittatus ophryticus*, *T. vulgaris lantzi*, *Mertensiella caucasica*, *Pelobates syriacus*, *Pelodytes causicus*, *Bufo verrucosissimus*, *B. viridis*, *Hyla arborea schelkownikowi*, *H. savignyi*, *Rana macrocnemis*, *R. camerani*, *R. ridibunda*. Drei Arten (*M. caucasica*, *P. causicus*, *B. verrucosissimus*) und zwei Unterarten (*T. vulgaris lantzi*, *H. arborea schelkownikowi*) sind für den Kaukasus und das nordöstlich angrenzende Anatolien endemisch. Vier Arten (*T. vittatus*, *H. savignyi*, *R. macrocnemis*, *R. »camerani«*) sind auf die klein- und vorderasiatische Region beschränkt. Zwei Arten (*T. karelinii*, *P. syriacus*) sind in Vorderasien und Südosteuropa und zwei weitere Arten (*B. viridis*, *R. ridibunda*) sind über weite Teile Eurasiens verbreitet. Die Analyse der **Verbreitungsmuster** der Amphibien innerhalb und außerhalb der Kaukasusregion **läßt** fünf zoogeographische Gruppen erkennen, die in zwei Großgruppen eingeteilt werden können: (1) in vorderasiatische Arten und (2) in Arten der zoogeographischen Kaukasus-Region. Zwei Artenpaare der Gattungen *Hyla* und *Rana* bilden Hybridzonen in Georgien.

Schlagworte: Amphibienverbreitung, Ökologie, Kaukasus, Georgien, Hybridzonen, Biogeographie.

Summary

The republic of Georgia is situated in the central-western part of the Caucasus Isthmus in between the Black and Caspian Seas. The country has thirteen **amphibian** species: *Triturus karelinii*, *T. vittatus ophryticus*, *T. vulgaris lantzi*, *Mertensiella caucasica*, *Pelobates syriacus*, *Pelodytes causicus*, *Bufo verrucosissimus*, *B. viridis*, *Hyla arborea schelkownikowi*, *H. savignyi*, *Rana macrocnemis*, *R. camerani*, *R. ridibunda*. Three species (*M. caucasica*, *P. causicus*, *B. verrucosissimus*) and two subspecies (*T. vulgaris lantzi*, *H. arborea schelkownikowi*) are endemic to the Caucasus. Four species (*T. vittatus*, *H. savignyi*, *R. macrocnemis*, *R. »camerani«*) are restricted to the Near East region. Two (*T. karelinii*, *P. syriacus*) are distributed throughout south-eastern Europe and the Middle East, **while** two (*B. viridis*, *R. ridibunda*) have a wide Eurasian distribution. The analysis of amphibian distribution patterns, both within and outside the Caucasus region, **leads** to the recognition of five **zoogeographic** groups that in **term** can be arranged into the larger **units** of (1) amphibians of the Near East and (2) amphibians of the Caucasian **zoogeographic** district. Two pairs of closely related species (or subspecies) (*Hyla* and *Rana*) produce hybrid zones in Georgia.

Key words: Amphibian distribution, amphibian ecology, Caucasus, Georgia, hybrid zones, biogeography.

1 Introduction

The republic of Georgia extends over the western and central parts of the Transcaucasus, which region includes the southern slopes of the Great Caucasus, the northern part of the Caucasus Minor Plateau and the intervening lowlands in between the Black and Caspian seas. Of the 15 amphibian species distributed throughout the Caucasus (FROST 1985) all but two are found in Georgia. However, this count includes two pairs of closely related taxa, the taxonomic status of which is as yet unclear. *Mertensiella caucasica* and *Pelodytes causicus* are endemics of the Caucasus and north-eastern Anatolia. Other Caucasian endemics are *Bufo verrucosissimus* (with two subspecies, *B. v. circassicus* and *B. v. turowi*) and, at the subspecific level, *Triturus vulgaris lantzi* and *Hyla arborea schelkownikowi*. Four species are endemics of the Middle East: *Triturus vittatus* (represented here by the subspecies *ophryticus* which is distributed through the western Caucasus and northern Turkey), *Hyla savignyi*, *Rana macrocnemis* and *Rana »camerani«*. Two species are distributed throughout the Near East and south-eastern Europe: *Triturus karelinii* and *Pelobates syriacus*. Finally, two species (*Bufo viridis* and *Rana ridibunda*) are widely distributed across Eurasia.

Hyla savignyi and *Rana »camerani«* possess a number of morphological peculiarities within geographically distinct ranges and may represent real monophyletic taxa. Wide hybrid zones with sister groups (*H. arborea* and *R. macrocnemis*, respectively) appear to be formed with specimens of intermediate character found frequently. A distinct lack of reproductive isolation would challenge their status as full species, but in both cases the situation requires further study. ISHCENKO (1978, 1987), who studied the morphometric variability of Caucasian brown frogs, supposes that *R. »camerani«* should not be given species status because it falls within the variation shown by *R. macrocnemis*.

Mertensiella caucasica, *T. vulgaris lantzi*, *P. causicus*, *B. verrucosissimus*, are allopatric relatives to their sister taxa within the Caucasus. Caucasian populations within the ranges of *T. karelinii*, *H. arborea schelkownikowi* and *R. macrocnemis* are probably isolated from other populations of these species. Hence, a better understanding of the distribution of amphibians in Georgia and the ways these ranges are formed requires a basic knowledge about their distribution throughout the whole of the Caucasus and adjacent regions.

2 Geophysical characteristics of the Caucasus region

The Caucasian Isthmus is composed of three parts that differ in their orogenic origins: the Great Caucasus mountain system, the mountain plateau of Caucasus Minor, and the lowlands situated between these two systems. Traditionally (and following political borders) the northwestern foothills of Elburs Mountains, which do not belong to Great nor to the Minor Caucasus, are included in the Caucasus region. Following BERUCHASHVILI (1979), the Caucasus includes parts of two different physico-geographical domains: the Crimea-Caucasus and the mountain plateaus of Near East (Fig. 1, cf. LEYSIER & CHURSIN 1924). However, the distribution of biogeographic, landscape, ecological and geomorphological regions does not follow this division.

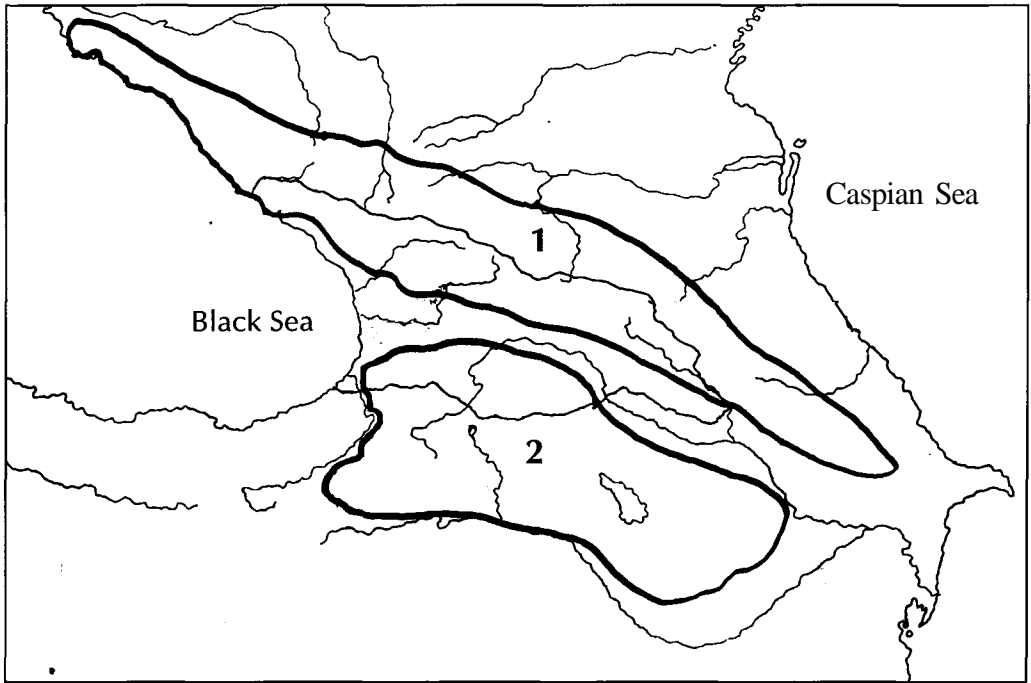


Fig. 1: Approximate borders of the Great Caucasus mountain system (1) and conditional borders of the Caucasus Minor (2). The southern border of the last region is rather unclear, because the mountain plateaus of the Caucasus Minor continually pass to the mountain plateaus of Near East.

Ungefähre Grenzen des Großen (1) und Kleinen Kaukasus (2). Die südlichen Grenzen des Kleinen Kaukasus sind unklar, da die Bergplateaus fließende Übergänge nach Vorderasien besitzen.

From the faunistic point of view (VERESHCHAGIN 1958), all of the Transcaucasus and the mountains of the northern Caucasus belong to the east Mediterranean province of the Palaearctis, and its territory belongs to the two different regions, the Caucasus proper and Near East. The Caucasus proper covers the mountains of the Great Caucasus, the northern slopes of Caucasus Minor and the Elburs mountains and covers three zoogeographic districts. The Caucasian Part of Near East region is composed of the plateaus of the Caucasus Minor and the lowlands of east Transcaucasus, and covers another three zoogeographic districts (Fig. 1). TUNIYEVS (1990) is of the opinion that the western part of Transcaucasus, the Colchis district may represent an independent centre of speciation.

The distribution of landscape types appears to be an important parameter influencing the distribution of animal species. Especially important for amphibians is the presence of forest, the degree of humidity and the type of relief. On the basis of these criteria the seven most important landscape types identified in the Caucasus region are (1) the humid, swampy and forested lowlands such as found in the Colchida, Alazani and Lenkoran valleys, (2) the foothill and mountain forests, (3) the subalpine meadows of the Great Caucasus, (4) the treeless uplands of Caucasus Minor, (5) the semi-arid foothills, (6) the arid and semi-arid lowlands (i. e. steppes and deserts) and (7) the forested valleys at the lower reaches of the river Kura. It should be noted that the bor-

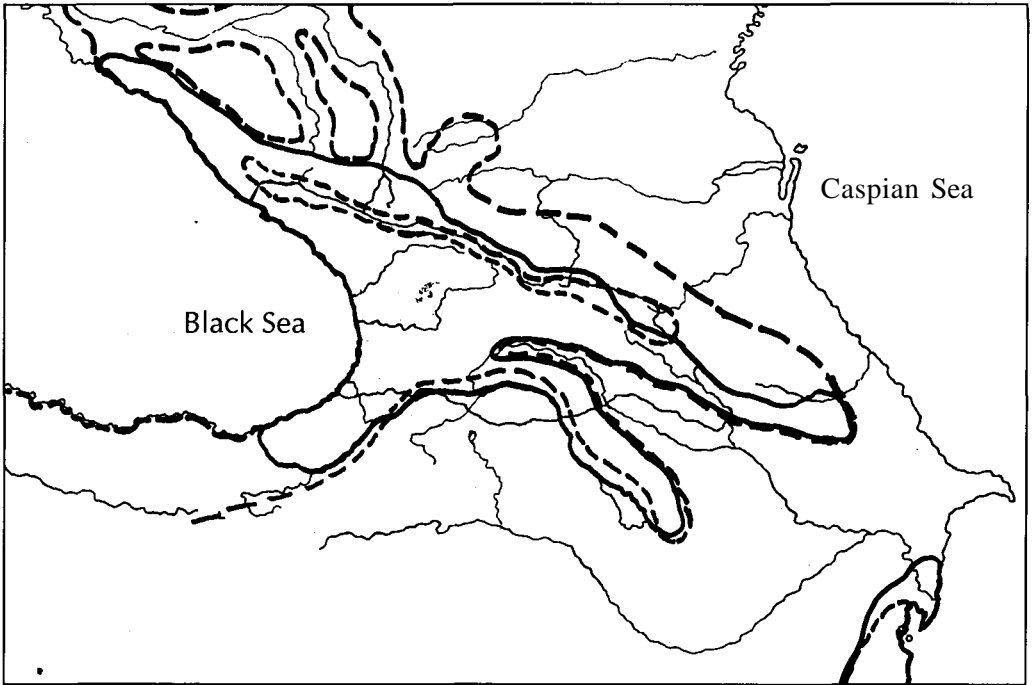


Fig. 2: Conditional borders of the Caucasus proper zoogeographic district (solid line; according to GAJIEV 1986, modified) and approximate borders of the distribution of forests or forest-type vegetation (interrupted line).

Vorbehaltliche Grenzen der zoogeographischen Kaukasus-Region (durchgezogene Linie; verändert nach GAJIEV 1986) und die ungefähren Grenzen der Wald und Wald ähnlichen Formationen (gestrichelte Linie).

ders of landscapes of the first and second types correspond more or less to the borders of the Caucasian faunistic region (Fig. 2).

Sixteen geomorphological regions in Transcaucasus are outlined by MUSEIBOV (1986) among which the main types are (1) the lowlands, (2) the low mountains, (3) the medium and high altitude mountains, and (4) the plateaus of volcanic origin. The eastern borders of the high and middle mountains approximately coincide with the borders of the Caucasian faunistic region.

Across the Caucasian Isthmus the level of precipitation varies between less than 200 mm/year to more than 3 500 mm/year. The humidity gradually increases from east to west, from low to high elevations, and from the northern Caucasus to the Transcaucasus (VLADIMIROV et al. 1991) (Fig. 3).

3 Historical notes

The first reference to the amphibians of Georgia stems from the 18th century encyclopedist SULKHAN-SABA ORBELIANI. In his Dictionary of the Georgian Language («Lexiconi Kartuli») this author lists five Georgian names, referring to three genera of amphibians: the frog (*Rana*), the toad (*Bufo*) and the treefrog (*Hyla*) (ORBELIANI 1991).

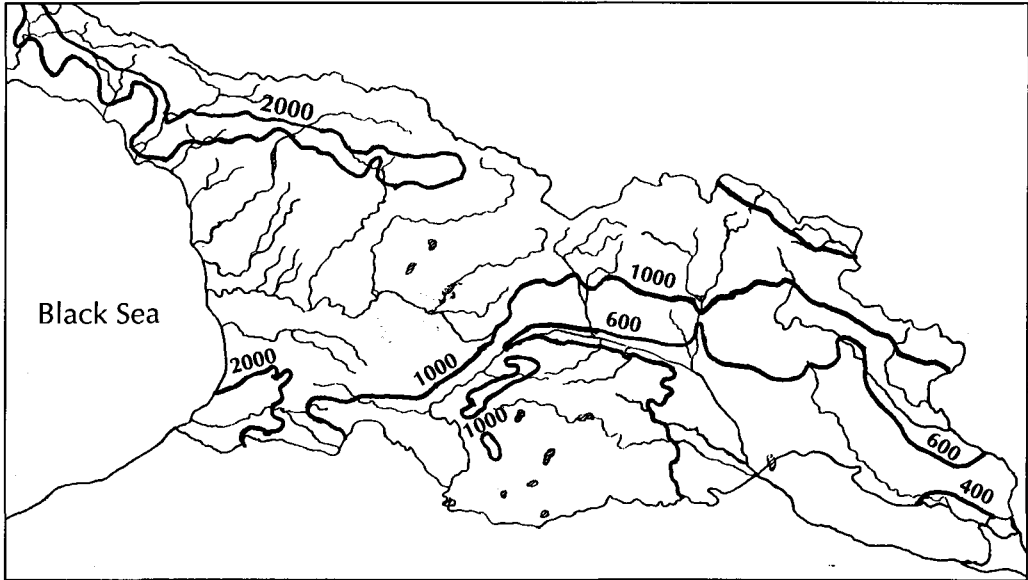


Fig. 3: Isoclines of the level of annual precipitations in Georgia (according to VLADIMIROV et al. 1990).
Isoklinen der jährlichen Niederschlagsmengen in Georgien (nach VLADIMIROV et al. 1990).

PALLAS (1831) described the Colchic toad, probably from western Georgia. His expeditions lead EICHWALD (1831, 1841) to list seven amphibian species and three were added by KESSLER (1878), WAGA (1876) and GRIMM (1876). NIKOLSKY (1913) summarized the information on Caucasus amphibians, listing 14 species. *Pelobates syriacus* was not yet included, whereas *Rana dalmatina*, a species superficially similar to *R. macrocnemis* was included by mistake. MERTENS (1923) established the presence in Georgia of *P. syriacus*. Finally, valuable contributions to the Caucasian batrachology were made by BEDRIAGA (1879, 1882), BOETTGER (1889) and BERG (1910).

Clarifications to the taxonomic status of Caucasian amphibians were brought about by WAGA (1876), who described the Caucasian salamander and WOLTERSTORFF (1925) who allocated it to the genus *Mertensiella*. BOULENGER (1885, 1886, 1896) described *Rana macrocnemis*, *Rana camerani* and (almost simultaneously with NIKOLSKY 1896) *Pelodytes caucasicus*. SHELKOWNIKOW (1910) demonstrated the existence of substantial differences between *Hyla arborea* and *H. savignyi*. CHERNOV (1926) described *H. a. schelkownikowi* as a subspecies. WOLTERSTORFF (1914) described the subspecies *T. vulgaris lantzi*, which taxonomic position was recently discussed by RAXWORTHY (1990). GUMILEVSKY (1939), TERENTYEV (1960) and SCHNEIDER (1974) discussed the taxonomic status of various Caucasian treefrogs in detail. WOLTERSTORFF (1906), BODENHEIMER (1944) and SCHMIDTLER & SCHMIDTLER (1967) did the same for *Triturus vittatus* and DELWIG (1928b), BARAN (1969) and ISHCENKO (1978, 1987) for brown frogs from the Near East. BUCCI-INNOCENTI et al. (1983) made suggestion to increase the taxonomic status of *Triturus karelinii*. TARTARASHVILI & BAKRADZE (1989) described the new subspecies of Caucasian salamander from BATUMI, with reduced pigmentation, *Mertensiella caucasica janashvili*. Finally, ORLOVA & TUNIYEV (1989) revised the taxonomic status of the Colchic toad.

Data on amphibian distribution were compiled by SOBOLEVSKY (1929) for south-eastern Azerbaijan, GUMILEVSKY (1939) for Armenia and the Nakhichevan region of Azerbaijan, DJANASHVILI (1956) for Georgia, EISELT (1965) for north-eastern Turkey, ALEKPEROV (1978) for Azerbaijan and VISOTIN & TERTISHNIKOV (1988) for the northern Caucasus. The distribution of amphibians over separate districts was described by BOETTGER (1892), BARACH (1925), KRASSOVSKY (1929), ROSTOMBEGOV (1930), EKVTIMISHVILI (1940), MUSKHELISHVILI (1959) ORLOVA (1973), TUNIYEV (1985), TARKHNISHVILI & THIESMEIER (1994). Reviews dedicated to the distribution of single species or species groups were prepared for *Hyla* spp. (GUMILEVSKY 1939), for *Pelobates syriacus* (PAPANYAN 1956), *Pelodytes caucasicus* (DAREVSKY et al. 1971, GOLUBEV 1980), *Rana macrocnemis* (TERTISHNIKOV et al. 1979) and for *T. vittatus* (TERTISHNIKOV & GOROVAYA 1985, TUNIYEV et al. 1987). Data on fossil amphibians were summarized by CHKHIKVADZE (1984). Complementary data are provided by LANTZ (1911), PAPANYAN (1952, 1961), ROTTER (1958), ALEKPEROV (1961), BAKRADZE (1985), BORKIN (1977), TERTISHNIKOV et al. (1979), GOLUBEV (1981), GOROVAYA & TERTISHNIKOV (1983), TUNIYEV (1983), BELOVA (1985), LEONTYEVA (1987), RUDIK (1989), TARKHNISHVILI & THIESMEIER (1994), KUZMIN (1995). The geography of the Caucasian herpetofauna is reviewed by BORKIN (1987) and TUNIYEV (1985, 1987, 1990, 1995).

4 • Amphibian distribution

In the following chapters, the known localities in Georgia for 13 amphibian species will be enumerated and the general distribution throughout the Caucasus will be described. Some obviously erroneous data are omitted (such as the reported presence of *Hyla savignyi* in the western Caucasus and *Mertensiella caucasica* in the Great Caucasus). Other doubtful cases are discussed.

Caucasian salamander — *Mertensiella caucasica* (WAGA, 1876)

Mertensiella caucasica is distributed along the Meskheta and Shavsheti mountains in Georgia, as well as across the western foothills of the Trialeti mountains. Outside Georgia it is found along the Arsian, Lasistan and Ponto mountains in northeastern Turkey. For Georgia, 17 localities are known (Fig. 4): (1) Zekari mountain pass (WAGA 1876), (2) the valley of the Baniskhevi, (3) mountain Lomis, (4) Borjomi canyon, (5) Keda, (6) Makhuntseti (Ajara), (7) Sairme and (8) Abastumani, Meskheta mountains (NIKOLSKY 1913), (9) mountain Mtirala near Batumi (OBST & ROTTER 1961), (10) The valley of the Nedzura (DAREVSKY & POLOZHIKHINA 1966), (11) Kintrishi reserve, (12) Goderdzi mountain pass (BAKRADZE 1985), (13) Chitakhevi and (14) Kvabiskhevi (TUNIYEV 1985), (15) valley of the Kamisvakistskali (16) the valley of the river Charnali, in foothills of Lasistan mountains and (17) the Batumi Botanical Garden (pers. comm. of M. BAKRADZE, TARKHNISHVILI unpubl. data). Outside Georgia this species is recorded from eight localities in north-eastern Turkey (ATATUR & BUDAK 1982). *Mertensiella caucasica* has the narrowest range among all Caucasian amphibian species. Its presence appears to be associated with high humidity (a precipitations of over 1000 mm/year) and with the subtropical forests of north-western Caucasus Minor. *Merten-*

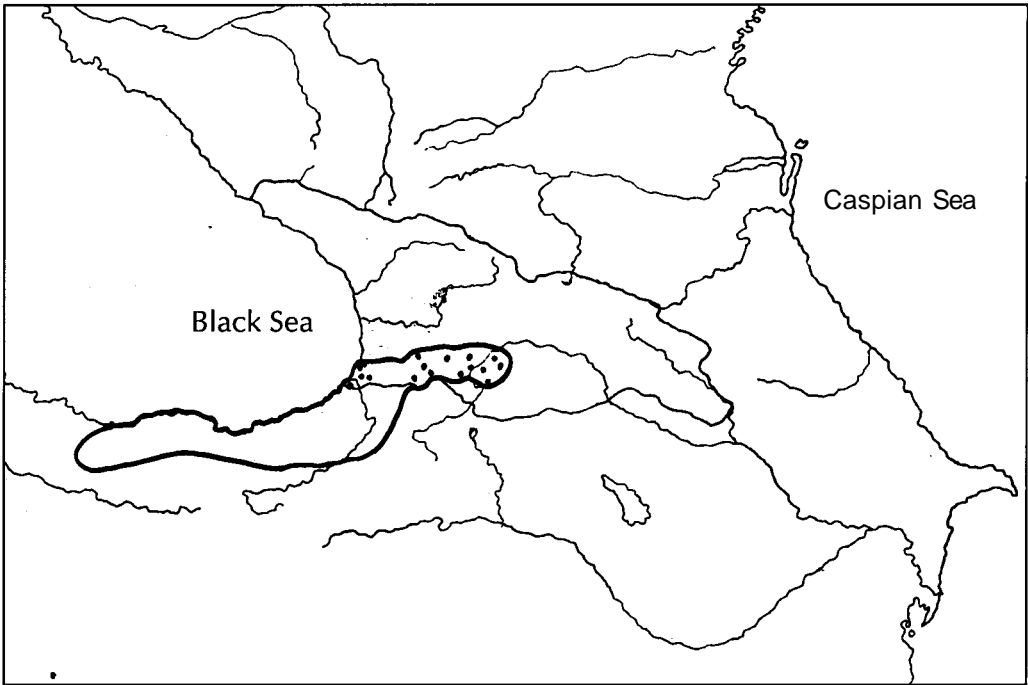


Fig. 4: Distribution of *Mertensiella caucasica*. The points indicate only documented Georgian localities, and the bold line the extrapolated range within the considered area, constructed on the base of known localities and appropriate landscapes for this species. Scale 1: 5 000.

Verbreitung von *Mertensiella caucasica*. Die Punkte zeigen dokumentierte Fundorte in Georgien an. Die kräftigen schwarzen Linien umreißen die ungefähre Verbreitung der Art im behandelten Gebiet, ermittelt auf der Grundlage bekannter Fundorte und geeigneter Lebensräume. Maßstab 1 : 5 000.

siella caucasica is absent from the Great Caucasus range (e. g. SHUGUROV 1909) and from central and eastern Transcaucasus. The easternmost known locality (Borjomi) is in the basin of the river Kura, draining into the Caspian Sea. The other localities are in the basins of the Chorokh, and other rivers discharging into the Black Sea.

Banded newt — *Triturus vittatusophryticus* BERIHOLD, 1846

Triturus vittatus ophryticus is known from the western and central Transcaucasus and from the north-western Caucasus, up to the upper ranges of the river Kuban. The species is known from 36 localities in Georgia (Fig. 5): (1) Betania, (2) near Turtle Lake, (3) Batumi, (4) Poti, (5) Gagra, (6) Sukhumi, (7) Kutaisi, (8) Lechkhumi, (9) Kodiani, (10) Baniskhevi, (11) mountain Lomis (NIKOLSKY 1913), (12) Jagoras-Veli (Lantz 1911), (13) Akhaldaba lake, Tskhheti (ROSTOMBEGOV 1930), (14) the Sakochavi Lakes, (15) Didi Mitarbi, (16) the village Tba, (17) Ozurgeti district and (18) the lake Chiantba (Telavi) (DJANASHVILI 1956), (19) the village Mtis Kalta, (20) the village Tskhvarichamia (upper ranges of Rioni) (TUNIYEV et al. 1987), (21) Gumista reserve (Abkhaseti), (22) Ajameti reserve near Kutaisi, (23) Kazbegi reserve, (24) Kintrishi reserve (Ajara), (25) upstream of the river Liakhvi, (26) Mariamjvari reserve near Sagarejo, (27) near lake Ritsa, (28) the Saguramo reserve near Tbilisi and (29) Lake Ertso (DAREVSKY

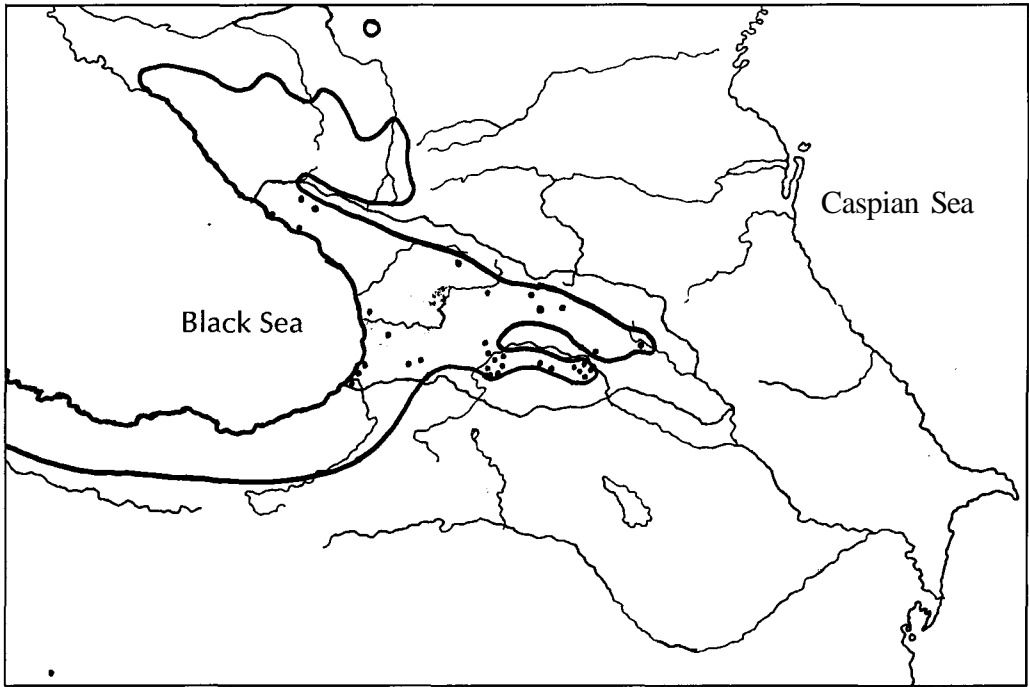


Fig. 5: Distribution of *Triturus vittatus ophryticus*. Further explanations see fig. 4.
 Verbreitung von *Triturus vittatus ophryticus*. Weitere Erläuterungen siehe Fig. 4.

1987), (30) the village Akhaldaba, (31) Ertatsminda lake, (32) Pitsesi Lake (Kaspi), (33) Tsodoreti Lake, (34) Satovle mountains, (35) Lake Chili-Tba (Tbilisi) and (36) the valley of the river Charnali (TARKHNISHVILI & THIESMEIER 1994, TARKHNISHVILI unpubl. data). Outside Georgia the banded newt is known from 35 Caucasian localities (NIKOLSKY 1913, GOLUBEV 1981, TUNIYEV 1985, TUNIYEV et al. 1987, TERTISHNIKOV & GOROVAYA 1985, DAREVSKY 1987, VISOTIN & TERTISHNIKOV 1988, KUZMIN 1995). The banded newt is widely distributed throughout the mountain forests of the western Caucasus. Along the northern slopes of the Great Caucasus it is found upstream in the tributaries of the river Kuban and an isolated population lives in the vicinity of Stavropol. Along the southern slopes of Great Caucasus the range of this species reaches Telavi. It is also distributed along the northern slopes of the Trialeti and Meskheti mountains, but it does not seem to occur in Armenia. In eastern Georgia the occurrences are sporadic whereas in western Georgia the distribution is more or less continuous. The Caucasian part represents the north-eastern border of the species range.

Lantz's smooth newt — *Triturus vulgaris lantzi* WOLTERSTORFF, 1914

Triturus vulgaris lantzi is distributed in the west and central Transcaucasus, the western part of the northern Caucasus, in southeastern Azerbaijan and in the northern foothills of the Elburs mountains. There are 17 known Georgian localities (Fig. 6): (1) Batumi, (2) Sukhumi, (3) Gagra, (4) Pitsunda, (5) Kutaisi and (6) Bakuriani (NIKOLSKY 1913), (7) near Poti (Kulagin-see, EKVTIMISHVILI 1940), (8) Mukheri, (9) the Sakochavi

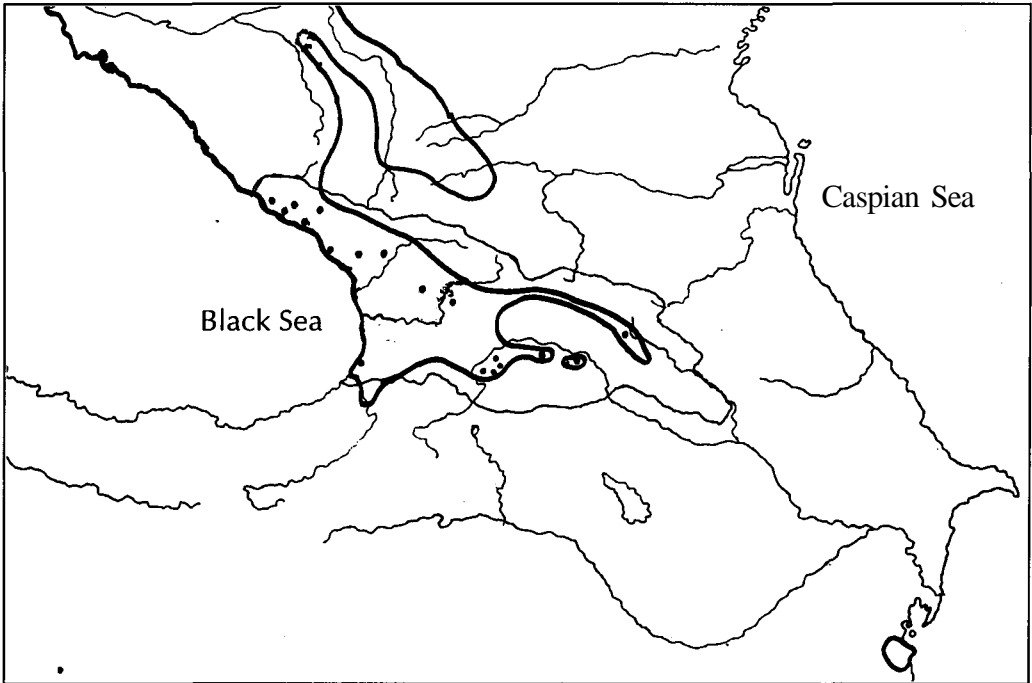


Fig. 6: Distribution of *Titurus vulgaris lantzi*. Further explanations see fig. 4.
Verbreitung von *Titurus vulgaris lantzi*. Weitere Erläuterungen siehe Fig. 4.

lakes, (10) Didi Mitarbi, (11) the village Tba (EKVTIMISHVILI 1940), (12) Kobuleti (DJANASHVILI 1956), (13) Lagodekhi and (14) Sataplia (DAREVSKY 1987), (15) Chiantba lake near Telavi, (16) Satovle mountains near Tbilisi and (17) Ertatsminda lake in the central part of the Trialeti mountains (TARKHNISHVILI & THIESMEIER, 1994). The reported occurrence in Armenia may be erroneous (NIKOLSKY 1913). It appears that several populations in east Georgia (e. g. near Kvareli) have recently gone extinct.

Outside Georgia, this species is known from two localities in southeastern Azerbaijan near Lenkoran (ALEKPEROV 1978) and in over 30 localities in the north-western Caucasus (BANNIKOV et al. 1977, TUNIYEV 1987, VISOTIN & TERTISHNIKOV 1988, KUZMIN 1995). Lantz's smooth newt is widely distributed in the western half of the Caucasian Isthmus, in the north reaching downstream of the river Don and in the lowland forests of the river Kuban. In eastern Georgia, its distribution strongly coincides with that of the banded newt. The presence of Lantz's smooth newt in the foothills of the Elburs ridge is remarkable. The range of *T. vulgaris lantzi* appears to be geographically isolated from other *T. vulgaris* and it is itself divided into two parts.

Karelin's crested newt — *Triturus karelinii* STRAUCH, 1870

The range of *Triturus karelinii* covers south-eastern Europe and the Crimea, western and central Anatolia, the western and central Caucasus and the Elburs mountains. There are 33 known Georgian localities of this species (Fig. 7): (1) Poti, (2) Sukhumi, (3) Kutaisi, (4) Senaki, (5) Ajara (?), (6) Baniskhevi, (7) Borjomi, (8) Bakuriani, (9) Betania,

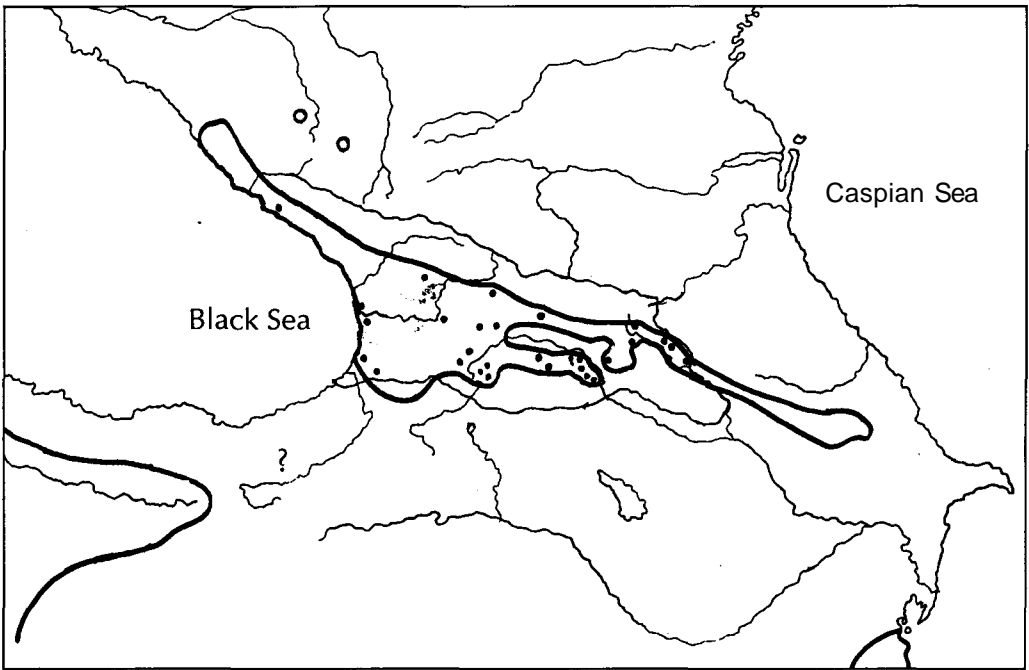


Fig. 7: Distribution of *Titurus karelinii*. Further explanations see fig. 4.
 Verbreitung von *Titurus karelinii*. Weitere Erläuterungen siehe Fig. 4.

(10) Surami and (11) the valley of the river Tana (NIKOLSKY 1913), (12) Sakochavi Lakes, (13) Didi Mitarbi, (14) the village Tba, (15) Kodiani, (EKVTIMISHVILI 1940), (16) Gagra, (17) Kobuleti, (18), Akhaldaba Lake near Tbilisi and (19) Chiantba lake near Telavi (DJANASHVILI 1956), (20) Batsara reserve, (21) the Ajameti reserve, (22) Lagodekhi, (23) the Liakhvi reserve, (24) the Pskhu reserve, (25) the Ritsa reserve (Abkhazeti), (26) the Saguramo reserve (DAREVSKY 1987), (27) Tsodoreti lake, (28) Satovle mountain ridge, (29) Lake Chili-Tba, (30) Ertatsminda lake, (31) Pitsesi Lake (Kaspi), (32) the man-made lake of Duruji and (33) Bursa valley (Kvareli). The locality near Batumi (DJANASHVILI 1956) appears to be erroneous.

Outside Georgia, *T. karelinii* is known from seven localities in northern, four in south-eastern Azerbaijan, and from at least six localities in the Krasnodar region of Russia. In the west Caucasus the range of *T. karelinii* stretches up to the foothills of Great Caucasus, at some places reaching into the basin of the river Kuban. In the east Transcaucasus its range reaches Tbilisi along the Trialeti mountains and the eastern foothills of the Great Caucasus in Azerbaijan. The species is found in forests of the Elburs mountains in northern Iran and southeastern Azerbaijan. In the humid forests of the western Transcaucasus Karelin's crested newt is rare and its populations usually small. The species appears to be absent in the extreme south-west of Georgia. In both parts of its Caucasian distribution Karelin's crested newt appears to be allopatric from other crested newt taxa.

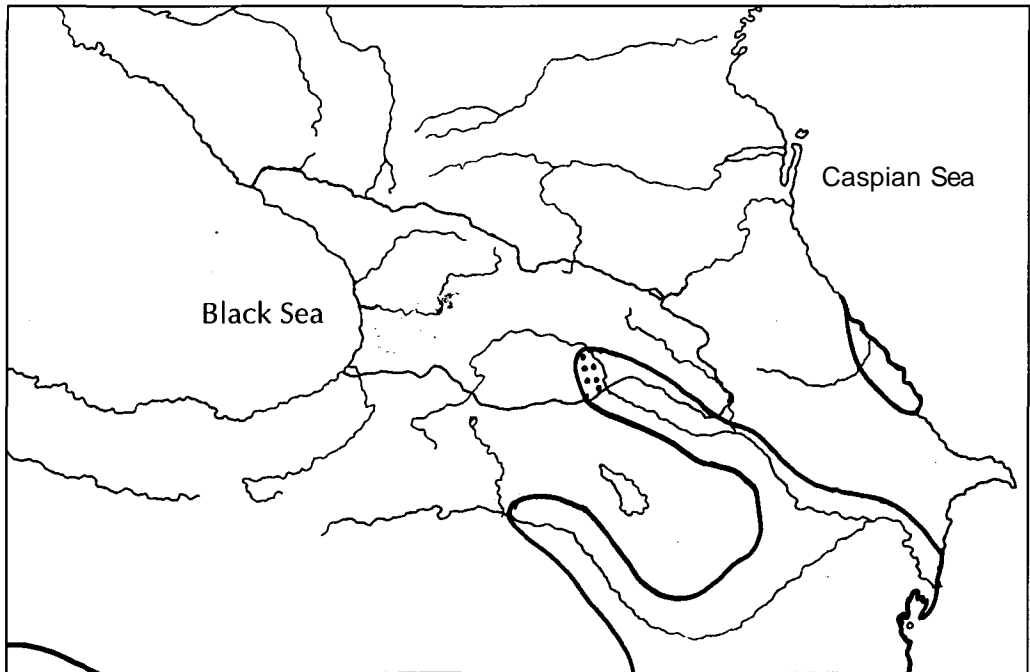


Fig. 8: Distribution of *Pelobates syriacus*. Further explanations see fig. 4.
 Verbreitung von *Pelobates syriacus*. Weitere Erläuterungen siehe Fig. 4.

Eastern spadefoot toad — *Pelobates syriacus syriacus* BOETTGER, 1889

The nominative subspecies of the Eastern spadefoot toad, *Pelobates s. syriacus* is known from Anatolia and the Middle East, including south-eastern Transcaucasus. The range is bordered by the valleys of the river Arax (up to the eastern border of Armenia), the Kura (up to Tbilisi) and by the Samur (up to its mouth at the Caspian Sea). In Georgia the Eastern spadefoot toad is known from eight localities (Fig. 8): (1) Turtle lake near Tbilisi (DELWIG 1928a), (2) Manglisi (DJANASHVILI & ZHORDANIA 1960), (3) surroundings of the lake Kumisi and (4) lake Chili-Tba (BAKRADZE et al. 1987), (5) Tsodoret lake, (6) Akhaldaba lake and (7) between Tbilisi and Rustavi (TARKHNISHVILI & THIESMEIER, 1994). Fossil bones of this species were found (8) downstream of the river Khrami. All these populations of *P. syriacus* are endangered and some may have gone extinct already. The reported finding of this species in Manglisi needs checking because locally the landscape type (mainly mixed forest) may be too humid for this animal and it certainly is atypical for the species. Outside Georgia the Eastern spadefoot toad is known from 15 dispersed Caucasian localities (PAPANYAN 1956, ALEKPEROV 1961, ANANYEVA & NIKITIN 1977, DAREVSKY 1987, LEONTYEVA 1987). Though the distribution of *P. syriacus*' populations in the Caucasus appears to be sporadic, a tendency is displayed for the species to occur in dry lowland and foothill territories around the Kura and Arax river beds, as well as along the Caspian Sea coast. The species appears to be absent from the Caucasian part of the Black Sea basin and from the forest belt of the Great Caucasus. Due to its secretive mode of life the Eastern spadefoot toad may

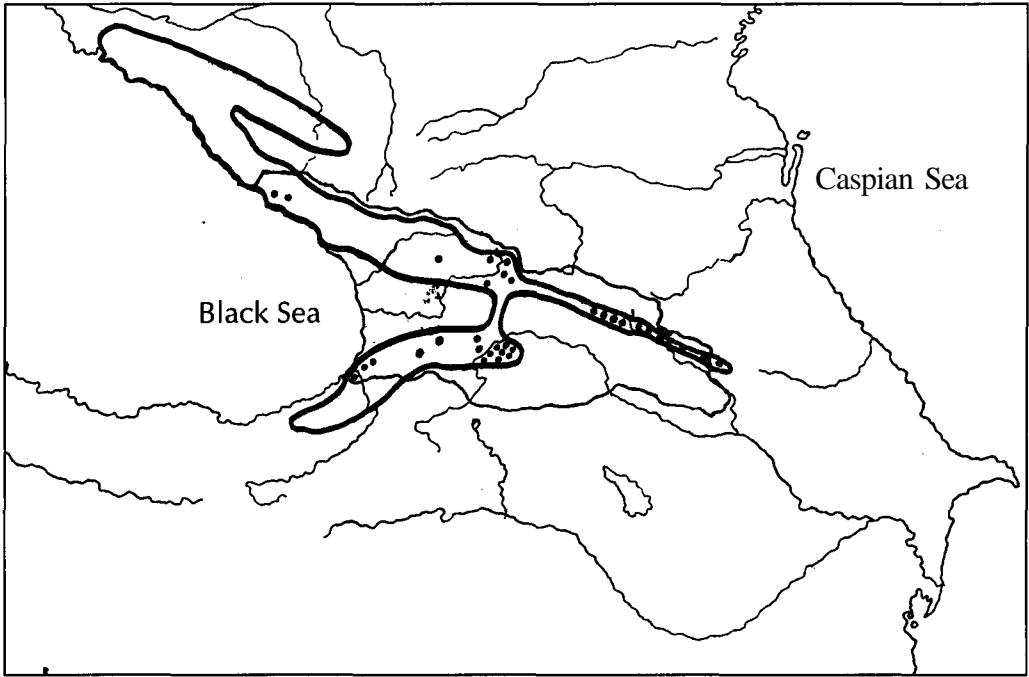


Fig. 9: Distribution of *Pelodytes caucasicus*. Further explanations see fig. 4.
 Verbreitung von *Pelodytes caucasicus*. Weitere Erläuterungen siehe Fig. 4.

be underrepresented in the survey. The south-east Transcaucasus covers the north-eastern part of the specific range, which spreads over the large part of the Near East and south-eastern Europe.

Caucasian parsley frog — *Pelodytes caucasicus* BOULENGER, 1886

The range of *Pelodytes caucasicus* is for the most part situated in Georgia where 33 out of 50 known localities of this species are situated (Fig. 9). GOLUBEV (1980) summarized the existing distributional data with 20 Georgian localities of *P. caucasicus* from four bibliographic sources (NIKOLSKY 1913, ROTTER 1958, CHANTURISHVILI 1940, ZHORDANIA 1960) and his own data: (1) Bakuriani, (2) Borjomi, (3) village Tba, (4) Akhaldaba, (5) Tsikhisdjvari, (6) Batumi, (7) Bagdadi, (8) Gagra, (9) Sukhumi, (10) Shovi, (11) Kvaisi, (12) Oni, (13) upstreams of the river Rioni near Kvemo-Khvtse, (14) Magaroskari, (15) Zemo-Artani, (16) Birkiani, (17) Pshaveli, (18) Shilda, (19) Akhalsopeli and (20) Lagodekhi. Localities not on GOLUBEV'S list are: (21) Zekari Mountain Pass and (22) Kintrishi reserve (BAKRADZE 1985), (23) Kvereti (SERBINOVA pers. comm.), (24) the canyon of the river Gujareti, (25) upstreams of the river Nedzura, (26) the river Charnali valley at the northern foothills of the Lasistianian mountain ridge and (27) vicinity of Kvareli (TARKHNISHVILI unpubl. data).

Outside Georgia, the Caucasian parsley frog is known from the north-western Caucasus, from one locality in north-western Azerbaijan and from two localities in north-eastern Turkey (GOLUBEV 1980, VISOTIN & TERTISHNIKOV 1988, SCHULTSCHIK, 1992).

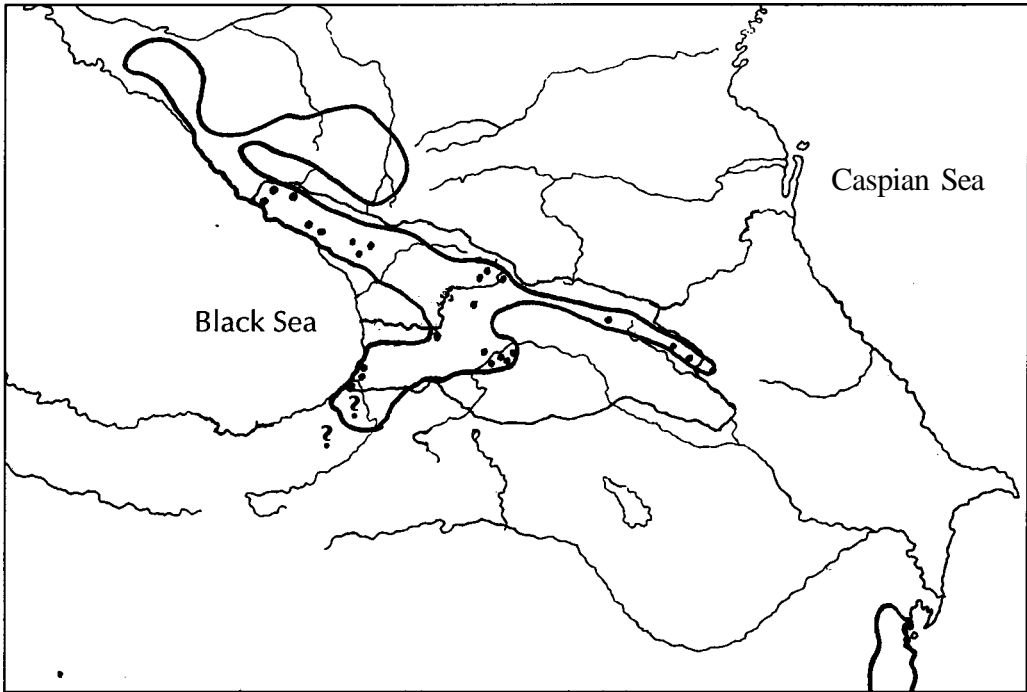


Fig. 10: Distribution of *Bufo verrucosissimus*. Further explanations see fig. 4.
 Verbreitung von *Bufo verrucosissimus*. Weitere Erläuterungen siehe Fig. 4.

The range of *P. caucasicus* covers a major part of the southern slopes of the Great Caucasus, up to the north-western Azerbaijan, upstreams of the river Kuban and its tributaries in the north-western Caucasus, the north-western slopes of the Lasistanian and Meskheti mountains and the extreme west of the Trialeti mountains. Altogether, the Caucasian parsley frog has a small distribution that appears to be restricted to the humid subtropics of the western Caucasus of the so-called »Colchic« vegetation type. Locally the species may be common or even abundant. Its range may be disjunct over the Great and Minor Caucasus.

Colchic toad — *Bufo verrucosissimus* (PALLAS, 1831)

Bufo verrucosissimus is known from 20 Georgian localities (Fig. 10): (1) Akhali Atoni, (2) Sukhumi, (3) Gagra, (4) Bedia, (5) Gudauta, (6) Tsebelda (Abkhazeti), (7) Kvaliti, (8) Kutaisi, (9) Lagodekhi and (10) Batumi (NIKOLSKY 1913), (11) Baniskhevi (EKVTIMISHVILI 1940), (12) the Jupshara and (13) the Lashipse river (TUNIYEV 1985), (13) Kvereti near Chiatura (SERBINOVA pers. comm.), (14) Kharagauli (DJANASHVILI 1956), (15) Akhaldaba, (16) Tsagveri (17) valley of the river Aragvi, (18) valley of the river Bursa (Kvareli), (19) mountain Mtirala and (20) the Charnali valley at the north-eastern foothills of the Lasistans (TARKHNISHVILI unpubl. data). The reported presence of this species near Tbilisi (DJANASHVILI 1956) is likely to be in error.

Outside Georgia, the Colchic toad is known from the north-western Caucasus, from two sites in north-western Azerbaijan and from three sites in south-eastern Azerbai-

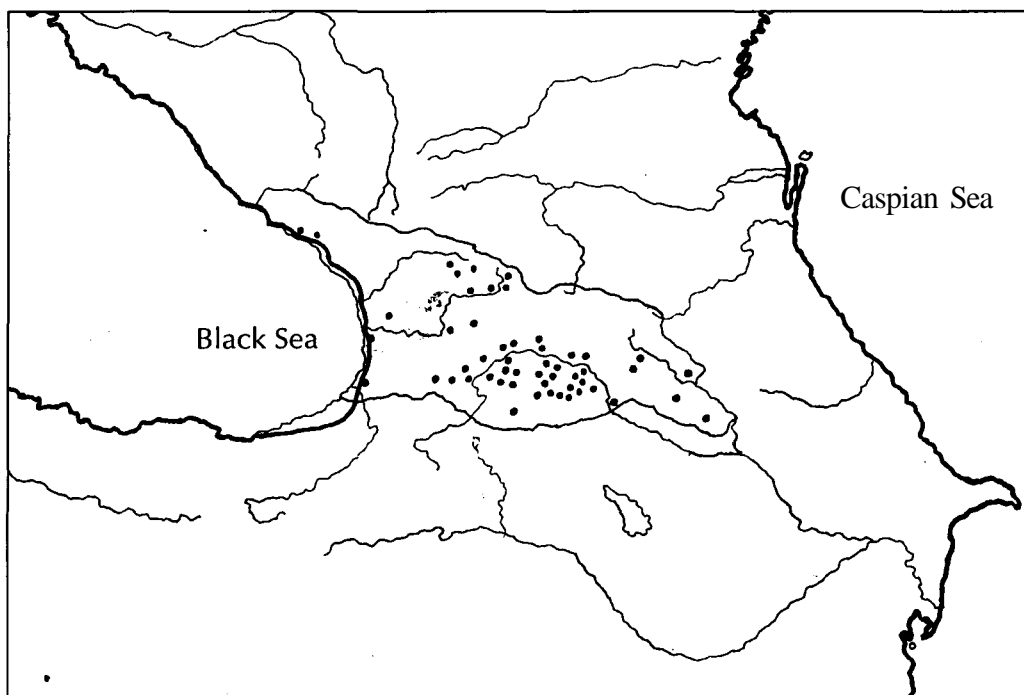


Fig. 11: Distribution of *Bufo viridis*. Further explanations see fig. 4.
Verbreitung von *Bufo viridis*. Weitere Erläuterungen siehe Fig. 4.

jan (ALEKPEROV 1978, VISOTIN & TERTISHNIKOV 1988, ORLOVA & TUNIYEV 1989). Toads from the two localities in the north-western Caucasus were described as separate subspecies, *B. v. circassicus* and *B. v. turowi* (ORLOVA & TUNIYEV 1989).

The range of the Colchic toad is disjunct over parts coined »Colchic« and »Elburs«, respectively (Fig. 10). Its range covers most of the southern slopes of the Great Caucasus, from the north-western foothills to northern Azerbaijan; upstream of the river Kuban and its tributaries, with a separate occurrence near Stavropol, the Meskheta mountains and the western foothills of the Trialeti mountains in Georgia. The range of this species resembles that of *P. caucasicus*, but it extends farther over the western part of the Elburs mountains.

Green toad — *Bufo viridis* LAURENTI, 1768

Bufo viridis is distributed all over the Caucasian Isthmus, throughout the Transcaucasus and the northern Caucasus in all landscapes types and from forests to deserts into urbanized areas. However, the green toad appears to avoid closed-canopy forests, though it may be found in forest clearings, and it is rare in the more humid areas of the Black Sea coast. The green toad is recorded from 28 localities throughout eastern Georgia and 14 localities from western Georgia (Fig. 11), including localities situated on the Black Sea coast such as Batumi and Poti (NIKOLSKY 1913, EKVIIMISHVILI 1940, DJANASHVILI 1956, MUSKHELISHVILI 1959, KUZMIN 1995) (Fig. 11). Listing the known sites would reveal the intensity of faunistic research rather than the actual distribution

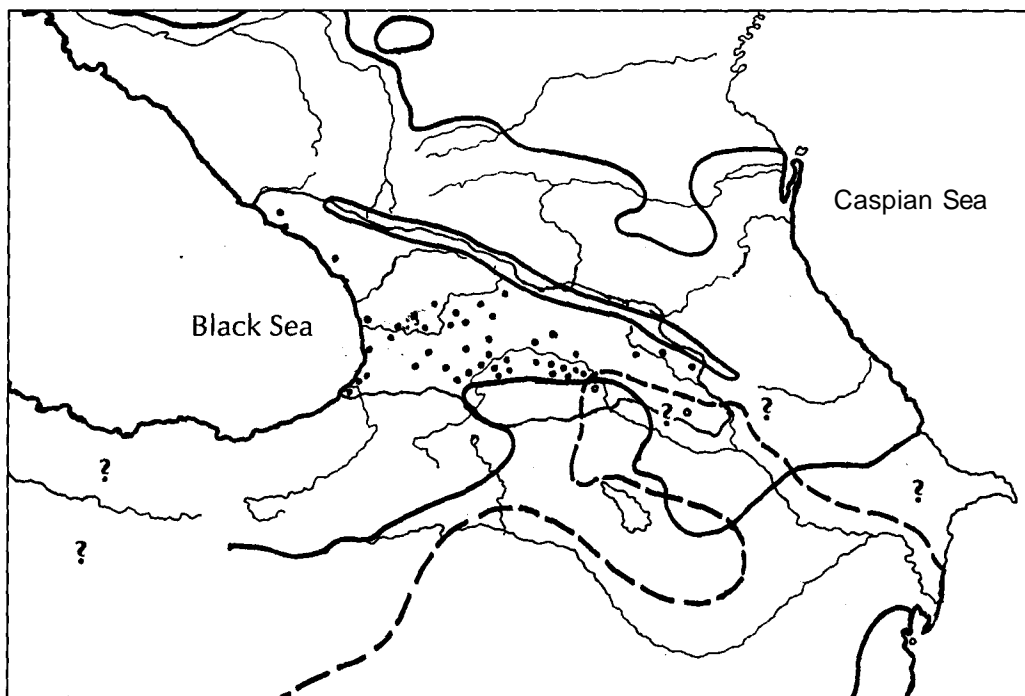


Fig. 12: Distribution of *Hyla* sp.: solid points; *Hyla arborea schelkownikowi*: solid line; *Hyla savignyi*: open circles and dotted line. Further explanations see fig. 4.

Verbreitung von *Hyla* sp.: Punkte; *Hyla arborea schelkownikowi*: durchgehende Linie; *Hyla savignyi*: Kreise und unterbrochene Linie. Weitere Erläuterungen siehe Fig. 4.

of the species and is therefore not attempted. *Bufo viridis* is abundant all over Georgia, except for the Black Sea coast in the south-west of the country. Some marked morphological differences appear to exist between toads from the south-east of Georgia and those from other parts of the country. The green toads from Armenia differ morphologically from toads inhabiting the other parts of the Caucasus. GUMILEVSKY (1939) distinguished three varieties: the typical form, *stmuchi* and *pewzowi*. Toads inhabiting the arid regions in south-eastern Georgia show a more pronounced sexual dimorphism while certain differences in skin structure and coloration (including a narrow mid-dorsal strip) can also be observed.

Outside Georgia, the green toad is known from at least 162 Caucasian localities (NIKOLSKY 1913, GUMILEVSKY 1939, BANNIKOV et al. 1977, ALEKPEROV 1978, KUBANTSEV et al. 1979, VISOTIN & TERTISHNIKOV 1988, LEDENISOV & MELKUMYAN 1987, KUZMIN 1995).

Common treefrog — *Hyla arborea schelkownikowi* CHERNOV, 1926

Hyla arborea schelkownikowi, the common treefrog or Shelkownikow treefrog, is recorded from the following Georgian localities (Fig. 12): (1) Gagra, (2) Batumi, (3) Kobuleti, (4) Poti, (5) Sukhumi, (6) Kutaisi and (7) Rioni, (8) Mukhrani and (9) Tbilisi (NIKOLSKY 1913), (10) Chakva, (11) Gebi, (12) Kharagauli, (13) Bakuriani, (14) Borjomi,

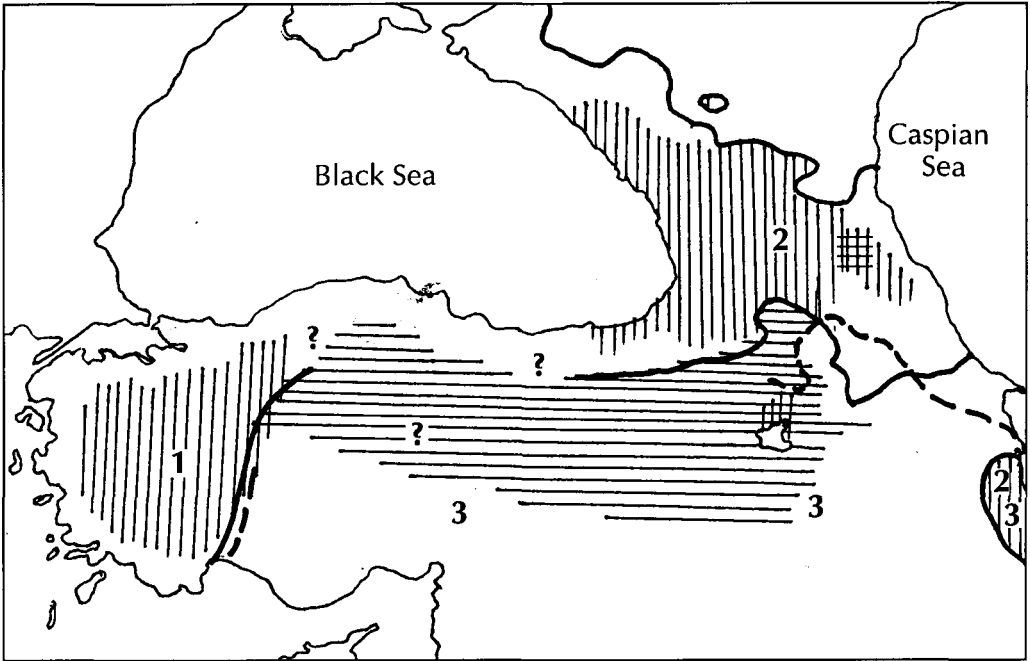


Fig. 13: The distribution of brown frogs and treefrogs throughout the Near East region (according to BODENHEIMER 1944, ZALOGLU 1968, BARAN & ATATUR 1986, and data presented in this article). Horizontal shaded areas: distribution of *Rana »camerani«*, vertical shaded areas: distribution of *Rana macrocnemis*. Bold lines: borders of distribution of *Hyla arborea* (1) and *H. arborea schelkownikowi* (2); interrupted line: conditional northern border of the distribution of *Hyla savignyi*. Scale 1 : 10000.

Die Verbreitung der Braun- und Laubfrösche in Vorderasien (nach BODENHEIMER 1944, ZALOGLU 1968, BARAN & ATATUR 1986 und Daten der vorliegenden Arbeit). Horizontale Schraffur: Verbreitungsgebiet von *Rana »camerani«*; vertikale Schraffur: Verbreitung von *Rana macrocnemis* complex. Durchgezogene Linie: Verbreitungsgrenzen von *Hyla arborea* (1) und *Hyla arborea schelkownikowi* (2); unterbrochene Linie: vorbehaltliche nördliche Verbreitungsgrenze von *Hyla savignyi*. Maßstab 1 : 10000.

(15) Surami, (16) Gori, (17) Kaspı, (18) Mtskheta (east Georgia), (19) Avchala, (20) Tskhneti, (21) Akhaldaba near Tbilisi, (21) Kojori, (22) Lake Lisi, (23) Lake Korki, (24) Lagodekhi (DJANASHVILI 1956), (25) the village Tba (EKVTIMISHVILI 1940), (26) Ajameti, (27) Kintrishi, (28) Kolchida reserve, (29) Pitsunda, (30) Psphu, (31) Ritsa, (32) Gumista, (33) Sataplia, (34) Algeti, (35) Babaneuri, (36) Kazbegi, (37) Liakhvi and (38) Mariamjvari (DAREVSKY, 1987), (39) Charnali river valley, (40) mountain Mtirala (Ajara), (41) upper currents of Rioni, (42) Oni (43) Gujareti valley, (44) Nedzura valley, (44) upstream the river Tedzami, (45) Manglisi, (46) Satovle mountain (47) Digmistkali river (Trialeti mountains), (48) the surroundings of Telavi (49) Kvareli and (50) the village Dzevera between Gori and Tskhinvali (TARKHNISHVILI & THIESMEIER, 1994).

According to GUMILEVSKY (1939), the range of *H. arborea* covers all of the northern Caucasus, the southern foothills of the Great Caucasus, western and central Georgia, Lazistanian and the Ponto mountains in Turkey. The northern border of the distribution coincides with the line running from the lower stretches of the river Don to the mouth of the river Kuma. Eastern Azerbaijan (including the north-western foothills of the Elburs mountains) is populated with treefrogs morphologically intermediate be-

tween *H. a. schelkownikowi* and *H. savignyi* (see below). ALEKPEROV (1978) assumes *H. a. schelkownikowi* to be present in northern, western and south-eastern Azerbaijan.

The Shelkownikow treefrog is distributed throughout landscapes covered with natural forests and agricultural areas (mainly orchards). The Caucasian range of this treefrog is isolated from that of other treefrog subspecies in both northerly and southerly directions. Treefrogs from the Caucasus are generally considered to belong to one and the same subspecies (GUMILEVSKY 1939, TEREPTYEV 1960, BORKIN 1987, GUTIEVA 1989) but a more detailed taxonomic study is required.

In summary, it is concluded that the range of common treefrog covers the northern Caucasus, northern and south-eastern Azerbaijan, northwestern Armenia and all of Georgia except for the extreme south-east. The unforested uplands of Near East limit the range of common treefrog to the south and, similarly, so do the steppes of southern Russia to the north (Fig. 12). In the central part of the Near East region the distribution is limited to south-eastern and central Anatolia (ZALOGLU 1968) (Fig. 13).

Yellow-lemon treefrog — *Hyla savignyi* AUDOUIN, 1827

Hyla savignyi was until recently seen by most authors as a subspecies of the common treefrog. SHELKOWNIKOW (1910) documented its presence in the Transcaucasus and showed that it is distinct from that of other treefrogs. More recently its taxonomic rank has been elevated to the species level (see FROST 1985). *Hyla savignyi* differs from *H. arborea* by its smaller size and different bodily proportions, in its shorter dorsolateral line without the bend in the area of the groin, and a light green dorsal coloration with no spots (GUMILEVSKY 1939, ZALOGLU 1968, TARKHNISHVILI & GOKHELASHVILI unpubl. data). A single well-documented locality for Georgia is (1) south of Tbilisi (ROSTOMBEGOV, 1930, GUMILEVSKY 1939, TARKHNISHVILI unpubl. data). It is known from the (2) valley of the river Alazani (GUTIEVA 1989), but without precise locality indication (Fig. 12). The (3) forests along the river Iori (NIKOLSKY 1913) and (4) the Vashlovani Reserve (DAREVSKY 1987) are also mentioned. The population from Telavi in eastern Georgia shows characters intermediate between *H. savignyi* and *H. arborea* and may be of hybrid origin (TARKHNISHVILI & GOKHELASHVILI unpubl. data). GUMILEVSKY (1939) showed that the Caucasian range of the yellow-lemon treefrog is restricted to most of Armenia, western Azerbaijan (including Nakhichevan but not the Elburs mountains) and south-eastern Georgia up to Tbilisi in the northwest. According to BANNIKOV et al. (1977) *H. savignyi* is distributed over the southern Transcaucasus.

Just to rely on the dorsolateral line to distinguish between *H. arborea* and *H. savignyi* may lead to erroneous interpretations such as by EKVIMISHVILI (1948) and TUNIYEV (1985). Even in some *H. arborea* populations from the Caucasus some specimens possess dorsolateral lines without the bend in the groin (GUMILEVSKY 1939, Tarkhnishvili unpubl. data). The eastern Azerbaijan is populated with treefrogs intermediate between *H. a. schelkownikowi* and *H. savignyi* (GUMILEVSKY 1939). In the Talish mountains of Azerbaijan the species are reported to occur in sympatry with no obvious indications of hybridization (ALEKPEROV 1978). The conclusion is warranted that the range of yellow-lemon treefrog in Transcaucasus is limited from the north and northwest by semi-arid unforested landscapes whereas in the belt of natural forest it is displaced by the common treefrog.

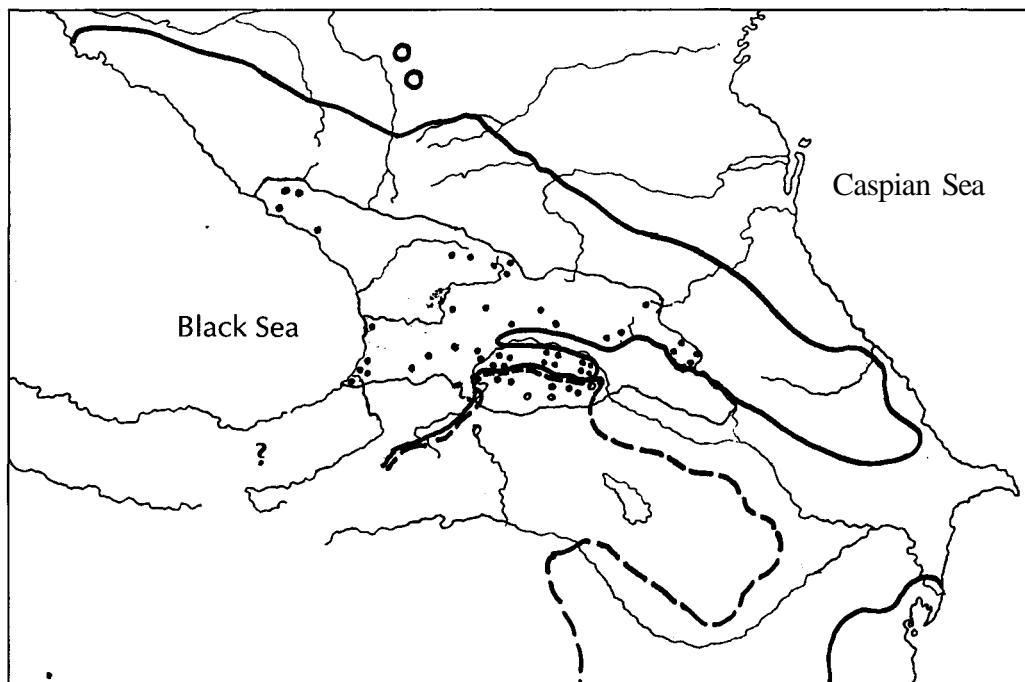


Fig. 14: Distribution of the *Rana macrocnemis* group. *Rana macrocnemis*: solid points and solid line; *Rana »camerani«*: open circles and dotted line. Further explanations see fig. 4.

Verbreitung der *Rana macrocnemis*-Gruppe. *Rana macrocnemis*: Punkte und durchgehende Linie; *Rana »camerani«*: Kreise und unterbrochene Linie. Weitere Erläuterungen siehe Fig. 4.

Brown frogs — *Rana macrocnemis* BOULENGER, 1885 and *Rana »camerani«* BOULENGER, 1886

Since the taxonomic status of the brown frog *Rana »camerani«* is unclear it is treated here alongside with its congener *R. macrocnemis*. Forty two Georgian locations are known of typical *R. macrocnemis*, and 11 of typical *R. »camerani«* (Fig. 14). Specimens with intermediate characters are reported from 13 localities. Records of *R. macrocnemis* are: (1) Sukhumi, (2) Gagra, (3) Batumi, (4) Tkibuli, (5) Ajameti, (6) Lomis Mt. in the Borjomi district, (7) Turtle Lake near Tbilisi, (8) Kazbegi, (9) Lagodekhi, (10) Eniseli, (11) Lake Saikhvie (NIKOLSKY 1913), (12) Jagoras-Veli (Bakuriani), (13) Didi Mitarbi, (14) village Tba, (15) the valley of Baniskhevi (EKVTIMISHVILI 1940), (16) Chazhashi, (17) Zeshkho, (18) Khoruldashi (Svaneti) (MUSKHELISHVILI 1959), (19), (20) two localities in upstream of the river Bzipi (TUNIYEV 1985), (21) northern foothills of the Lazistan mountains, (22) near Kobuleti, (23), (24) eastern Ajara, (25) near Pitsunda, (26) upper currents of Rioni, (27), (28) the Surami mountains, (29) near Tskhinvali and (30) upper currents of Alazani (from BANNIKOV et al. 1977, without identification of the prime source). *Rana macrocnemis* has further been found in (31) the valley of the river Nedzura, (32) Ertatsminda in the Trialeti mountains, (33) Akhaldaba Lake, (34) Betania, (35) Tsodoreti, (36) Satovle mountains (37) mountain Mtirala near Batumi, (38) Mamisoni mountain pass, (39) surroundings of Kvareli, (40) near Omalo, (41) vicinity

of Telavi, (42) Datvisjvari mountain pass (TARKHNISHVILI & THIESMEIER 1994, TARKHNISHVILI unpubl. data).

Outside Georgia, the typical form of the *R. macrocnemis* is known from 67 localities in the northern Caucasus, from 19 localities in northern Azerbaijan and from eight localities in the foothills of the Elburs mountains (NIKOLSKY 1913, EISELT & SCHMIDTLER 1971, BANNIKOV et al. 1977, BORKIN 1977, ALEKPEROV 1978, TERTISHNIKOV et al. 1979, VISOTIN & TERTISHNIKOV 1988) Its distribution appears to be uninterrupted throughout the forest belts of the Great Caucasus, the Meskheta, Trialeti and Elburs mountains, probably including the Colchida valley. Outside the Caucasus, it is found in the western part of Anatolia (BARAN & ATATUR, 1986), but does not reach into the Balkan Peninsula. The range of *R. macrocnemis* appears to be disjunct over the mountain plateaus of Caucasus Minor and Anatolia. *Rana »camerani«* appears to be less widespread: (1) Turtle lake, (2) Lake Tabatskuri, (3) the river Ktsia, (4) Lake Khanchali, (5) Lake Paravani (NIKOLSKY 1913), (6) Lake Sagamo (ISHCHENKO 1978), (7) Lake Bareti, (8) Imera, (9) Lake Tba in the Tsalka district, (10) Tskhratskaro pass, (11) Gogoti in the Trialeti mountains (TARKHNISHVILI unpubl. data). Outside Georgia *R. »camerani«* is reported from Armenia and south-western Azerbaijan. It appears that *R. »camerani«* has a more or less continuous distribution throughout the mountain plateaus of the Caucasus Minor, the Near East and Anatolia. Brown frogs in central Anatolia belong to *R.»camerani«* (BARAN & ATATUR 1986). Typical *Rana macrocnemis* is distributed all along the Great Caucasus, in the Colchis, and along the Elburs mountain ridge into north-eastern Azerbaijan. *Rana »camerani«* inhabits the mountain plateaus of the Middle East, including East Anatolia and the Caucasus Minor. Where the two forms, *camerani* and *macrocnemis*, meet specimens with intermediate characters are found, such as at the northern slopes of the Trialeti mountains.

Lake frog — *Rana ridibunda* PALLAS, 1771

Rana ridibunda is found all over Georgia, with probably a wider distribution than any of the other amphibian species. There are 62 documented localities of the lake frog in Georgia (NIKOLSKY 1913, DJANASHVILI 1956, 1956, BANNIKOV et al. 1977, TARKHNISHVILI unpubl. data) (Fig. 15). As in fact the lake frog is found almost everywhere and exhaustive enumeration of known localities is not attempted (NIKOLSKY 1913, ALEKPEROV 1978, GUMILEVSKY 1939, BANNIKOV et al. 1977, VISOTIN & TERTISHNIKOV 1988). Subfossils of *R. ridibunda* are known from Kudaro, East Georgia (CHKHIKVADZE 1984).

The lake frog is found in a wide variety of landscapes, from deserts to humid subtropical forests. It is found in agricultural landscapes and urban agglomerations where it can be abundant. Lake frogs can be found in canals, streams and ponds but in treeless uplands of the Caucasus Minor they are restricted to relatively large pools and lakes. In altitude its range is from sea level to over 2 500 m. At high altitude the population density of the species declines and in the subalpine and alpine belts of the Great Caucasus the species is rare. A morphologically distinct form of the lake frog with short hindlimbs and a high frequency of striped phenotypes in the populations is known from the arid areas of south-eastern Transcaucasus. Such morphs, by some

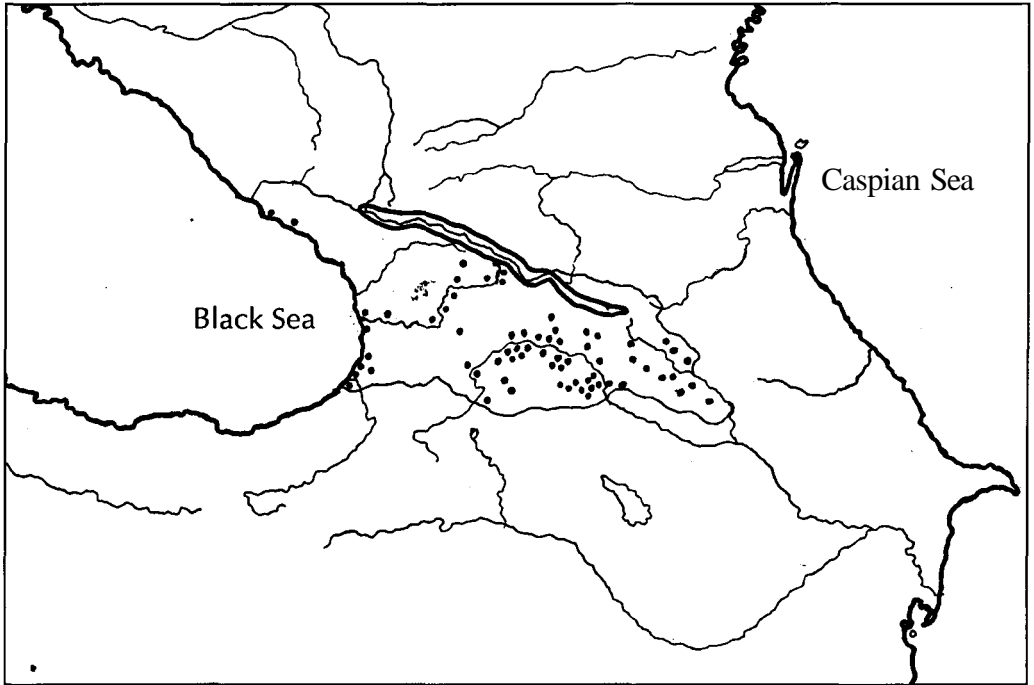


Fig. 15: Distribution of *Rana ridibunda*. Further explanations see fig. 4.
 Verbreitung von *Rana ridibunda*. Weitere Erläuterungen siehe Fig. 4.

(e. g. BANNIKOV et al. 1977) considered to represent a different subspecies *R. r. saharica*, can found near Tbilisi in the north-western edge of the subspecific range (e. g. EKVTIMISHVILI 1948).

5 Contemporary biogeography

The most explicit theories with regard to the zoogeography of amphibians of the Caucasus are those expressed by BORKIN (1987) and TUNIYEV (1987, 1990, 1995). Following BORKIN most species were formed by the end of the Pliocene and reached the Caucasus through the Balcans and Asia Minor. Boreal species with wide distributions reached the Caucasus at later times from the north, when the Peninsula joined with the plains of eastern Europe. In three cases clear similarities are observed between endemic Caucasian and European species. *Pelodytes caucasicus*, *M. caucasica* and *P. syriacus* are found in the Caucasus and have taxonomic counterparts *P. punctatus*, *Chioglossa lusitanica* and *P. cultripes* in south-western Europe. Moreover, in Mid-Sarmatian sediments of the northwestern Caucasus vertebrae of *Triturus* aff. *marmoratus* were found (ESTES & DAREVSKY 1977) whereas *T. marmoratus* in its present day distribution is restricted to France and the Iberian Peninsula. BORKIN concludes that Asia Minor served as a »bridge« allowing faunistic exchange between the Caucasus and Europe. Care should be taken with such an interpretation because, as BORKIN reminds us, some narrow-ranged species may have been more widely distributed in the past.

For example, *T. marmoratus* and *M. aff. caucasica* were once distributed in central Europe (SANCHIZ & MLYNARSKI 1979, HODROVA, 1985). The unification of these Caucasian species in one faunistic group on the basis of them possessing related forms in western Europe may be artificial, because it does not pay attention to the distribution of species throughout the Caucasus. For example, the distribution of *P. syriacus* in the Caucasus does not even overlap with that of *M. caucasica* and *P. causicus* whereas it strongly coincides with the range of *H. savignyi*.

TUNIYEV (1987, 1990, 1995) distinguishes four groups of western Caucasian amphibian species as »Colchic«, »European«, »Caucasian« and »Eastern-Mediterranean«. The Colchic group is of autochthonous origin and includes *M. caucasica*, *T. vittatus ophryticus*, *T. vulgaris lantzi*, *P. causicus* and *B. verrucosissimus*. The Caucasian group (*H. arboreaschelkownikowi*, *R. macrocnemis*) also may be of autochthonous origin. The Mediterranean group includes *T. karelinii*, which may have moved into the Caucasus from the Crimea. The European group includes the widely distributed species *B. viridis* and *R. ridibunda* (TUNIYEV 1990). The fact that faunistic and floristic complexes of the Colchic refugia are analysed simultaneously provides additional power to TUNIYEV'S analysis. However, some deficiencies in the scenario are also apparent. For instance, the range of *T. vittatus* covers not only the Colchis but almost all of north and west Anatolia, and the same is true for *R. macrocnemis*. To be convincing, the hypothesis of an autochthonous origin for these two forms would need additional support. Moreover, it cannot be excluded that ancestors of some forms have reached the Caucasus from more than one direction. This problem can only be analysed through the study of intraspecific variability of amphibians.

6 Biogeographical analysis

Considering the zoogeography of the Caucasus it is important to keep the following methodological aspects in mind: i) the Caucasus is a large and geographically complex region, and for any firm conclusions to be reached the distribution of the species have to be studied throughout the region; ii) species colonizing the region by similar routes does not necessarily imply that they did so at the same time; iii) species may have colonized the Caucasus in more than one way. If genetically different groups merged it may be possible to reconstruct parts of their geographical histories through the analysis of geographic variation. Alternatively, stable hybrid zones may have formed. This shows that the study of intraspecific variation is important for the development of biogeographic hypotheses. Finally it must be noted that available palaeontological data do not point to marked differences in the past and present distribution of the Caucasian amphibians (CHKHIKVADZE 1984) and the information, by consequence, does not bear to the discussion.

Historical events in the formation of the amphibian fauna of the Caucasus region are reflected in their contemporary distribution. On the other hand the distribution of species also depends on their ecological requirements not necessarily reflecting historical traits. It is not easy to separate ecological from historical causes. Some progress can be made by the simultaneous analysis of the species' ecological preferences, their

Tab. 1: Scheme of the zoogeographical classification of the Caucasus amphibians.
 Schema der zoogeographischen Klassifizierung der Amphibien des Kaukasus.

Super-group	Group	Supposed time of penetration	Supposed way of penetration	Preferential landscapes	Species/Subspecies
Near East	(1) East-Transcaucasia	?	South, South-East	Treeless lowlands, foothills	<i>P. syriacus</i> , <i>H. savignyi</i> , <i>R. ridibunda saharica</i> , <i>B. viridis</i>
	(2) Caucasus Minor	?	South	Treeless uplands	<i>R. »camerani«</i> , <i>B. viridis</i> , <i>R. ridibunda</i>
Caucasian	(3) Caucasus-Anatolian	Pliocene	South-west	Forests	<i>H. arborea schelkownikowi</i> , <i>R. macrocnemis</i> , <i>T. vittatus ophryticus</i>
	(4) Euro-Caucasian	Miocene	South-west or North-west	Forests	<i>T. vulgaris lantzi</i> , <i>T. karelinii</i> , <i>B. verrucosissimus</i>
	(5) European	Permanent	South-west and North	Euritopic	<i>B. viridis</i> , <i>R. ridibunda</i>
	(6) Pyrenean-Caucasian	?	South-west	Mountain Forests	<i>M. caucasica</i> , <i>P. caucasicus</i>

range across the Caucasus and their general distribution. The 13 species to be dealt with fall into five separate groups (Tab. 1).

Group 1: Amphibians of the plains and the foothills of the eastern Transcaucasus. Two species belonging to this group are *P. syriacus* and *H. savignyi*. They are distributed along the valleys of the rivers Arax and Kura, reaching Tbilisi in the north-westernmost part of their distributions. They are both found along the western coast of Caspian Sea, albeit sporadically. Outside the Caucasus they are distributed throughout the Near East, reaching Israel in the south and southern Anatolia at the west (BODENHEIMER 1944, ZALOGU 1968). *Rana ridibunda* from the southern and south-eastern regions of the Transcaucasus with its short hind limb length resemble the subspecies *R. ridibunda saharica* (ALEKPEROV 1978). Relative hind limb length increases to the north-west in clinally fashion. Short-legged *R. ridibunda* are also found in eastern Georgia (EKVTIMISHVILI 1948). The remarkable coincidence of the ranges of the three amphibians forms in this group, together with their similar ecological requirements suggests a common route of dispersal into the Caucasus region — probably through the river Arax valley historically connected with the basin of Mediterranean sea and Parthian Gulf (CKHIKVADZE & BAKRADZE 1991). In the Caucasus, they met a number of other amphibian forms. The north-western border of the range of *P. syriacus* is a sharp border whereas *H. savignyi* forms a zone of hybridization with *H. arborea schelkownikowi* in the east of Georgia (TARKHISHVILI unpubl. data). The latter species arrived from the opposite direction. Finally, the »short-legged« variety of *R. ridibunda* mixed with ordinary, long-legged lake frogs which arrived into the Caucasus region from the north and west, but remained shortlegged in the southernmost part of the Caucasus.

Group 2: Forms of Caucasus Minor Mountain highlands in the Sevan district. The typical representative of this group is *R. »camerani«* together with the nominative form of *R. ridibunda* and *B. viridis*. *R. »camerani«* and *B. viridis* may have colonized the region following similar routes, taking into consideration morphological peculiarities of green toads from this district. *R. »camerani«* formed a wide hybrid zone with the closely related species *R. macrocnemis*, whereas populations of the green toad fully merged with the groups arriving in the Caucasus by different routes, which is reflected in the current variability of the species.

Group 3: Two species with comparable distributions (*Hyla arborea schelkownikowi* and *Rana macrocnemis*) belong to this group. Their range covers the northern foothills of the Great Caucasus, the western Transcaucasus and the forested areas of the eastern Transcaucasus, including the Elburs foothills. In the foothills and plateaus of Caucasus Minor and in the uplands of Asia Minor that are devoid of forestation, they are displaced by the closely related *R. »camerani«* and *H. savignyi*, respectively, to re-appear in western Anatolia (Fig. 13). *Rana macrocnemis* is absent in the Balkans whereas *H. arborea* is distributed throughout the most of Europe. Whether the Anatolian treefrog belongs to the same subspecies as those of the Caucasus remains to be investigated (see BODENHEIMER 1944, TERNIYEV 1960, ZALOGU 1968, VISOTIN & TERTISHNIKOV 1988, BORKIN 1987).

Triturus v. ophryticus which is absent in the eastern Transcaucasus but present in western Anatolia may also belong to this group. On the other hand it can be seen as belonging to the Colchic species group (TUNIYEV 1987, 1990). The question may be raised why *T. v. ophryticus* is absent from the south-east of Azerbaijan, despite the fact that the ecological conditions in this region appear to be appropriate for the species. In the Miocene, the forest landscapes of Elburs mountains and Colchis were joined by the »Karabagh Bridge« (TUNIYEV 1990). It may be that the banded newt reached the Caucasus later, in the Pliocene, from the south-west, when the »Karabagh Bridge« had disappeared already. *Rana macrocnemis* and *Hyla arborea* could have colonized the Elburs before as well as after the disappearance of the »Karabagh Bridge«, at the expense of their, in comparison with *T. v. ophryticus*, wider ecological tolerance. The species group under consideration is called »Anatolian-Caucasian«, although TUNIYEV (1987) called it »Caucasian«.

Group 4: A group of species, termed here »Euro-Caucasian«, with a range including the Caucasus have in common that their ranges in the Caucasus are isolated to the north and to the south and disjunct in a Caucasian and Elbursian part. Taxa included in this group are *T. vulgaris lantzi*, *T. karelinii* and *B. verrucosissimus*. The separation may result from their residence in the Caucasus during the Miocene, or at any rate for longer than the species of the previous group. The ranges of these species in the western part of the Caucasus do not fully coincide, due to their different ecological requirements. *B. verrucosissimus* is the most humidophilous species among them, whereas *T. karelinii*, is a rather xerophilous form. TUNIYEV (1987) includes this species in the East-Mediterranean group, which may have colonized the Caucasus through the Crimea, whereas the other two species are assumed to be representatives of the Colchic fauna. It should be noted that all taxa of group 4 form part of bigger species groups or superspecies (represented by *Bufo bufo*, *T. vulgaris* and *Triturus cristatus*)

with wide distributions in Europe. The shared characters of the species in group 4, including their interrupted range and the isolation in the Caucasus points to a shared history. *Triturus karelinii* differs from the other two representatives of group 4 on the basis of its presence in Anatolia and south-eastern Europe (ARNIZEN 1995).

Group 5: Two species widely distributed in Eurasia, *B. viridis* and *R. ridibunda*, colonized the Caucasus from the north, the south-west and the south. Most of the Caucasus is inhabited by the nominative forms of these species, pointing to a continuous exchange between the Caucasian, Anatolian and European populations of green toad and lake frog. Probably it would be a mistake to unify all populations of these species in the separate zoogeographic group. Part of populations can be incorporated with different groups described earlier.

Group 6: Two species unique to the Caucasian fauna but with Pyrenean affinities, *Mertensiella caucasica* and *Pelodytes causicus*, are placed in group 5. This group is termed the »Pyrenean-Caucasian« group. Although the present day distributions of *M. caucasica* and *P. causicus* only overlaps in south-western Georgia, the following facts point to a shared history: i) the range of both species is restricted to the West Transcaucasus (although the range of *P. causicus* reaches into the northern slopes of the Great Caucasus and the eastern Georgia); ii) ecologically the species are associated to forested mountain streams, and, iii) the species represent regressive taxa with sister-species *Chioglossa lusitanica* and *Pelodytes punctatus*, inhabiting south-western Europe. As evidenced by fossil data, *M. caucasica* was widely distributed in Europe during the Pliocene (SANCHIZ & MLYNARSKI 1979). After the last glaciation (13 000 YBP, DJANELIDZE 1970) it did not restore its former range.

Group 1 and 2 may be joined in the higher-order unit of species of the Near East on the basis of: i) their overall distribution pattern, and ii) the general similarity of the eastern and southern Transcaucasian fauna (GAJIEV 1986). They are limited in their distribution to the Near East region (in the wide sense). The distribution of brown frogs and treefrogs in Anatolia deserves special attention. In western Anatolia, *R. »camerani«* and *H. savignyi* are displaced by the closely related *R. macrocnemis* and *H. arborea* (ZALOGU 1968, BARAN & ATATÜR 1986).

Accordingly, the following taxa compose the »Middle East« group: *P. syriacus*, *H. savignyi*, *R. »camerani«*, *R. r. saharica*, perhaps *B. viridis strauchi* and *B. v. pewzowi*. It is likely that these forms colonized the Caucasus from the south along the mountain plateaus of the Near East, through valleys such as those of the river Arax. The Arax therefore may be included in the basin of the Parthian Gulf (CKHIKVADZE & BAKRADZE 1991). Groups 3, 4 and 6 may be taken together as a »Caucasian« unit on the basis of parallel present-day distributions, although the constituent groups have different histories. Attention is to be paid to the following aspects of their distribution: i) the isolation of the Caucasian part of the range; ii) the presence in the north-western foothills of the Elburs ridge in south-eastern Azerbaijan (i. e. isolated from the Great Caucasus by extensive steppe areas); and iii) the range of the species and its close relatives outside the Caucasus.

The biogeographic classification given here does not pretend to be the final word in the analysis of the amphibian fauna of the Caucasus. However, previous studies did not pay attention to the character of distribution of Caucasian species throughout Near

East region and Anatolia nor to their intraspecific variability, which highlights the differences between the present and previous biogeographic classifications.

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