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A Comparative Study on the Morphological Characters of Adult Specimens of the Grass Frog *Rana temporaria temporaria* LINNAEUS, 1758 and Moor Frog *Rana arvalis arvalis* NILSSON, 1842

[Pp. 217—282, with 5 text-figs.]

Badania porównawcze nad cechami morfologicznymi dorosłych osobników żaby trawnej (*Rana temporaria temporaria* LINNAEUS, 1758) i żaby moczarowej (*Rana arvalis arvalis* NILSSON, 1842)

Сравнительные исследования морфологических признаков взрослых особей лягушки травяной (*Rana temporaria temporaria* LINNAEUS, 1758) и лягушки остромордой (*Rana arvalis arvalis* NILSSON, 1842)

Abstract: Twenty-nine morphological and morphometrical characters, generally given in keys and descriptions and used to distinguish the grass frog from the moor frog, were studied. The author showed that only four of these characters are suitable for the correct determination of adult grass and moor frogs. These characters are the length ratio of the inner metatarsal tubercle to toe I, the development of the inner metatarsal tubercle, the shape of the snout, and the development of the longitudinal dorso-lateral folds. The use of these four characters alone visibly reduces the number of specimens considered to be hard to identify and treated by some authors as hybrids. The author denies the existence of such natural hybrids.

CONTENTS

A. Theoretical Part

Two species of brown frogs occur in Poland: *Rana temporaria* LINNAEUS (common or grass frog) and *Rana arvalis* NILSSON (moor frog). The presence of a third species, namely, the jumping or agile frog (*Rana dalmatina* BONAPARTE, 1839) is questionable, for lately it has not been found within the present frontiers of Poland, whereas the earlier data are either unreliable or unconfirmed. Having stated the rare occurrence of this species, UDZIELA (1910) records it from the region of Babia Góra Mt., the Pieniny Mts., and makes a general remark about its occurrence in the territory of the former Kingdom of Poland and the Prussian sector of partitioned Poland, more or less as far south as 51° N latitude. TENENBAUM (1913) writes about finding single specimens of the agile frog in many places of the Zamość District. GRIMME (1916) reports a find of one specimen at Antoniówka in the upper course of the River Wieprz. PAX (1917) is of the opinion that it is just the southern part of the Lublin Province that this frog occurs in. FEJÉRVÁRY (1923) gives 3 localities of the agile frog: 1) between Działoszyce and Miechów (1917), 2) at Dęblin (1918) and 3) at Olkusz (1918). With respect to these 3 specimens (each locality is represented by only one specimen) the author writes that they were typical in so far as their morphology and coloration were concerned.

Unfortunately, in the period between the two World Wars there was no confirmation of these records except for information provided by FUDAKOWSKI (1933) about a very rare occurrence of this species at Uher near Chełm Lubelski.

BERGER and MICHAŁOWSKI (1963), however, believe that the occurrence of the agile frog in the south-eastern part of this country is very probable, since, according to TARASHCHUK (1959), it has been found in the Western Ukraine. This last author writes that its distribution in the Western Ukraine is limited to several localities and even these are poorly known. The occurrence of the agile frog in this area, adjacent to the East Carpathians and, besides, traversed by the eastern boundary of the distribution of this species (approximately as far as the Dnieper), was also reported by UDZIELA (1910), TERENTEV and CHERNOV (1949), TERENTEV (1950), KHOZATSKII (1950), POLUSHINA and TATARINOV (1952), ANDREYEV (1953), KOLYUSHEV (1956, 1959), DIDUSENKO (1959), and recently by Polushina and KUSHNIRUK (1963). However, according to POLUSHINA and KUSHNIRUK (1963), some reports, e. g., that by TARASHCHUK (1959) on the occurrence of this frog in the Lvov and Stanislav Provinces, need confirmation.

This species is also encountered in other territories borderring upon Poland, i. e., in Czechoslovakia and the G. D. R.

The presence of the agile frog in Czechoslovakia has been reported, among other authors, by WOLTERSTORFF (1890), SCHREIBER (1912), RUST (1941), ŠTĚPÁNEK (1949), STERNFELD (1952), DOBRORUKA, and DANIEL (1953), and LAC (1959, 1963). LÁC mentions as many as 119 localities in Slovakia, where this

frog appears to be particularly common. It is absent only from the northern part of this country, including the central part of the Carpathians, the High and Low Tatra Mts., Oravia, and the river-basins of the upper Hron, Hnik, Hornad, and Torysa, but, as LÁC writes in another paper (1959), it may well be that single specimens occur in the Tatra region, in the proximity of thermal springs. On the other hand, these frogs are met with in large numbers in southern Slovakia, where they often predominate over the grass frog. They are also fairly numerous in Moravia (ŠTĚPÁNEK, 1949; LÁC, 1959) but rather rare in other parts of Czechoslovakia (ŠTĚPÁNEK, 1949).

Not very detailed data obtained so far in Germany show that the distribution of the agile frog is only insular. It is chiefly known from the south-western part of the country (Rhineland, Baden, Bavaria — especially its southern part — Württemberg and Hesse), but also from the Thüringer Wald, south-eastern Harz, Lower Saxony, Hamburg region, Mecklenburg, Rügen Island, and the region of Dresden (Saxony) (SCHREIBER, 1912; FROMMHOLD, 1953/54; 1959a, b, 1965; KLINGELHÖFFER, 1955; FREYTAG, 1961, FRITZSCHKE and OBST (1961). In addition, many authors (SCHREIBER, 1912; WERNER, 1922; KLINGELHÖFFER, 1931; „Raniden", 1941; WERNER and HERTER, 1944, HERTER, 1955) report the occasional occurrence of the agile frog in Silesia, and, therefore, in the area which now belongs to Poland. However, PAX (1921, 1925) decidedly rejects the possibility of its occurrence in both Upper and Lower Silesia. At any rate, the earlier data on the meeting of specimens of this species in the forefield of the Sudetes (Sobótka, former Zobten) and in the Izerskie Mts. have not been confirmed. As to SCHREIBER'S data, they refer only to the part of Silesia that then belonged to the Austro-Hungarian Monarchy.

The possibility of occurrence of the agile frog in the Polish areas neighbouring upon Byelorussia, Lithuania and the Kaliningrad Province is unambiguously negative. The recent studies carried out by SAPOZHENKOV (1916) have not supported the report of FEDOROWICZ (1930) about its presence in Byelorussia. On the other hand, KROLL'S statements about his observing large numbers of specimens of this species in the region of Pinsk have met with essential reservations appended to this very report by WOLTERSTORFF. The lack of this frog in the Białowieża Forest has already been reported by KOŻMIŃSKI (1928). Discussing the distribution of this species in the U. S. S. R., neither TERENTEV and CHERNOV (1949) nor TARASHCHUK (1959) makes mention of Byelorussia.

So far there is no mention about its occurrence in Lithuania except for an unconfirmed reference made by BAYGER (1937).

Neither are there any data concerning the presence of the agile frog in the area of former the East Prussia. PAGAST (1939, 1941) does not mention this species, nor do WERNER and HERTER (1944). I did not meet with the agile frog during my herpetological excursions in the Olsztyn, Gdańsk and Bydgoszcz Provinces, and for this reason I shall not deal with it in this paper.

Both the grass frog and the moor frog are represented in this country only by their nominal forms.

FEJÉRVÁRY (1923) and DELY (1953, 1964a) write also about the occurrence of the subspecies *Rana arvalis wolterstorffi* FEJÉRVÁRY, 1919 in Poland, which form is relatively larger and more slender and, above all, its hind limbs are longer.

The problem is significant inasmuch as KAURI (1959) and STUGREN (1966) have recently questioned the distinction of this subspecies within *Rana arvalis*. KAURI did that on the basis of the theory put forward by him that the changes in body size and hind limb (shank) length are exclusively clinal modifications without any taxonomic value and that being chiefly functions of temperature they may at the most characterize southern populations only. STUGREN finds a support of the opinion that the species *R. arvalis* is uniform in the presence of isolated „colonies" of *R. arvalis wolterstorffi* in the territory of Poland (Zawada, Bratków) inhabited by *R. arvalis arvalis*, and a similarly isolated „group" of *R. arvalis arvalis* in Romania (Reci) populated by *R. arvalis wolterstorffi*, for he excludes the possibility of the passage of these isolated „race groups" over the Carpathians (altitudes!) or their taking a roundabout way across the Czechoslovakian lowlands, and, consequently, the possibility of the presence of two centres of formation of the race.

KAURI'S (1959) opinion has been criticized by FUHN (1962). Unfortunately, the fundamental defect of FUHN'S work is the small number of specimens used by him for measurements and calculations, which, what is more, are followed by a statistical analysis. In the case of *R. arvalis arvalis* FUHN had at his disposal 39 males, 8 females and 7 juveniles, whereas the subspecies *R. arvalis wolterstorffi* was represented by 16 males and 12 females. The geographical criterion shows the expediency of the distinction of this subspecies more convincingly, since, according to FUHN, in Transylvania both these subspecies occur at the same geographical latitude, living under similar ecological conditions, and they are separated from each other by a meridionally extending ridge of mountains. STUGREN, however, writes that the ecological conditions are not uniform in this region. In his final estimation of the morphological characters examined in *R. arvalis arvalis*, *R. arvalis wolterstorffi* and *R. dalmatina*, DELY (1953, 1964a) arrives at the conclusion that *R. arvalis wolterstorffi* has an intermediate position between *R. arvalis arvalis* and *R. dalmatina* and even that it has more characters in common with this last species.

Tables I and II summarize the most significant biometrical and taxonomic differences between the subspecies under study. In addition to the quantitative differences between the two races juxtaposed in Table II, some authors take into consideration also the biological differences, e. g., FEJÉRVÁRY (1919) writes that at rest the specimens of *R. arvalis arvalis* have their „heels" moved away from each other and their knees are far from the elbows, whereas those of *R. arvalis wolterstorffi* have their „heels" overlapping each other or nearly overlapping and their knees touch the elbows. They also differ in their manner of leaping: *R. arvalis arvalis* performs numerous short leaps, whereas *R. arvalis wolterstorffi* leaps remarkably farther and higher, in which it resembles the

agile frog (FEJÉRVÁRY, 1913; CALINESCU, 1931; SOCHUREK, 1953; FROMMHOLD, 1959a).

The subspecies *R. arvalis wolterstorffi* is specific to southeastern Europe: north-eastern Yugoslavia (Croatia and Slovenia), eastern Austria (Burgenland, Carinthia, north-eastern Styria and Lower Austria), Hungary (where they are distributed chiefly north of Budapest), Romania (central and north-western Transylvanian Upland) and southern Slovakia. Thus, *R. arvalis wolterstorffi* occupies the southern part of the range of this species and *R. arvalis arvalis* its northern part, including central and northern Europe, up to the Polar Circle in the north and to Siberia in the east, where the boundary of the distribution has not been defined exactly.

The nominal race, therefore, occurs in the European part of the U. S. S. R. except for the Caucasus, in Poland, Germany, Denmark, Sweden, Finland, Belgium, Holland, Luxemburg, north-eastern France, Switzerland, Czechoslovakia and partly in Romania (eastern Transylvania and northern Moldavia). Opinions differ as to the occurrence of this subspecies in Hungary and Austria. Both races live in Czechoslovakia and Romania, perhaps also in Hungary and Austria.

In Poland, as has already been mentioned, the occurrence of *R. arvalis wolterstorffi* is assumed after FEJÉRVÁRY (1923) and DELY (1953). FEJÉRVÁRY worked out and identified the specimens collected by A. PONGRACZ: a) adults from Zawada near Zamość and Bratków near Tomaszów (one specimen from either of these localities), b) 8 larvae from Łysa Góra near Kielce and 4 larvae from Suchedniów; however, he was not quite certain if the larvae belonged to the subspecies under discussion. Dely osteologically confirmed the identifications performed by FEJÉRVÁRY. BAYGER (1937) did not record this subspecies from Poland, and BERGER and MICHAŁOWSKI (1963) regarded its occurrence in south-eastern Poland only as possible. Neither do TERENTEV and CHERNOV (1949) take it into account in connection with the European territory of the U. S. S. R., nor does TARASHCHUK (1959) mention it from the Ukraine and SAPOZHENKOV (1961) from Byelorussia. DELY (1964a), however, informs that *R. arvalis wolterstorffi* lives in Transcarpathia and LÁC (1956) has reported its occurrence in southern Slovakia (Zahorska Lowland, the north-western part of the Danube Lowland). Earlier, its presence was signalled by FEJÉRVÁRY-LANGH (1953, after LÁC, 1956) from the environs of Bratislava and, in addition, SOCHUREK (1953) numbered the specimens of the moor frog from the Danube-Morava area in this race. LÁC writes about his interesting discovery of specimens with characters intermediate between the characters of the *wolterstorffi* race and those of the nominal race, or such as only little differ from this last race and eventually occasional ones which are identical with it, north-east of Košice in eastern Slovakia. An analogous situation has also been reported from Romania (VANCEA, 1959; STUGREN and POPOVICI, 1960; STUGREN and KOHL, 1961; FUHN, 1962), from Bukovina (Chernovtsy region, U. S. S. R.) and Hungary. These facts induced LÁC to infer that all the specimens living

in the parts of Slovakia situated farther to the north must belong to the nominal race. So far it is impossible to define the exact boundary between the areas inhabited by these two subspecies in Slovakia on the basis of LÁC's studies.

On the other hand, an analysis of some systematic characters of the specimens of *R. arvalis arvalis* from Poland (Poznań region), Slovakia (eastern part of this country and one of the islands in the Danube, Žitno-Ostrovský) and Romania carried out by LÁC (1963) showed that the Polish specimens differ markedly from those obtained from the above-mentioned Danubian island, especially in the length ratio of body (L.) to shank (T.) and that of shank (T.) to inner metatarsal tubercle (C. int.), and only slightly from the specimens from eastern Slovakia. The Polish specimens should, therefore, be regarded, according to this author, as typical members of the nominal subspecies, whereas the East Slovakian populations unquestionably hold an intermediate position or, in sporadic cases, they already belong to the typical form. The Romanian specimens differ in nothing from those from Žitny-Ostrov.

The occurrence of this subspecies in the regions of Poland explored by PONGRACZ has not as yet been confirmed.

However, basing himself on the results of a comparative analysis of the outer morphology and biometric variation of moor frogs from various parts of Europe, obtained from his own studies and from those carried out by FUHN (1956, 1962), GISLEN and KAURI (1959) and STUGREN and POPOVICI (1960), DELY (1964a) has unexpectedly postulated the occurrence of *R. arvalis wolterstorffi* also in the eastern part of Central Europe, and thus, above all, in Poland and north-eastern Germany [1].

The above-mentioned specimens collected by PONGRACZ and two other ones from Międzyrzecze (Zielona Góra Province) from the collection of the Berlin Museum prompted this author to include Poland in the range of the race *wolterstorffi*, whereas his identification of one specimen from Friedersdorf (east of Berlin) as *R. arvalis wolterstorffi* became a basis for his supposition that this subspecies may inhabit the south-eastern region of Germany. In DELY's opinion, there are undoubtedly transitional forms in the borderland between the ranges of the two subspecies of the moor frog (*R. arvalis arvalis* — western, northern and eastern Europe — and *R. arvalis wolterstorffi* — south-eastern and eastern parts of Central Europe). Among such transitional forms he reckons, in addition to other specimens, the juvenile specimen from Eutin (north of Lübeck) and those from Denmark (Jutland) and southern Sweden (Smaland).

The two species of brown frogs inhabiting Poland are very much alike in respect of morphology. Sometimes it is even difficult to distinguish them decisively, which is particularly true of juvenile specimens. This is due to the fact

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[1] In order to distinguish the two subspecies of the moor frog DELY used 5 biometrical characters: L., F., T., D_4 p (L. p.) or the length of the 4th toe = foot length, and C. int. He also took into consideration the results of the two variants of the „heel" test.

that a large number of characters which we use to distinguish these species from each other develop, especially in the grass frog, with time. This concerns both meristic and quantitative characters.

Generally speaking, young grass frogs have often the ventral side of the body light and spotless or only slightly maculated; similarly, their back is not usually strongly maculated and the dorso-lateral folds are marked much more distinctly, which characters are attributed to the moor frog. In its youth the grass frog has also often its snout more pointed, like that in the moor frog. On the other hand, as already mentioned above, young moor frogs often resemble the grass frog in the form of the inner metatarsal tubercle and also in the length ratio of the first toe to the inner metatarsal tubercle $\left(\frac{D_1 p}{C.\ int.}\right)$.

Neither is the distinction of adult frogs of these two species always quite certain. FROMMHOLD (1953/54), for instance, writes that most doubt may be raised when only one of the generally accepted characters essential to the discrimination of our brown frogs is used for identification. Further he arrives at the obvious conclusion that in identification it is indispensable to apply many characters, even such as are considered to be very subtle and, consequently, hard to distinguish.

Another cause of this situation is, as emphasized by BERGER (1957), the fact that the authors of keys to Central European frogs do not share each other's opinions on the value of particular specific characters used for determination. Some of these characters are, in addition, unascertainable on the factual material, or they are not distinctive enough. As a result, we often hesitate in which of the species to number a specimen under examination. Occasional specimens are even unidentifiable, since, as BERGER and MICHAŁOWSKI (1963) write, „their characters are intermediate between those of the grass frog and the moor frog" and „it is difficult to say whether we are concerned here with extreme individual variation in either of these frogs, evading appropriate taxonomic criteria, or whether they are hybrids derived from crosses of these two species". As early as the nineteenth century PFLÜGER and SMITH (1883) and BORN (1883, 1886) attempted to solve this problem. For this purpose they carried out a number of successful crosses between female *R. arvalis* and male *R. temporaria*. And thus PFLÜGER and SMITH brought up 3 small hybrid frogs; unfortunately, two of them ran away, but the remaining one went on developing. BORN (1883) achieved metamorphosis in more than 200 larvae, which, however, did not outlive the winter. According to DÜRKEN (1935), BORN'S unpublished data show that he obtained satisfactory results in his further experiments of this sort, carried out in 1886—1891.

The first thing that struck BORN (1883) in the newly metamorphosed hybrids was their similarity to the mother (*R. arvalis*), though some paternal characters were also visible; these last became more pronounced, as the animal developed. However, this resemblance to the moor frog seems to have been connected, above all, with the presence of such characters in most of the hybrids as a) light

dorsal stripe and b) certain morphological features which, unlike BORN, DÜRKEN did not take into consideration on account of their variation with growth (e. g., shape of snout).

Opposite crosses (*R. temporaria* ♀ × *R. arvalis* ♂) performed by PFLÜGER and SMITH (1883) and BORN (1883, 1886) failed to produce any hybrids.

Far more precise studies conducted by DÜRKEN (1935, 1938) seem to have been a long step forward. He, too, obtained hybrids by crossing female *R. arvalis* (form „striata") with male *R. temporaria*. All the specimens of the F_1 generation were males; they attained maturity in the fourth year of life and copulated normally. They also went through the mating season in the next years. At first sight, right after their metamorphosis, these hybrids were similar to grass frogs in external appearance (coloration and pattern) except for the poorly developed light dorsal stripe, and they still resembled them, when they were 2 years old. It, however, appeared on close examimation that in the details of coloration and pattern of the dorsal side some specimens came near to the grass frog and others to the moor frog. Later, simultaneously with the differentiation of general coloration, these differences became still more pronounced.

The coloration and maculation of the ventral side of the body were as a rule similar to those in the grass frog, whereas the body size was taken after the moor frog.

No distinct predominance of the characters of one of the species was observed by DÜRKEN with respect to the inheritance of other morphological characters, which fact allowed him to distinguish a number of transitional groups, from the specimens completely similar to the grass frog to those resembling the moor frog. The breeding colour develops according to the group to which the given hybrid belongs, but it is always different from those typical of the parental species. The voices also vary parallel to the changes in the appearance of the hybrids.

DÜRKEN'S (1938) attempts to obtain progeny by crossing these hybrids with female moor frogs came to naught. However, in spite of the earlier experiments he (DÜRKEN, 1935) succeeded in crossing these frogs in opposite direction (*R. temporaria* ♀ × *R. arvalis* ♂), but only 5 larvae lived to metamorphose, which, not unlike his prodecessors, he referred to the occurrence of clear-cut differences in the morphology of spermatozoa between the species under discussion (spermatozoa of the grass frog have far narrower and more pointed, long thread-like heads, whereas those in the sperms of the moor frog are cylindrical, slightly thickened in the middle and blunt at the anterior end). The different structure of the vitelline membrane in eggs (it is thicker in the grass frog) may also cause differences in percentages of fertilized eggs. In DÜRKEN'S (1935) opinion, the fertilization of an egg with thin membranes by a sperm with a thin pointed head (*R. arvalis* ♀ × *R. temporaria* ♂) is naturally more effective than that of an egg with a thick membrane by a sperm with a bluntly-ending head (*R. temporaria* ♀ × *R. arvalis* ♂).

DÜRKEN also attempted to find the cause of hybrid infertility. For this purpose he carried out cytogenetic studies of both parental partners as well as of their hybrid offspring (1938).

As a result of his studies on spermatogonia DÜRKEN established a set of 22 chromosomes for *R. arvalis arvalis*, though WITSCHI (1933) claimed that they are 24. On the other hand, DÜRKEN confirmed the previously published number of 26 chromosomes in *R. temporaria temporaria* (WITSCHI, 1922a, b, 1924; TCHOU-SU, 1931; DALCQ, 1932; MAKINO, 1932; GALGANO, 1933; PROKOFEVA, 1935). DÜRKEN found only 24 chromosomes in the hybrids (11 from the moor frog and 13 from the grass frog). He took it that with these numerical relations in chromosomal sets between the parents the phenomenon of poorer production of sperms in their hybrids and the inability of the hybrid sperms to stimulate the moor frog eggs to proper development are natural. Dürken finds another cause of this infertility in the fact that at the time when female moor frogs attain maturity the hybrid sperms are already somewhat too old, since in the hybrids the mating season occurs a little earlier.

In the light of the foregoing, cytogenetic studies might provide sound arguments to settle the question of specific membership of controversial brown frog specimens under discussion or that of possible occurrence of hybridization among them. However, the cytogenetic studies carried out by other authors on both the grass frog and the moor frog show that there are still a great many obscure points in this problem.

Apart from the number of 26 chromosomes given above for the grass frog and confirmed by WICKBOM (1945), GUILLEMIN (1967) and ULLERICH (1967), other authors (KAWAMURA, 1943; KOBAYASHI, 1946, 1962; WITSCHI et al., 1958; SETO, 1965;) found only 24 chromosomes in this species. These last results, however, concern the grass frog from Japan (Hokkaido) and Sakhalin. This was, among other things, the reason why the Japanese form has recently been separated and regarded as a distinct species (KAWAMURA, 1962). On the other hand, WICKBOM (1945), KOBAYASHI (1962) and ULLERICH, 1967 confirmed the data published by WITSCHI for the moor frog, i. e., its having a set of 24 chromosomes, though CEI (1946) claimed that the number of chromosomes is 26 in this species.

In addition to DÜRKEN, KAWAMURA and KOBAYASHI (1960) have lately carried out experimental studies on the crosses of these frog species. They performed crosses between *R. temporaria temporaria* ♀ from Japan and *R. arvalis* ♂ and between *R. temporaria temporaria* ♀ from Japan and *R. temporaria* ♂ from Europe. All the hybrids obtained from the first cross were sterile males having a small number of spermatozoa, of which none proved normal, most probably owing to some disturbances during meiosis. The tadpoles received from the second cross did not attain metamorphosis (difference in sets of chromosomes). This last result has been corroborated by KAWAMURA and NISHIOKA (1962), who, besides, demonstrated that it does not come to fertilization at all

in the inverse crosses (*R. temporaria temporaria* ♀ from Europe × *R. temporaria temporaria* ♂ from Japan).

In view of the results of crosses described by KAWAMURA and KOBAYASHI (1960), this last author (1962) is of the opinion that *R. temporaria temporaria* from Japan approximates rather to *R. arvalis* than to *R. temporaria temporaria* from Europe, which fact has already been suggested by KAWAMURA (1943) and WITSCHI et al. (1958) in connection with their above-mentioned results of karyogamic studies on *R. temporaria temporaria* from Japan and the ascertainment of the occurrence of 24-chromosome sets in both these species. Moreover, these species (*R. arvalis* and *R. temporaria temporaria* from Japan) correspond to each other in a large number of morphological characters.

CUKIERZYS (1938) holds an individual and utterly unilateral view, according to which 43 per cent of the specimens of brown frogs collected by him in the Troki region were natural hybrids between the moor frog and grass frog. One of the fact which induced him to make this conclusion was that all the hybrids examined by him were, like DÜRKEN'S experimental specimens, males.

B. SYSTEMATIC PART

I. PURPOSE, MATERIAL, AND METHOD

1. Purpose

The difficulties in identification of our brown frogs, expounded above and resulting, among other things, from the inaccuracy of their specific descriptions, aroused my interest in this problem.

The objective of my study has been to check the taxonomic criteria so far used to distinguish the grass frog from the moor frog from the Central European territory, in a practical manner. Besides, I was concerned exclusively with adult specimens, i. e., from the moment when they began their first mating season, which in Central European grass and moor frogs usually occurs in the third year of life or after the second hibernation (Poland: BERGER and MICHAŁOWSKI, 1963; U. S. S. R.: TERENTEV, 1961; Germany: FREYTAG, 1961; Sweden: KAURI, 1959).

The minimum body length (L.) assumed in the present study is 44 mm for the grass fog and 40 mm for the moor frog. The choice of these minimum values of body length in the frogs under study is connected with the criterion of „adultness" presented above for these anurans. In males of our brown frogs the nuptial pad and, for the most part, the contrast coloration of the throat as compared with that of the belly are fairly lasting marks of „adultness". The nuptial pad appears, even before the specimen attains its complete maturity, and loses its specific colour at the end of the mating season, though its size

undergoes a relatively slow reduction and only very rarely disappears utterly. Hence, together with the swelling of the finger and the limb on which it occurs, this is a fairly important diagnostic character associated with the maturation of males. In Olsztyn I observed such distinct sexual characters even in 46-millimetre males of the grass frog and 43·5— mm males of the moor frog. As a rule, I did not make mistakes in determining the sex of somewhat smaller specimens with less marked sexual characters, either, which I next checked at dissection. Females of the same body lengths were generally identified by the lack of any male marks. The values of L. accepted for both species are somewhat smaller than those actually ascertained on account of some data from literature, according to which 4 cm is the lower limit size in the moor frog (MÉHELY, 1894; GERLACH, 1960; DELY, 1964a), and some authors (DÜRIGEN, 1897; HEMPELMANN, 1908; RAMMNER, 1956) assume a length of 4—5 cm as normal (average) in this species, which, however, does not correspond with the facts.

It is well known that in metamorphosed frogs particular body parts do not grow proportionally. TERENTEV (1945) and KANEP (1965) write that in the grass frog the growth of the head is inhibited earlier than that of the remaining parts of the body, whereas the hind limbs grow longest. Similar results concerning the growth rate of the head and shanks in relation to the body length were virtually obtained by TOPORKOVA (1966) for the moor frog. It should be emphasized that, in SCHUSTER'S (1950) opinion, although the hind limbs actually become relatively longer with age in the *Ranidae*, in some of the species (among them in the grass frog) there occur sexual differences in the growth of the limbs. As a result of such developmental properties of frogs, nearly all indices naturally change with age, which TERENTEV (1936) has already observed far earlier. However, these changes are not, as a rule, significant in so far as measurements of the taxonomic characters in adult specimens of the genus *Rana* are concerned.

The subject of my study has included the nominal forms of the species in question, as they are the only members of this genus found in the territory of Poland. Since there are also some data in literature indicating the occurrence of *Rana arvalis wolterstorffi* in this country, this subspecies has been taken into consideration in some analyses of the taxonomic characters of the species under study.

2. Material

The material for study came from the north-eastern Poland (regions of Toruń, Gdańsk, and Olsztyn). Totals of 600 adult grass frogs (Toruń — 83, Gdańsk — 218, and Olsztyn — 299) and 292 adult moor frogs (Toruń — 156, Gdańsk — 56, and Olsztyn — 80) were used for observation. The sex distribution of the specimens obtained from the particular regions is given in Table III.

Different numbers of these specimens were used for analyses of individual characters (detailed numerical data given in the text).

3. Methods

Observations were carried out on living animals. Measurements were taken to an accuracy of 0·1 mm, using calipers. In a case of symmetrical characters the right measurements were taken into consideration. „Heel" tests A were made on the right limb also, the left limb being measured only exceptionally, when the right one was damaged.

The present observations and measurements cover the characters commonly used for the distinction of the species in question in keys and descriptions. In defining the measurements and biological indices I have adopted the generally accepted Latin nomenclature (see the „List of Systematic Characters Examined" and „Explanation of Measurements and Tests Performed") in accordance with that applied by TERENTEV (1950) and DELY (1964b). The analysis of some characters was carried out by statistical methods (dispersion of values or their maximum-minimum range, arithmetic mean (M), standard deviation (δ), graphs). Photographs and drawings are given for some qualitative characters.

a. List of Systematic Characters Examined

The following morphological and morphometrical characteristics have been examined in this study: 1. General body shape; 2. Occurrence of outer metatarsal tubercle (C. ext.); 3. Shape of inner metatarsal tubercle (C. int.); 4. Length ratio of inner metatarsal tubercle to toe I $\left(\frac{\text{D, p.}}{\text{C. int.}}\right)$; 5. „Heel" test A; 6. „Heel" test B; 7. Development of swimming webs; 8. Development and form of tips of fingers and toes; 9. Ratio of upper eyelid width to interorbital space $\left(\frac{\text{Lt. p.}}{\text{Sp. p.}}\right)$; 10. Ratio of internasal space to interorbital space $\left(\frac{\text{Sp. n.}}{\text{Sp. p.}}\right)$; 11. Shape of snout; 12. Arching of snout, upper surface of head (regio frenalis) and frons; 13. Distinctness (projection and colour) of dorso-lateral folds; 14. Course (shape) of dorso-lateral folds; 15. Shape of dark nasal stripe; 16. Occurrence of longitudinal light stripe on the back; 17. Development of light labial spot; 18. Occurrence of dark transverse interorbital stripe; 19. Development of angular spot; 20. Colour of the back; 21. Appearance of dark transverse stripes on dorsal side of hind limbs; 22. Occurrence of dark marbling on body flanks; 23. Colour and pattern of ventral side of body; 24. Presence of yellow colour in the groin.

In addition, I shall discuss the following characteristics, which being, as a rule, secondary, have been taken into consideration by some authors, but I shall not examine them in detail on a definite number of specimens:

1. Ratio of head length to its width $\left(\frac{\text{L. c.}}{\text{Lt. c.}}\right)$
2. Ratio of distance of nostrils from top of snout to that from eyes $\left(\frac{\text{D. n. r.}}{\text{D. n. o.}}\right)$
3. Length ratio of finger I to finger II.

b. Explanation of Measurements and Tests Performed

L. — Longitudo corporis (body length)
From snout tip to middle of cloacal opening; to be measured a specimen is placed with its ventral side up and slightly pressed with a finger in the sacral region.

Lt. p. — Longitudo palpebrae (width of upper eyelid)
Greatest width of upper eyelid; measurement taken on an eyelid flattened by a press.

Sp. p. — Spatium palpebralis (interorbital space)
Smallest distance between bulging inner edges of upper eyelids

Sp. n. — Spatium internasale (internasal space)
Distance between external nostrils

D_1 p — Primus digitus (length of toe I)
From distal base of inner metatarsal tubercle to toe tip

C. int. — Callus internus (length of inner metatarsal tubercle)
Greatest measurement

„Heel" test A — with hind-limb stretched along body. The „heel" (tibio-tarsal joint) marks the point of reach of the limb. The drum, eye, nostril, and tip of snout have been assumed as reference points.

„Heel" test B — with hind-limbs arranged perpendicularly to the long body axis (thigh and shank lying parallel to each other) Three positions of the „heels" were thus found: they either touch each other, or overlap each other, or lie quite clear of each other.

II. RESULTS

1. Body Build

The body of the grass frog is stocky, relatively sturdier than that of the slimmer moor frog. These actual differences have been recorded by a clear majority of the authors (Wałecki, 1882; Knauer, 1883; Wolterstorff (1888), Bedriaga, 1889; Lachmann, 1890; Méhely, 1894; Szarski, 1939; Frommhold, 1953/54; Młynarski, 1966). The stocky build of the grass frog was also mentioned by Bedriaga (1898/1912). As I have observed on my abundant material, there are marked individual deviations from this general rule. They probably made Siebold (1852) and Štěpánek (1949) think that the grass frog is, for the most part, slimmer than the moor frog. Hence I consider this character to be practically of little use in the identification of these species.

2. Occurrence of Outer Metatarsal Tubercle (C. ext.)

Grass frog

Many authors claim that this tubercle occurs unchangeably as a hardly visible swelling (Table IV).

The results of my investigation carried out in this respect on 586 specimens are given in Table V.

As will be seen from these data, the outer metatarsal tubercle occurs mostly in the grass frog (74·5%), being very distinct in many specimens, often merely in the form of a greyish white or whitish patch, but sometimes in a vestigial form or on one foot only (11% — developed to a various degree), or even missing completely (14·5%).

Moor frog

Nearly all the authors assume that this tubercle does not appear in the moor frog (Table IV). My own investigation, made on 276 specimens, showed the relations presented in Table V. The tubercle was found in many specimens (54·5%), though it was mostly poorly developed as a greyish white or whitish patch. Sometimes it was hardly perceptible and on one of the feet only (15·5%). At times, however, it was quite distinct.

In no case can, therefore, the occurrence of the outer metatarsal tubercle be used as a criterion for distinction of these two species from each other.

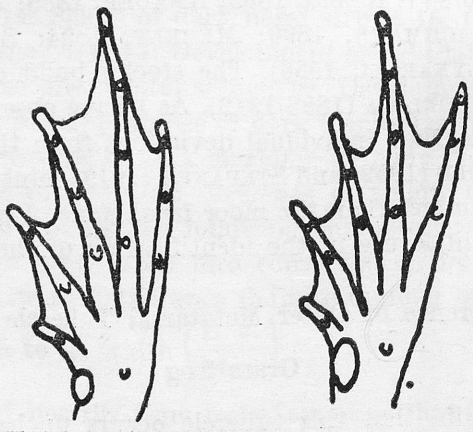
The supposition that all the specimens with outer metatarsal tubercles identified as *R. arvalis* were hybrids must be refuted, for they had every other character of the moor frog without exception.

3. Shape of Inner Metatarsal Tubercle (C. int.)

Grass frog

The inner metatarsal tubercle is roundish to oval, or digitate in shape, low and soft (Fig. 1a).

Only in one out of the 600 specimens examined this tubercle deviated from the type and resembled that of the moor frog.



a b

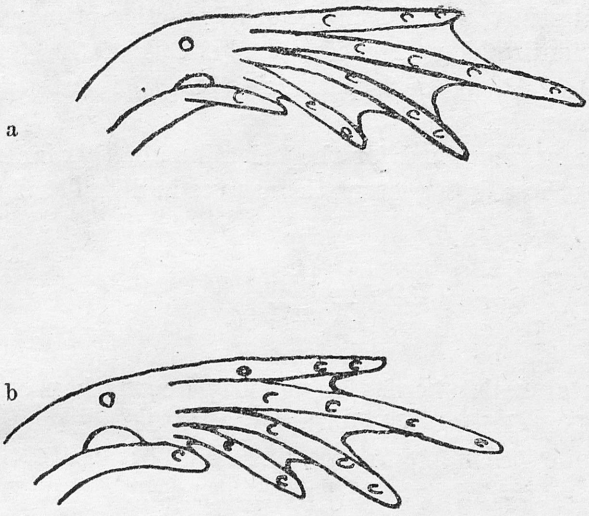


Fig. 1. Feet. a. — *R. temporaria* L., b — *R. arvalis* NILSS.

Moor frog

The inner metatarsal tubercle is distinctly crescent and similar to the tubercle in *Pelobates fuscus* (LAURENTI). It is squeezed from the sides, high, hard and with a projecting longitudinal edge in the middle of the top part (Fig. 1b).

In 276 specimens examined there were no deviations from the standard.

4. Length Ratio of Inner Metatarsal Tubercle to Toe I $\left(\frac{D_1\ p.}{C.\ int.}\right)$

Grass frog

The inner metatarsal tubercle is shorter than half the length of toe I, i. e., the inner toe (Fig. 1a).

BOULENGER (1898), FROMMHOLD (1953/54) and FREYTAG (1961), giving the same ratio, mention that this tubercle usually measures about one-third of the length of toe I, and according to BEDRIAGA (1899), it is even a quarter of this length, though it may also attain half of it.

According to TERENTEV and CHERNOV (1949), TERENTEV (1950) and BERGER and MICHAŁOWSKI (1963) this tubercle goes into the length of toe I 1·9—4·5 times. At the same time BERGER and MICHAŁOWSKI (1963) as well as TERENTEV (1945) found this value higher in the male than in the female. TERENTEV and TERENTEV and CHERNOV, in other places of their publications, and TARASHCHUK (1959) give somewhat different values of this index, ranging from 2·00 to 4·47.

FUHN (1960) offers the following measurements for Romanian specimens (in mm.):

	min.	M	max.
$D_1p.$	9·0	(11·9)	13·0
C. int.	3·0	(3·7)	4·5

In the present study and also in the field practice of many years this regularity has been confirmed nearly completely. Out of the 476 specimens, 467 (98%) had C. int. $< \frac{1}{2} D_1p$. In 8 specimens (1·75%) it was equal to and in one (0·25%) larger than $\frac{1}{2} D_1p$.

In the specimens examined for the behaviour of this index and characters associated with it these data present themselves in detail as shown in Tables VI and VII.

Moor frog

The inner metatarsal tubercle is evidently longer than or, rarely, equal to half the length of toe I (Fig. 1b). BOULENGER (1898), BEDRIAGA (1899), ANGEL (1946), FROMMHOLD (1953/54) and FREYTAG (1961) write that this tubercle does not exceed two-thirds of the length of toe I.

According to TERENTEV and CHERNOV (1949), TERENTEV (1950) and BERGER and MICHAŁOWSKI (1963), the tubercle goes into the length of toe I 1·2—2·1 times, but TERENTEV and CHERNOV, TERENTEV, elsewhere in the papers quoted, and TARASHCHUK (1959) give somewhat different values of this index:

1·31—2·13 (TERENTEV, TERENTEV and CHERNOV)
1·31—2·15 (TARASHCHUK)

The absolute values of the corresponding measurements (in mm.) in the Romanian specimens are, after FUHN (1960), as follows:

		min.	M	max.
R. arvalis arvalis:	D_1 p.:	7·0	(8·3)	9·0
	C. int.:	3·0	(4·0)	4·5

This regularity has almost as a rule been confirmed by the results of my study and in the field practice. Out of the 292 specimens, 287 (98·25%) had their C. int. longer than $\frac{1}{2} D_1p$. In 3 specimens (1%) C. int. was equal to and in 2 (0·75%) smaller than $\frac{1}{2} D_1p$. Tables VIII and IX show in detail the behaviour of this index and the characters connected with it in the specimens under study.

Estimating the taxonomic usability of this character positively, I, naturally, keep in mind also these small and very rare deviations from standard as regards the numerical index $\frac{D_1 p.}{C. int.}$, which deviations are of no major importance, for the concord of both the characters connected with the inner metatarsal tubercle is decisive. Thus, if the index $\frac{D_1 p.}{C. int.}$ is, for instance, close below the minimum value of the grass frog and, at the same time, the inner metatarsal tubercle resembles that in the grass frog in shape, we are concerned with the grass frog. Additional support is, certainly, given by other taxonomic characters important to the discrimination of the two species from each other.

5. „Heel" Test A

In so far as the character examined in this test is concerned, the opinions of different authors vary largely (Table X). Some of them assume that this character is quite distinctive (MAKUSHOK, 1926; CALINESCU, 1931; BAYGER, 1937) or almost quite distinctive (NIKOLSKII, 1918; TARASHCHUK, 1959; BERGER and MICHAŁOWSKI, 1963) in these two species. According to them, the „heel" of the hind-limb reaches the snout tip (BAYGER) and the snout tip or nostrils (the other authors) in the grass frog and only as far as the eye and nostrils in the moor frog. Other investigators do not, however, find this character distinctive (e. g., FATIO, 1872; ANGEL, 1946; FUHN, 1960; DELY, 1964a), and still others hold that, on the contrary, a leg stretched in this way has its „heel" placed farther to the front more often in the moor frog than in the grass frog (LENZ, 1878; BOETTGER, 1885; FROMMHOLD, 1959a). On the other hand, WALECKI (1882), DÜRIGEN (1897), STERNFELD (1952), KLINGELHÖFFER (1955) hold an opinion which is opposite to that put forward by BAYGER and the other above-mentioned authors, namely, they consider the hind-limbs of the moor frog to be relatively somewhat longer than those of the grass frog (STERNFELD writes that the „heel" in a hind-limb stretched along the trunk often reaches beyond the snout tip in this species), which may be due to the fact that the moor frog is characterized by a far greater jumping ability than the grass frog. The results obtained in this respect on my material are summarized in Table XI.

In the light of these observations the relations under discussion in the moor frog practically agree with the rule postulated by Bayger and the first group of authors mentioned above. This concordance occurs also, in a sense, in reference to the grass frog (the „heel" extends to the snout tip or nostrils), but in a relatively great proportion (17%) of the specimens the „heels" reach only as far as the eyes, which is considered to be a character of the moor frog.

After all, the present study does not corroborate the opinions of the authors who hold that the relatively longer hind-limbs pertain to the moor frog (STERNFELD, KLINGELHÖFFER and others) [1], though, certainly, some particular specimens of this subspecies may have hind-limbs relatively longer than single specimens of the grass frog. They also show clearly that the character in question is not distinctive, because in this test in a great percentage of the specimens of both species the „heel" of the hind-limb reaches the nostrils (54% in the grass frog and 61% in the moor frog), not to mention the specimens of the moor frog with the „heels" reaching the snout tip on the one hand and,

[1] These relations, naturally, refer not only to *R. arvalis arvalis* but, as will be seen from the results obtained by some authors (out of the recent ones, FUHN, 1960, and DELY, 1964a), another European subspecies, *R. arvalis wolterstorffi*, has its hind-limbs actually relatively longer than both the nominal race of the moor frog and the nominal race of the grass frog, which, according to DELY, is especially true of males.

on the other hand, those of the grass frog, whose „heels" do not go beyond the eyes. A confrontation of the data obtained by a number of authors with regard to this criterion partly corroborates my observations (Table X).

A comparative analysis of the values given by various workers for the index L. : T., which is equivalent to this character, leads to the same conclusions. The taxonomic value of this index has been shown in the study made by TERENTEV (1943) on *R. ridibunda* PALLAS and that by SCHUSTER (1950) on — among other species — *R. temporaria* and *R. arvalis*. These authors found that in the *Ranidae* both the length of the whole hind-limb and that of its particular sections (femur, tibia, etc) in relation to the body length change with geographic position (this is, above all, associated with the influence of temperature on their growth). NIKOLSKII (1918) claims that both in the grass frog and in the moor frog the length of the tibia is larger than half the body length. According to KIRITZESCU (1903), in the grass frog the tibia is smaller than the half of the body length, equal to it, or only very rarely somewhat larger, whereas TERENTEV and CHERNOV (1949) give the value of L. : T. as 1·8—2·3 [1].

DELY (1964a) calculated this index in the form of 2T. : L. and admitted that the double length of the tibia of the grass frog only slightly exceeds the body length if it exceeds this measurement at all. He concluded that in this species the character discussed has the level of intermediate specimens between *R. arvalis arvalis* and *R. arvalis wolterstorffi* from the Reci region (Romania).

Below are given the biometric data (after FUHN, 1960) for the measurements L. and T. in the grass frog from Romania (in mm.):

	min.	M	max.
L.	62·0	(68·5)	79·0
T.	31·0	(37·6)	41·0

The values of this index (in both its forms) calculated in a similar way by various authors for *R. arvalis arvalis*, and both the scatter of the results and their mean values for particular measurements used to form it have already been given above (Tables I and II).

The results obtained are undoubtedly conditioned by individual variation in the length of hind-limbs, especially in the grass frog, as has been emphasized by BEDRIAGA (1898/1912) and FEJÉRVÁRY (1921).

Thus, this character, which KLINGELHÖFFER (1955) treated even as the most important in distinguishing many species of frogs („das wichtigste Unterscheidungsmerkmal für viele *Rana* Arten ist das Verhältniss der Beinlänge zur Körperlänge"), being indistinctive, should rather not be applied for the discrimination of our two brown frogs from each other.

With reference to the variation observed in the length of limbs, I should mention that some authors report the sporadic occurrence of specimens of the

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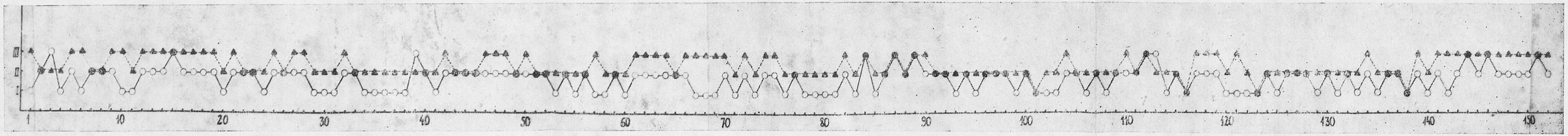
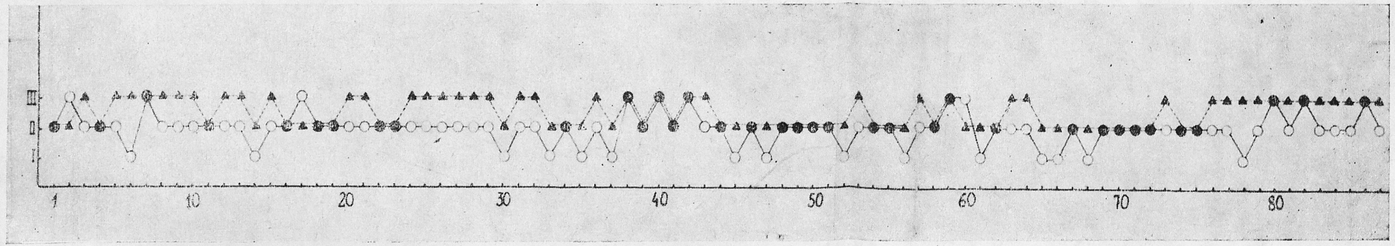
[1] Having estimated the mean value of L. : T. as 2·03 for the grass frog populations examined, Terentev (1945) stated it to be 2·01 for males.



a



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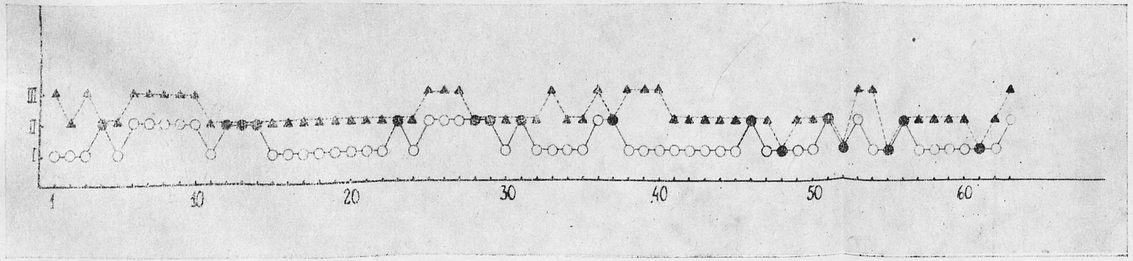
b



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c

Graph Fig. 2 „Heel" tests for *R. temporaria* L. — a, b, c (b — in males and c — in females)

○ „heel" test A
▲ „heel" test B
● „heel" tests A and B show the same degree (I, II or III)
I — „heels" up to the anterior margin of the eye; „heels" clear of each other
II — „heels" up to nostrils; „heels" touching each other
III — „heels" up to snout tip; „heels" overlapping
1, 2, 3, ... particular specimens

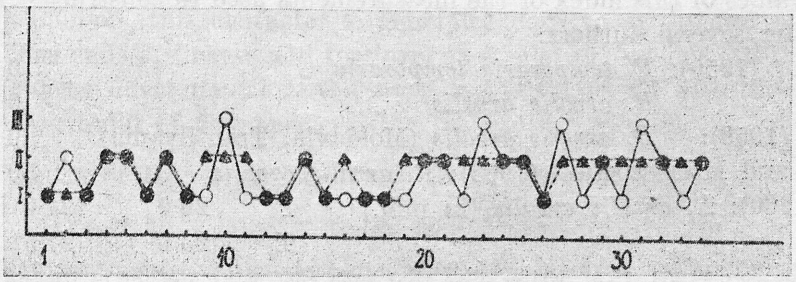
grass frog with very strongly elongated limbs (MÜLLER, 1885, after BOULENGER, 1898; KIRITZESCU, 1903, 1930 [1]; Rendahl and Vestergren, 1939; Schulz [2]; Frommhold, 1953/54). On account of this property MÜLLER (o. c.) distinguished the specimens marked by this character as var. longipes. Similarly, distinctly longer hind-limbs were also attributed to the mountainous form of this species, described as *Rana fusca honnorati* HERON-ROYER, 1881 (its special characters are, in addition, a pointed snout, somewhat different coloration, and a different dental formula in tadpoles — HERON-ROYER, 1881). BEDRIAGA (1889) and KIRITZESCU (1903, 1930) considered *R. fusca honnorati* and var. *longipes* to be identical.

KNOEPFFLER and SOCHUREK (1956) have resumed this problem, distinguishing the form *honnorati* from the nominal form of the grass frog. They treated it as *Rana honnorati*, and so did CAHET and KNOEPFFLER (1963), who found the sterility of crosses between the specimens of the nominal race and those of honnorati. Both these forms live in the Basses Alpes Department (south-eastern France) at altitudes ranging from 700 to 2000 m. a. s. l. (ARILLO and BALLETTO, 1966, write about their meeting with a frog showing the characters of *R. honnorati* also in Liguria). BALCELLS (1956), too, mentions this frog, calling it *R. temporaria honnorati*, and so do MERTENS and WERMUTH (1960).

6. „Heel" test B

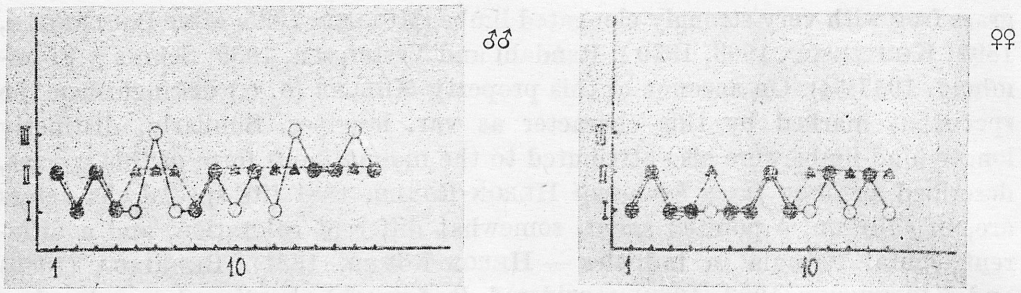
Some authors use the so-called „heel" test B instead of the „heel" test A (e. g., TERENTEV and CHERNOV, 1949) or in addition to it (e. g., TARASHCHUK, 1959; FUHN, 1960; BERGER and MICHAŁOWSKI, 1963).

The denomination of this test by TOPORKOVA (1965) as the index of long-leggedness (In) seems unsuitable. The test rather shows the length relation of the thigh bone to the tibia (F. : T.), which TOPORKOVA treats separately, whereas the „heel" test A serves to expose the index of long-leggedness. The lack of equivalence of the two „heel" tests (A and B) is also corroborated by my results of these tests juxtaposed in graphs (Fig. 2 a, b, c; Fig. 3 a, b, c). The varying results obtained by TOPORKOVA for the „heel" test B and index F. : T. in *R. arvalis arvalis* should most likely be referred to the scanty material she had



a

Graph Fig. 3a



b c

Graph Fig. 3. „Heel" tests for R. arvalis Nilss. For explanations see fig. 2

at her disposal (22 and 18 specimens for particular indices). As in the case of the „heel" test A, the authors differ in opinion on the taxonomic value of the „heel" test B (Table XII).

Some of the authors assume this character to be completely distinctive (e. g., TARASHCHUK, 1959; FUHN, 1960), others nearly completely distinctive (e. g., TERENTEV and CHERNOV, 1949; BERGER and MICHAŁOWSKI, 1963), and still others do not regard it as distinctive at all (SCHREIBER, 1912; DE WITTE, 1948). With respect to *R. arvalis arvalis*, FEJÉRVÁRY (1919) and CALINESCU (1931) write that at this test the „heels" touch each other in females and slightly overlap each other in males. The males of this subspecies would, therefore, have their hind-limbs relatively longer than the females. DÜRKEN (1935) supports this view only that, unlike most authors who refer this phenomenon to the fact that females shanks are shorter, he claims that in this case this is thighs that are shorter in females.

The statements made by FUHN (1960) and DELY (1964a) that at the „heel" test B the „heels" do not touch each other in the specimens of the nominal form of *R. arvalis* are surprising and they have not been confirmed by my results (Table XIII).

Similar values are given for the index F. : T., which is more or less equivalent to this test. According to BOULENGER (1898), SCHREIBER (1912) and FUHN (1960), the shank (T.) is somewhat longer than the thigh (F.) in both the species, whereas DE WITTE (1948) claims that in the grass frog the shank is shorter than the thigh and in the moor frog it is somewhat longer.

The values of this index or the measurements used to construct it are given below after several authors:

TERENTEV (1950):	*R. temporaria temporaria*			0·83—1·05
	R. arvalis arvalis			0·90—1·07
VANCEA (1959):	*R. arvalis arvalis* (Moldavia, Transilvania)			0·88—0·92
BERGER and MICHAŁOWSKI (1963):	*R. arvalis arvalis*			0·95—1·07
FUHN (1960):	*R. arvalis arvalis* (in mm.)	F	20·0 (24·0)	30·0
		T	25·0 (27·5)	30·0

[1] KIRITZESCU (1903, 1930) writes even that such specimens are not rarities in Romania.

[2] I quote after BERGER (1955), who, however, did not confirm the occurrence of long-legged specimens of this kind in the Wielkopolska Province.

Thus, as can be seen from the data from literature, an analysis of the relations under study in the aspect of the F : T index shows that this character does not allow the definitive discrimination of the two species of frogs examined (DE WITTE'S views on the F : T index in these frogs are an exception).

7. Development of Swimming Webs

Some authors, e. g., LEYDIG (1877), BOETTGER (1885), BEDRIAGA (1889) DÜRIGEN (1897), NIKOLSKII (1918), ADOLPH (1927), STERNFELD (1952), FROMMHOLD (1954) and GARMS (1962), consider the degree of development of the swimming webs to be a criterion permitting the distinction of the two species of brown frogs from each other. In the nominal form of the grass frog the webs are well developed and strong. Their colour, as a rule, agrees with the general ground colour of the dorsum, the edge-line is weakly indented, and they extend at best up to the base of the last phalanx of the 4th toe in the mating season, leaving the last two phalanges, or somewhat less, free in the interval between these seasons. In the nominal form of the moor frog the webs are generally worse developed and more delicate, their colour being often very light with a weak reddish tinge. Their edge-line is strongly indented, especially in females, and they reach at most to the base of the penultimate phalanx of the 4th toe in the mating season. This character, that is to say, the range of the web, is, however, often unreliable for its variability in the periods between the mating seasons and for this reason it has not usually been taken into account recently. By the end of the previous century PFLÜGER and SMITH (1883) had already called its usability for identification in question.

8. Development of Fingers and Toes

The fingers and toes of the grass frog are sturdier, evidently thicker and bluntly ended (somewhat swollen at tips) (Bedriaga, 1889; Mehely, 1894).

The fingers and toes of the moor frog are relatively thinner, much more sharply ended than those of the grass frog, and they become uniformly darker towards the tips. Their poorer development has also been emphasized by ANGEL (1946), whereas BOULENGER (1898) and FUHN (1960) found the toes of this species to be more slender. BOULENGER (1898) writes also about the bluntly ended toes of the moor frog.

In my opinion, this character is generally hard to apply and practically unuseful. The ends of fingers and toes are, as a rule, similar in both the species and their poorer development in the moor frog is connected with the generally more delicate build of this species.

9. Ratio of Upper Eyelid Width to Interorbital Space $\left(\frac{\text{Lt. p.}}{\text{Sp. p.}}\right)$

Grass frog

In many keys, especially the older ones, the interorbital space (Sp. p.) is mostly given as equal to the width of the upper eyelid (Lt. p.) and only rarely as larger or smaller than this measurement (Table XIV).

Similar relations in this respect are shown by the measurements given by FUHN (1960) (in mm.):

	min.	M	max.
Lt. p.:	4·0	(5·5)	6·0
Sp. p.:	4·0	(5·1)	6·0

The results obtained in my investigation, carried out on 367 specimens, are as follows:
Lt. p. < Sp. p. in 52 specimens (14%); Lt. p. = Sp. p. in 140 specimens (38%); Lt. p. > Sp. p. in 175 specimens (48%)
Table XV shows the absolute values of measurements compared (in mm.).

Moor frog

The interorbital space is far smaller than the eyelid width (Table XIV), which is also confirmed by the biometrical data given by Fuhn (1960) (in mm.):

	min.	M	max.
Lt. p.:	4·0	(4·5)	5·0
Sp. p.:	3·0	(3·6)	4·0

The following relations have been revealed by my investigation made on 100 specimens:
Lt. p. < Sp. p. in 9 specimens (9%); Lt. p. = Sp. p. in 27 specimens (27%); Lt. p. > Sp. p. in 64 specimens (64%)
Table XVI shows the absolute values of measurements compared (in mm.).

As will be seen from the foregoing results, both in the grass frog and in the moor frog there occur all the three possible relations between the measurements being compared. The character attributed as appropriate to the moor frog (Lt. p. > Sp. p.) was found in only 64% of the specimens of this species. In the other specimens the relations resembled those regarded as characteristic of the grass frog. On the other hand, we encountered specimens of the grass frog with the interorbital space remarkably smaller the eyelid width, which is considered to be a character of the moor frog. Similar observations have already been published by earlier authors (Table XIV). Therefore, this character is not distinctive, either. The confirmation of the opinion of its taxonomic uselessness may also be attained by comparing the coefficients of variation calculated by me for this character $\left(\frac{\text{Lt. p.}}{\text{Sp. p.}}\right)$ in both these species of frogs with the values given by TERENTEV and CHERNOV (1949), TERENTEV (1950) or TARASHCHUK (1959) (Tables XVII and XVIII).

Thus, it seems that this character cannot be used to identify our brown frogs, either.

10. Ratio of Internasal Space to Interorbital Space (Sp. n.: Sp. p.)

Grass frog

The internasal space is said to be equal to or somewhat smaller than the interorbital space (Table XIX). Only BOULENGER (1910) and FUHN (1960)

found this character to be different in this species, that is, the internasal space exceeded or equalled the interorbital space.

Out of the 232 specimens examined in the present study, 84 (36%) had Sp. n. > Sp. p., 142 (61·5%) Sp. n. = Sp. p. and only 6 (2·5%) Sp. n. < Sp. p. Thus, the results obtained agree with those published by BOULENGER (1910) and FUHN (1960).

Moor frog

The internasal space is much larger than the interorbital space. From among the 76 specimens examined I distinguished 53 (69·5%) with Sp. n. > Sp. p., 22 (29%) with Sp. n. = Sp. p. and only one specimen (1·5%) with Sp. n. < Sp. p.

The absolute values of the measurements (in mm.) used to calculate the index for my specimens of the grass frog and moor frog and those of the index itself are given in Tables XV, XVI, XX, and XXI.

In the light of these results the internasal space is not absolutely always much larger than the interorbital space in the moor frog, since specimens are often met with such that they have both these measurements equal and, therefore, show a character ascribed to the grass frog.

11. Shape of Snout (dorsal aspect)

Grass frog

The snout is rounded, though KOCH (1872), LEYDIG (1877), DÜRIGEN (1897) and HEMPELMANN (1908) mentioned the occurrence of grass frog specimens with a pointed snout; hence, as DÜRIGEN has remarked, some specimens much resemble the agile frog. FATIO (1872) distinguished the specimens of this type as var. acutirostris, opposing it to the typical form with a blunt snout (obtusirostris). This author and also LEYDIG (1877), BEDRIAGA (1889) and BOULENGER (1898) write that this form rather retains the elongated snout appropriate to young or semi-grown-up specimens.

PFLÜGER and SMITH (1883), FEJÉRVÁRY (1921) and WITSCHI (1930) also mention this individual variation of the snout shape of the species. The groundlessness of the distinction of these forms was emphasized by LEYDIG (1877) and BOULENGER (1898) (disorderly occurrence):

Out of the 366 specimens examined only 3 (0·8%) had the transitional form of the snout.

The results obtained at present do not show anything particularly new, because BEDRIAGA (1889) and BOULENGER (1910) have already written that the snout of the grass frog is broadly rounded and only rarely slightly pointed.

Moor frog

The snout is, as a rule, more or less pointed. As has been recorded by many authors (GIEBEL, 1861; FATIO, 1872; LEYDIG, 1877; LENZ, 1878; WAŁECKI, 1882; BOETTGER, 1885; WOLTERSTORFF, 1888; BEDRIAGA, 1889, LACHMANN,

1890; MÉHELY, 1894; DÜRIGEN, 1897; DE WITTE, 1948), the upper jaw, in contradistinction to that of the grass frog, as a rule projects farther beyond the margin of the mandible.

PFLÜGER and SMITH (1883), however, write that occasional specimens may even have their snout more bluntly shaped than it is in the grass frog.

In 3 (1%) out of the 267 specimens examined the snout was rounded and in 7 (2·5%) intermediate in shape. The results obtained for this species also confirm the generally admitted regularity, which BOULENGER (1898, 1910), SCHREIBER (1912) and MERTENS (1917) define as follows: the snout is usually pointed and strongly projecting, and only exceptionally rather blunt and rounded.

The character discussed, generally quoted in the keys, is for the most part constant for either species and, therefore, it is very helpful to a research worker in their identification.

Some authors show differences in the shape of the snout using the index $\frac{\text{Sp. c. r.}}{\text{D. r. o.}}$, where Sp. c. r. (spatium canthi rostralis) is the mouth width and D. r. o. (distantia rostri oculi) the snout length. For example:

NIKOLSKII (1918): *R. temporaria* — Sp. c. r. = D. r. o.
R. arvalis — D. r. o. not larger than Sp. c. r.

TERENTEV and CHERNOV (1949), TERENTEV (1950) and TARASHCHUK (1959):

R. temporaria — $\frac{\text{Sp. c. r.}}{\text{D. r. o.}} = 0{\cdot}8—1{\cdot}12$

R. arvalis — $\frac{\text{Sp. c. r.}}{\text{D. r. o.}} = 0{\cdot}77—0{\cdot}98$

FUHN (1960) (in mm.):

		min.	M	max.
R. temporaria	— Sp. c. r.	9·0	(10·0)	11·0
	D. r. o.	8·5	(9·7)	12·0
R. arvalis arvalis	— Sp. c. r.	8·0	(8·7)	10·0
	D. r. o.	6·0	(7·0)	8·0
R. arvalis wolterstorffi	— Sp. c. r.	7·0	(7·6)	8·0
	D. r. o.	8·0	(8·6)	9·0

Other authors define this difference in the value of the index $\frac{\text{Sp. c. r.}}{\text{D. r. o.}}$ descriptively: the grass frog has a short snout, whereas in the moor frog the snout is elongated (HOFFMANN, 1874; SCHMIEDEKNECHT, 1906; BAYGER, 1937; SZARSKI, 1939). LACHMANN (1890), MÉHELY (1894), WERNER (1897), DÜRIGEN (1897), ADOLPH (1927) and SLOKA (1961) also write about a short snout in the grass frog.

12. Arching of the Dorsal Surface of the Snout, Head (regio frenalis[1]) and Frons

These characters have not been defined clearly enough. Descriptions of particular characters will be found in the papers by GIEBEL (1861), FATIO

[1] Regio frenalis — area between the nasal stripes.

(1872), KOCH (1872), HOFFMANN (1874), LEYDIG (1877), LENZ (1878), WAŁECKI (1882), KNAUER (1883), BORN (1883), BEDRIAGA (1889, 1898/1912), LACHMANN (1890), MÉHELY (1894), DÜRIGEN (1897), BOULENGER (1898, 1910), SCHREIBER (1912), ADOLPH (1927), DE WITTE (1948) and FUHN (1960).

In the light of my observations these characters are not very clear (arching of the head and frons) or they are quite indistinctive (arching of the dorsal surface of the snout) and so have no taxonomic value.

13. Distinctness of the Dorso-lateral Folds

Grass frog

The dorso-lateral folds are rather poorly developed, hardly projecting, and only slightly standing out against the surrounding region in both shape and colour. Sometimes, on the outer side and, more rarely, on the inner side these folds are marked by irregularly arranged dark spots, varying in shape and at times fused together to form a kind of border, especially on the outer side. LEYDIG (1877) described specimens in which these folds were light in colour, as in the moor frog.

Moor frog

The folds are more often than not distinctly marked, projecting, mostly of a lighter colour than the rest of the dorsum, whitish, yellowish, goldish or pinkish. They are broader than in the grass frog (BOULENGER, 1897; MEHELY, 1894) and often accentuated by a dark outer border or spots.

The results of my investigation show that this character is adequately distinctive and, therefore, it may play an important part in determining the species (1 specimen of the moor frog had its dorsal folds strongly reduced, that is to say, interrupted in several places).

14. Shape (Course) of the Dorso-lateral Folds (Fig. 4)

Grass frog

The folds are somewhat arcuately bent, approach each other in the region of the shoulder-blades and next they go slightly asunder up to the sacral region to converge again as far as the cloacal opening.

Moor frog

The folds are completely or nearly completely straight, since they slightly converge in the region of the shoulder-blades. This regularity has, as a rule, been confirmed, but rather hard to grasp, on the basis of the present material.

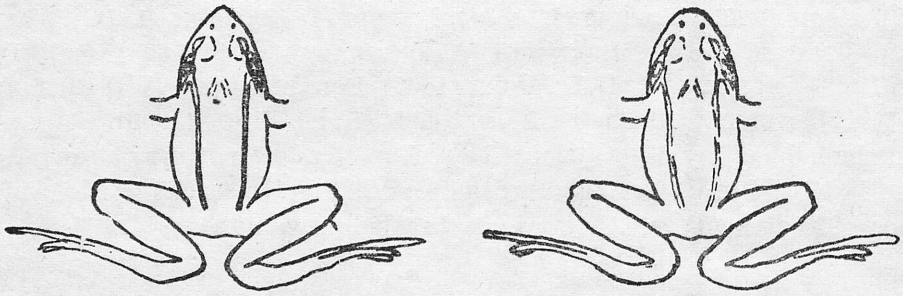


Fig. 4. The shape of the longitudinal dorso-lateral folds. a — *R. arvalis* NILSS., b — *R. temporaria* L.

15. Shape of the Dark Nasal Stripes

This stripe runs from the snout tip via the nostril to the anterior edge of the eye. It is usually dark in colour (dark-brown, dark-red-brown, blackish or sometimes even black). Its course is different in either of the species (Fig. 5).

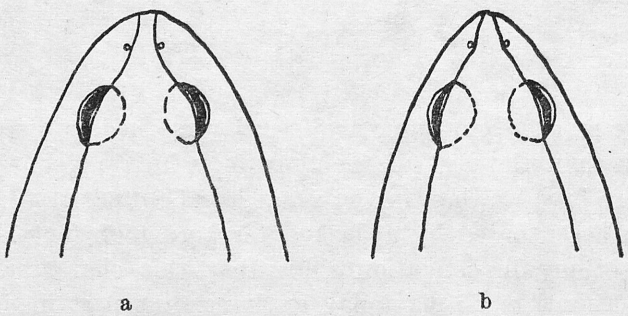


Fig. 5. Heads. a — *R. temporaria* L., b — *R. arvalis* NILSS.

However slight this difference was in the material examined, its stability was unquestionable. On the external side of the stripe I fairly often observed a light streak, sometimes hardly marked or interrupted or present only for a part of the stripe length.

16. Occurrence of Light Longitudinal Stripe on the Back

The light dorsal stripe is often encountered in the moor frog. It is a stripe, varying in width, which runs dorsally along the midline from the back of the head or the interorbital region or, still farther to the front, from the very snout tip, at first as a narrow line, next widening gradually towards the middle of the back, from where it extends to the proximity of the cloacal opening to narrow abruptly there. Such specimens with a stripe were distinguished as *R. arvalis* var. *striata* KOCH, 1872.

However, there are some specimens, and, what is more, they are relatively frequent, in which this stripe has developed only in the caudal portion of the back or is reduced to a thin line or, on the contrary, widened to the extent that it occupies nearly the whole back, while the dark dorsal patches dwindle to small dots or even disappear completely. It is a well-known fact that the striated form may be the only one in a region or it may occur together with the non-striated form. TOPORKOVA (1965) claims that in the Ural populations, consisting of both striated and non-striated specimens, the number of the striated frogs decreases in the S-N direction.

In the Olsztyn region this species was represented only by nonstriated specimens. The relations observed are summarized in Table XXII.

This stripe does not usually occur in the grass frog, but even in this species it may be seen, though very rarely and then in a less distinct or reduced form, limited to a portion, especially the caudal one, of the back. This stripe, as emphasized by BOULENGER (1898), WITSCHI (1930) and DÜRKEN (1935), is not very sharply delimited from the surrounding background, and specimens with as welldeveloped a stripe as that in the moor frog are met with only exceptionally (LEYDIG, 1877; BOULENGER, 1898; WITSCHI, 1930; FROMMHOLD, 1953/54).

Such striped specimens were distinguished as *R. temporaria* var. *striata* DÜRIGEN, 1897.

I have found this stripe, relatively well developed, scarcely in 2 out of the 600 specimens of the grass frog examined, and only slightly marked in another 6 specimens.

The frequency of grass frogs with a stripe of this kind being slight, whenever we deal with a brown frog with a dorsal stripe, it is most likely, especially in the presence of some other distinct characters typical of the moor frog, that this specimen belongs to this last species.

17. Development of Light Labial Spot

This is a light narrow streak between the temporal patch and dark nasal stripe and the dark border of the upper jaw. In the grass frog it is worse developed, shorter and less distinct in colour. At the front it extends at most to the anterior edge of the eye (MÉHELY, 1894; BOULENGER, 1898; BEDRIAGA, 1898/1912; de WITTE, 1940; ANGEL, 1949).

In the moor frog this spot is well developed and clear in colour. It reaches up to the snout tip and, at the back, to the base of the arm (HOFFMANN, 1874; BOULENGER, 1898; DE WITTE. 1948; ANGEL, 1949;). BOULENGER (1898), DE WITTE (1948) and ANGEL (1949) regard it even as a character which is particularly important to the discrimination of these species from each other.

As will be seen from my observations, no such distinctive relations can be found here for certain. I may only state that the percentage frequency of spe-

cimens with a distinct and long labial spot is much higher in the moor frog; on the other hand, there are relatively frequent cases in which this spot is distinct and extensive in the grass frog and poorly marked and small in the moor frog.

18. Occurrence of Dark Transverse Interorbital Stripe

In fact, here we are concerned with two stripes situated in the medial portion of the respective upper eyelid each. These stripes fairly often join in the middle to form a single transverse stripe, but not unfrequently they are reduced to a various degree and deformed, or completely absent.

WERNER (1897, 1929) considers this stripe to be characteristic of the moor frog, in which it is only rarely absent. Some other (e. g., BEDRIAGA, 1889, 1898/1912) mention the occurrence of this stripe also in the grass frog. My observations show that this stripe really occurs in the grass frog and very often at that (Table XXIII). Being indistinctive, this character is unfit for determination of species.

19. Development of Angular Spot

This spot lies in the scapular region, where it covers the area occupied by the cervical glands, arranged in two strings. It is, therefore, two folds, darker in colour than their surroundings and placed at an acute angle so that they more or less exactly resemble the inverted letter „V" closed or open at the top. However, it often occurs in a form reduced to a various degree, interrupted into a series of separate spots or continuous in one part, whereas the remaining portion is absent. In some cases it is distorted by irregular widenings. This spot is also fairly often lacking. It does not usually occur in the specimens with a light longitudinal dorsal stripe.

According to DÜRKEN (1935) and CUKIERZYS (1938) the angular spot is better developed and more distinct in the grass frog than in the moor frog. In this last frog, as DÜRKEN has described, it is formed of at most 2 small spots.

Grass frog

Out of the 551 specimens observed, 498 (90·5%) had this spot and in 53 specimens (9·5%), two of which with the longitudinal stripe, it was absent. From among the 498 specimens with the angular spot, 125 (25%) had it in a reduced form; this last figure, however, included 28 specimens with the spot in the form of 2 unjoined streaks (/\), which, in fact, also represents rather a typical appearance of this spot (Table XXIV).

Moor frog

Out of the 235 specimens examined, 120 (51%), including all the striped specimens (116), had no angular spots (Table XXV).

Out of the remaining 115 specimens, in which this spot occurred, 15 (13%)

had it reduced to a various degree (in this group I have also included the specimens with the spot in the form of the inverted letter V with open arms (/\)).

My observations show that the angular spot occurs in a similar form in both species (naturally, it is missing in the specimens with a longitudinal stripe). DÜRKEN's statement that this spot is less frequent in the unstriped forms of the moor frog than in the grass frog has not, as a rule, been confirmed.

20. Colour of the Back

The ground colour of the dorsal side of brown frogs may be any shade of brown; however, it may also be grey, yellow grey and, occasionally olive, but never green.

Both the ground colour and the pattern of maculation vary not only from specimen to specimen, but they may also vary with time in the same specimen, and rather considerably at that. This variability in coloration makes it impossible to distinguish the species under study from each other exclusively on the basis of the colour of the back. The changes in the coloration of the back are far intenser in the grass frog than in the moor frog.

The markings which are constant in colour and shape in both the species and are not subject to incidental influences include some dark dorsal spots, i. e., the temporal spot, nasal stripe, arm spot, angular spot, border of the upper jaw and interorbital stripe. Some of them (nasal stripe, interorbital stripe, angular spot), applied occasionally for the distinction of the two species from each other, are discussed separately in this paper.

The light dorsal markings, which owing to their distinctness are particularly characteristic of the moor frog, belong to the unchanging ones. They are the labial spot, light stripes on the back and longitudinal dorsal stripe. On account of their taxonomic value they have been discussed separately.

Some authors (e. g., DÜRKEN, 1935; FROMMHOLD, 1965) are of the opinion that the upper side of the grass frog has more spots than the back of the moor frog. In this last frog the spots are relatively indistinct. Although this opinion does not agree exactly with the actual situation, in the light of my observations it seems to prove correct to a fairly great extent.

Grass frog

The back is brown in colour, its shades varying from yellow-brown to red- and black-brown. Sporadically, there occur red, grey and green-grey specimens, whereas BOULENGER (1910) and DOTTRENS and AELLEN (1963) record even olive, and LEYDIG (1877), nearly lemon-coloured ones. Melanic specimens are also met with. The back is generally spotted in a dark (dark-brown to black) or red colour, rarely spotless. The number, shape, size and arrangement of spots range within very wide limits. On account of the various character of maculation of the back some authors distinguished colour varieties of these frogs (e. g., CAMERANO, 1883, MÉHELY, 1894, WERNER, 1897, SCHREIBER, 1912, MERTENS, 1917, ŠTĚPÁNEK, 1949).

Moor frog

Its coloration of the back is more monotonous than that in the grass frog. The colour of the back is any shade from yellowish to brown, or it may be greyish (bluish), sometimes brown-red (dark-brick-red), reddish and rarely, as recorded by FROMMHOLD (1953/54, 1965) blackish. Melanic specimens are also known. Grey and grey-brown colours may be found in males (WAŁECKI, 1882; WOLTERSTORFF, 1888; LACHMANN, 1890; MÉHELY, 1894; DÜRIGEN, 1897; HEMPELMANN, 1908; RAMMNER, 1956; and DELY, 1964a, for *R. arvalis wolterstorffi*, which subspecies does not differ in coloration and maculation from the nominal form and shows the same colour patterns only that they are, according to SOCHUREK, 1953, somewhat more prominent). LÁC (1956), however, claims that there is no such distinction in the colour of the back between sexes. He examined specimens of *R. arvalis wolterstorffi* and found that, although the ground colour was yellow or yellow-brown in most of the females, the sex ratio in the case of bluish coloration was approximately as 1:1.

There are no spots in this frog or, if present, the spots are small and dark (ranging from brown to black) and they differ in abundance, being larger on the flanks. The arrangement of spots is various, sometimes regular (BERGER and MICHAŁOWSKI, 1963).

Several colour varieties of these frogs have been distinguished on the basis of their coloration of the back and these varieties have also been observed by some contemporary authors (DELY, 1953; 1964a; VANCEA 1959; STUGREN and POPOVICI, 1960; FUHN, 1962).

21. Appearance of Dark Transverse Stripes on Dorsal Side of Hind Limbs

These stripes occur in varying numbers on the dorsal side of the hind limbs in the form of uniform transverse bands. They are sometimes disrupted into separate spots or may show tendency to vanish in particular parts.

According to some authors, there are certain differences in the number and distinctness of these stripes between the two species. The grass frog is said to have these stripes more numerous (DÜRKEN, 1935) and more distinct than the moor frog (BEDRIAGA, 1889; BOULENGER, 1910; DÜRKEN, 1935; DE WITTE, 1948). On the other hand, WERNER (1929) writes that the transverse stripes of the hind limbs of the grass frog are often less pronounced than those of the moor frog. DOTTRENS and AELLEN (1963) also emphasize the distinctness of these stripes in the moor frog.

I believe, and in this I agree with KLINGELHÖFFER (1931), that this character cannot be used to distinguish the two species under study from each other. All the descriptions of differences in this respect were most likely based on observations made on too small numbers of specimens.

22. Occurrence of Dark Marbling on the Flanks

Dark marbling or maculation, in which spots sometimes fuse into large patches or streaks, or resemble a kind of „quilting" on the flanks of the trunk, is attributed to the moor frog, and BEDRIAGA (1889), GAUPP (1904), WERNER (1922), ANGEL (1946), DE WITTE (1948), WERMUTH (1957) and BERGER and MICHAŁOWSKI (1963) consider this characteristic to be always present in this species, whereas other authors, e. g., DELY (1953), think that it is only very frequent. On the contrary, in the grass frog, as reported by STERNFELD (1952), this strongly marbled border-zone between the belly and the back is completely missing, and only large spots can at the most be seen on the flanks of its body (ANGEL, 1946). However, it will be seen from my observations made on abundant material that this type of maculation or marbling may be found in the grass frog, too, and it is not so very unfrequent in it. As early as the seventies of the nineteenth century FATIO (1872), and later WERNER (1897), BOULENGER (1898) and DE WITTE (1948) also met, and what is more, they often met with this sort of a coloured pattern of the flanks of the trunk in the grass frog, and FROMMHOLD (1959a) states indirectly that the marbling of the flanks is not a character confined exclusively to the moor frog when he writes that it frequently occurs in this last species and is for the most part missing in the grass frog. The occurrence of the dark maculation on the flanks of the trunk in both these species is, in addition, recorded by HOFFMANN (1874), LEYDIG (1877) and GAUP (1904), but these authors are of the opinion that in the moor frog it is to varying degrees — according to LEYDIG — and most frequently — according to HOFFMANN — divided in the middle by a kind of longitudinal spotless stripe, which, in their opinion, is not encountered in the grass frog.

Therefore, the occurrence of such maculation on the flanks of the body is not an exclusive characteristic of the moor frog, in which it may be missing, being at the same time present in the grass frog. This dark-coloured pattern on the flanks of the trunk of the moor frog is striking, above all, because it stands out in relief against the spotless or only slightly spotted back.

23. Colour and Pattern of the Ventral Side of Body

In most cases the ventral side of the body differs between these species at least either in ground colour or in maculation but, more often than not, the differences involve both these characteristics fairly evidently. Moreover, STERNFELD (1952) considers the differences in the maculation of the belly to be the most important taxonomic character (on a par with the shape of the snout) used for the distinction of the species under study. MÉHELY (1894), ŠTĚPÁNEK (1950), FUHN (1956), TARASHCHUK (1959), MERTENS and WERMUTH (1960), SLOKA (1961) and DOTTRENS and AELLEN (1963) are further authors who ascribe the taxonomic significance to this character. Earlier, MÉHELY (1890) treated the marbling of the belly in the grass frog as a very distinctive character; on the other hand, TERENTEV (1950) thinks that the uniformity of the colour of the belly is the fundamental character of the moor frog.

Grass frog

The ventral side of the trunk is

1. brownish-white, more often yellowish, or, rarely, ranging from greenish to orange; according to HOFFMANN (1874), LEYDIG (1877), LENZ (1878), MÉHELY (1894), BOULENGER (1910), DE WITTE (1948), GADOV (1958) and SERRA and ALBUQUERQUE (1963), in this last case we are concerned with females. Some specimens, nearly exclusively males, have a well-defined throat, which is white, white-grey, yellowish, or any shade from bluish to violet[1], not unfrequently with a light longitudinal stripe in the middle;

2. indistinctly spotted or marbled grey, bluish (FROMMHOLD, 1965), and grey-bluish (STERNFELD, 1952), which is seen mostly in males, or in shades ranging from yellow to brown, also orange and red, which, especially with reference to the last two colours, much more often characterizes the females. Brown spots may often be found also in males.

The yellow, red-brown and red spots sometimes fuse together over a large or even nearly whole area of their occurrence, ousting the ground colour. Such specimens with the entirely or nearly entirely uniform, red, red-brown or yellow ventral side of the body were distinguished as *R. flaviventris* MILLET, 1828 naturally, similar specimens very often found among females in the mating season are not included here).

There also occur specimens in which the spots are greenish, brownish-greenish and black (FATIO, 1872; GISLEN and KAURI, 1959), or, much more often, blackish (FATIO, 1872). One-coloured and spotless specimens are sporadic, though WOLTERSTORFF (1921) and BERGER (1955) met with them fairly often.

Moor frog

The ventral side of the trunk is

1. one-coloured, milk-white, more rarely yellowish, or, quite rarely, light-reddish; in some specimens it has a well-defined white or bluish-white throat, mostly characteristic of males and fairly often with a light longitudinal stripe in the middle;

2. generally spotless; if macular, the spots are small, indistinct, dark in colour: grey, various shades of brown, or red. These spots, varying in number, cover chiefly the throat and the sides of the breast region in most specimens, but very rarely the belly. The posterior portion of the belly is nearly always spotless, though there appear sporadic specimens with spots all over their bellies, in which they resemble the relations characteristic of the grass frog.

As there are occasional specimens of the grass frog with an entirely uniform spotless belly or a belly showing only a few spots and, on the other hand, moor frogs with a spotted belly, the use of this and only this character to distinguish

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[1] FROMMHOLD (1954) and SOCHUREK (1959) hold the opinion that the dark-blue colour of the throat is typical of old males.

the species under discussion (and this is how it is treated, e. g., by OLIGER, 1955) may lead to wrong identifications or at least raise doubts as to the correct determination of the species. The ascertainment of the ground colour of the belly may but need not help in each case to make a correct definitive diagnosis. Hence, in agreement with WOLTERSTORFF (1921), this character cannot be regarded as primary in distinction of these species. Being, however, easy in use, it is after all very helpful in preliminary identification, on condition that the above-mentioned precautions have been taken[1] [2].

Bolkay (1923) explains the occurrence of specimens of this kind by the affinity of the grass frog and moor frog, and also of the agile frog, to the three South-European species of the brown frogs, i. e., *R. latastei* BOULENGER, *R. iberica* BOULENGER and *R. graeca* BOULENGER, in which such marbling on the throat with a light stripe in the middle, is a constant character (*R. latastei*) or a very frequent one (*R. iberica* and *R. graeca*).

24. Presence of Yellow Colour in the Groin

The occurrence of yellow colour in the groin and on the sides of the posterior part of the belly, as well as on the ventral side of the thighs and legs, is considered by DÜRKEN (1935) and FUHN (1960) to be characteristic of the grass frog. The colour of these places in the moor frog is most often rusty or dull buff, which shades are rather rarely found in the grass frog. However, in my specimens of the moor frog I sometimes observed a yellow colour in the groins and, on the contrary, I often saw grass frogs without this yellow inguinal coloration.

25. Ratio of Head Length (L. c.) to Width (Lt. c.)

Grass frog

The head is usually wider than long (MÉHELY, 1894; DÜRIGEN[3], 1897; BEDRIAGA, 1898/1912; BOULENGER, 1910; SCHREIBER, 1912; ANGEL, 1945; DE WITTE, 1948; LEUTSCHER, 1952; FUHN, 1960; SERRA and ALBUQUERQUE, 1963). BEDRIAGA (1889), DÜRIGEN (1897) and ADOLPH (1927) are, besides, of the opinion that males have their heads somewhat narrower than females, for

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[1] Like other investigators (e. g., LÁC, 1961, in the grass frog and DELY, 1953, and FUHN, 1962, in the moor frog), in both our species of brown frogs I occasionally found specimens of both sexes, but oftener females (checked at autopsy), having a uniformly dark-coloured (grey to brown), as if smoky, throat, not unfrequently with a light longitudinal stripe in the middle.

[2] FUHN (1962) observed specimens of this kind also in the race „*wolterstorffi*".

These specimens should not be confused with those, chiefly males, with a light or bluish throat, often also spotted, but in bluishgrey, bluish, or even grey-brown but never smoky colours.

[3] However, some specimens, distinguished by FATIO as var. „*acutirostris*", are, according to DÜRIGEN characterized by a somewhat more elongated head.

instance, DÜRIGEN writes that the head of a male is by 1 or 2 mm wider than long, whereas in females this difference is 4—5 mm.

According to FUHN (1960), the corresponding values of these dimensions are as follows (in mm.):

	min.	M	max.
L. c.	20·0	(21·9)	25·0
Lt. c.	20·0	(22·5)	26·0

Moor frog

The head is as wide as long or somewhat wider (MÉHELY, 1894; DÜRIGEN, 1897; BOULENGER, 1910; SCHREIBER, 1912; DE WITTE, 1948; FUHN, 1960). BEDRIAGA (1889) and DÜRIGEN (1897) write that, as in the grass frog, the males of this species have the head somewhat narrower than the females.

FUHN (1960) gives the following values (in mm) for these dimensions in the nominal race:

	min.	M	max.
L. c.	16·0	(18·2)	21·0
Lt. c.	16·0	(18·0)	20·0

This character has, however, no practical application in identification of the species.

26. Ratio of Distance of Nostrils from Tip of Snout to That from Eyes $\left(\frac{\text{D. n. r.}}{\text{D. n. o.}}\right)$

The opinions of different authors on this character are presented in Table XXVI. In my opinion, it is not distinctive at all.

27. Length Ratio of Finger I to Finger II

In the grass frog finger I is only slightly longer than finger II, whereas in the moor frog this difference is far greater (BOULENGER, 1910; SCHREIBER, 1912; NIKOLSKII, 1918; CALINESCU, 1931; ANGEL, 1946; DE WITTE, 1948). These relations have also been confirmed for the grass frog, among other authors, by BEDRIAGA (1898/1912) and GADOV (1958), though according to the first of them, the fingers may sometimes be equal in length, and for the moor frog by DÜRIGEN (1897) and MAKUSHOK (1926).

In my opinion, the difference between the species examined is clear in this respect in many cases, but, all the same, fairly often it cannot be shown at all, and so it may be used only as an additional character.

III. CONCLUSIONS

Keeping in mind the results of the foregoing studies and observations on the essential morphological and morphometrical characters used in discrimination of the nominal forms of the grass frog and moor frog, I consider the follo-

wing of these characters to be the most reliable: 1. length ratio of inner metatarsal tubercle to toe I $\left(\frac{D_1p.}{C.\ int.}\right)$; 2. shape of inner metatarsal tubercle; 3. shape of snout, and 4. distinctness of dorso-lateral folds.

Some other characters taken into account in descriptions and keys are not, as I have found, contrastive or distinct enough and, consequently, they are hard to use. Among these I may number, e. g., 1. shape of nasal stripes; 2. shape of dorso-lateral folds; 3. ratio of head length to width $\left(\frac{L.\ c.}{Lt.\ c.}\right)$, and 4. shape of fingers and toes.

On the other hand, the characters which even now are often reckoned among those fundamental in discrimination of the two species under study but which, being indistinctive, do not suit this purpose are as follows: 1. „heel" tests A and B; 2. ratio of upper eyelid width to interorbital space $\left(\frac{Lt.\ p.}{Sp.\ p.}\right)$; 3. presence of outer metatarsal tubercle, whereas; 4. colour and maculation of the ventral side of the body may be used only with great caution, because there occur specimens in which this character has the appearance typical of the opposite species.

In addition, the „heel" tests A and B, rather often regarded as equivalent (index of long-leggedness), in fact, are not identical. The „heel" test B shows the length ratio of thigh (F.) to shank (T.) fairly exactly and the „heel" test A coresponds strictly to the index of long-leggedness.

Lastly, there is quite a number of characters, which are often indistinctive, e. g., because of their obvious variability, or do not prove true at all, and for this reason cannot be used in identification. These are, e. g., 1. development of swimming webs; 2. length ratio of finger I to finger II; 3. general body shape; 4. ratio of internasal space to interorbital space $\left(\frac{Sp.\ n.}{Sp.\ p.}\right)$; 5. distance of nostrils from snout tip and eyes $\left(\frac{D.\ n.\ r.}{D.\ n.\ o.}\right)$; 6. occurrence of dark transverse interorbital stripe; 7. development of light labial spot; 8. appearance of dark transverse stripes on dorsal side of hind limbs, and 9. presence of yellow colour in the groin.

The key and the survey of characters, presented below, in which the results of the present study have been included, may be used for the correct determination of adult specimens of our two species of brown frogs outside the mating season.

KEY TO THE BROWN FROGS OF POLAND

(to be used after the ascertainment that the specimen observed belongs to the group of brown frogs)

1. Inner metatarsal tubercle high, crescent, constricted on sides, hard, with projecting longitudinal ridge on top. Its length generally evidently larger than or, more rarely, equal to halflength of toe I. Snout, more or less pointed,

SURVEY OF CHARACTERS OF BROWN FROGS OF POLAND

Character	*R. temporaria temporaria*	*R. arvalis arvalis*
1	2	3
Length ratio of inner metatarsal tubercle to toe I $\left(\frac{D_1 p.}{C. int.}\right)$	Length of inner metatarsal tubercle smaller than half-length of toe I	Length of inner metatarsal tubercle conspicuously longer than or equal to half length of toe I
Shape of inner metatarsal tubercle	Inner metatarsal tubercle oval or digitate, low and soft	Inner metatarsal tubercle pronouncedly crescent, constricted on sides, high, hard, with a projecting longitudinal ridge on top
Shape of snout (seen from above)	Rounded	More or less pointed; upper jaw as a rule projecting beyond the end of the lower jaw
Dorso-lateral folds	They as a rule stand out in relief against surroundings less distinctly both in shape (at most they project only slightly) and in colour	They generally project and are much lighter in colour than their surroundings. Their course is quite or almost straight
Dark nasal stripes	As in the diagram	As in the diagram
Length ratio of finger I to finger II	Finger I only slightly longer than finger II	Finger I much longer than finger II
Light labial spot	In front it does not usually reach beyond the anterior eye margin and rarely farther, up to the snout tip; it is not, generally, very sharply marked	It often stretches from the base of the arm up to the snout tip and is usually well marked
Colour and maculation of ventral side of body	Ventral side greyish-white or ranging from yellow to orange, abundantly but indistinctly spotted or marbled in grey, yellow, orange or red colour; sporadically spotless or with only few spots; some specimens, nearly all of which are males, with white, white-grey, yellowish, or bluish, well-defined throat	Ventral side milk-white or, more rarely, yellowish, usually spotless or with few small spots, grey, brown, or red in colour, in most specimens only on throat and sides of breast region, very rarely on belly, but its posterior portion remains as a rule spotless; specimens having their ventral side thoroughly spotted are extremely rare; distinct white or bluish-white throat present in some specimens, nearly exclusively males
General body shape	Body for the most part stocky and strongly made	Body generally with slightly stocky outline and weakly made

with upper jaw as a rule projecting beyond the end of the lower jaw. Dorso-lateral folds, in principle, projecting and clearly lighter in colour than surroundings . . . . . *R. arvalis arvalis*

2. Inner metatarsal tubercle low, oval or digitate, and soft. Its length smaller than half-length of toe I. Snout usually rounded. Dorso-lateral folds poorly standing out in relief against their surroundings both in colour and in projection above the body surface or only slightly projecting . . . . . *R. temporaria temporaria*

It will be clearly seen from my observations made on adult specimens of our brown frogs which were hard to identify, since they showed characters of both species or intermediate ones between the species, and thus might be regarded as their hybrids, that, in contradistinction to the view held by CUKIERZYS (1938), who described intermediate specimens of this kind only among males, they are of both sexes.

IV. DISCUSSION

I am not completely solitary in mentioning the following four characters, the length ratio of toe I to inner metatarsal tubercle ($D_1p.$: C. int.), the shape of the inner metatarsal tubercle, that of the snout, and the development of the dorso-lateral folds, as the most important ones to the discrimination of our brown frogs. COCHRAN (1961), for instance, concludes that the essential morphological differences between the two species are the length ratio of the inner metatarsal tubercle to toe I and the form of this tubercle, beside the shape of the snout and maculation of the belly.

Similarly, FROMMHOLD (1953/54) treats the development of this tubercle as a particularly important character, and BOLKAY (?), after KLINGELHÖFFER, 1931) even attaches more importance to its shape and biological role than to the length relations. The significance of this criterion is, besides, emphasized by KLINGELHÖFFER himself. KOCH (1872), DÜRKEN (1935) and WERMUTH (1957), too, consider the development of this tubercle (its size and hardness) to be the most important character in discrimination of the two species under study.

On the other hand, KAURI (1959) believes that the size of the inner metatarsal tubercle in grass and moor frogs depends upon the mean annual temperature of the region in which they live. This opinion is connected with his theory, based on observations made on material from various parts of Sweden and, for comparative purposes, that from other regions of Europe, that the inner metatarsal tubercle, unlike the remaining parts of the body, grows also in the so-called resting season, which in the case of European frogs falls in the autumn. Hence its growth is far longer than that of the rest of the body and it becomes gradually larger and larger in relation to the other parts of the body. In the north, frogs grow more slowly because of lower temperatures and the shortness of the postmetamorphic period. For this reason, the northern frogs, as

compared with the southern specimens of the same size, have survived more autumnal growth intervals, which are, in addition, far longer than those in the south of Europe. Therefore, if we compare specimens equal in size, the northern frogs are older than the southern ones. As a result, a comparison of the values obtained for this tubercle within particular body-size groups of the specimens examined shows that its measurements are somewhat smaller in the south of Europe than in the north. However, as will be seen from the foregoing, the specimens of the same age belonging to the nominal races of both species have relatively larger tubercles in the south of Europe than in the north, though this difference is not very great.

Apart from the fact whether KAURI's view on the morphological variability of the inner metatarsal tubercle with age corresponds in substance with the actual situation, its value as a fundamental criterion in discrimination of the two species of our brown frogs can be established without impediment, since even if such variability occurs actually, it is weakly marked, which KAURI himself has emphasized.

This conclusion may also be strengthened by the study carried out by BALCELLS (1956), who, among other things, compared the development of the inner metatarsal tubercle of Central and South-European grass frogs with that of the tubercle in the agile frog. This investigator found that in the grass frogs from the south of Europe the tubercle is intermediate in respect of size and hardness between the grass frog from Central Europe and the agile frog. In the agile frog this tubercle, though well developed, is relatively smaller than in the moor frog. According to BERGER and MICHAŁOWSKI (1963), the index $\frac{D_1 p.}{C. int.}$ is 2.3—2·8 for the agile frog, 1·2—2·1 for the moor frog, and 1·9—4·5 for the grass frog.

Having rejected CUKIERZYS's (1938) opinion as to the existence of natural hybrids of the grass and moor frogs on account of the occurrence of specimens with intermediate characters in both sexes, not only in males, I must, basing myself on my observations and the data from recent literature, treat critically the argumentative part of his work. In the light of CUKIERZYS's conclusions, most males in the population of both species of brown frogs — at least in the area studied by him — were hybrids (43% of the total of specimens collected). The question arises whether this is possible at all.

DÜRKEN (1935) himself remarks that, despite his diligent quest, he failed to observe copulation between the grass frog and the moor frog, but he assumes the possibility of its occurrence under suitable climatic conditions (tardy spring), which bring their mating seasons closer. This assumption is, besides, supported by observations and opinions of some other investigators (BORN, 1883; HEMPELMANN, 1908; JOCKISCH, 1909).

An analysis of the studies made by JUSZCZYK (1938, 1959) and JUSZCZYK and ZAMACHOWSKI (1965) shows that the possibility of simultaneous egg laying by females of both the species under study cannot be ruled out. These authors

(JUSZCZYK, 1959; JUSZCZYK and ZAMACHOWSKI, 1965) experimentally demonstrated the capacity of female grass frogs for prolonged retainment of eggs.

However, even if it comes to such an interspecific amplexus, which DÜRKEN observed in his laboratory, to which he had transferred heterogeneous pairs of both species, irrespective of the direction of crossing (male *R. arvalis* with female *R. temporaria* or vice versa), the amplexus becomes concluded sooner or later without shedding eggs or sperms, though, as he found experimentally, his specimens were mature. Hence he concluded that hybrids of both species can be obtained only by artificial insemination.

Much earlier, BORN (1883) attempted to answer the question why hybrids between these species are not met with in nature. His experiments in hybridization between male *R. temporaria* and female *R. arvalis* show clearly that the positive result of experiments of this sort depends on the following circumstances:

1. the degree of concentration of spermatic fluid; the dilution of sperm which in normal mating (between specimens of the same species) still allows good results, in hybridization does not, as a rule, bring about fertilization. Born explains this by difficulties encountered by spermatozoa in penetration through the vitelline membrane alien to them. Hence, out of the large number of spermatozoa contained in the sperm only some succeed in getting inside the egg cell. In a case when the number of spermatozoa becomes reduced, the possibility of fertilization decreases with the dilution of the sperm and falls practically to naught. In nature it does not come to the action of a concentrated number of spermatozoa, since the males shed them over eggs laid in water and during the short time that the sperm has at its disposal to reach the eggs, especially those situated deeper in the water, it undergoes a dilution.

2. the fact whether the specimens used in hybridization have attained full heat or whether the eggs and spermatozoa are at the peak of development, as has already been emphasized by PFLÜGER and SMITH (1883). Eggs are particularly sensitive to this circumstance, whereas sperms are fit to fertilize heterogeneous eggs several weeks before and after period of highest development, and this presents far greater difficulties than normal intraspecific fertilization. BORN (1883) writes about cases in which the overmature grass frogs failed in the experiments of hybridization, but were still fit to have their eggs fertilized by males of their own species.

He (BORN, 1883), however, thinks that it should be checked, if in cases when the mating seasons of both species overlap there are any eggs that cleave after all but owing to the infecting effect of the dead unfertilized eggs in the spawn are deprived of the possibility of further development. If, as BORN concludes, under particularly favourable conditions it comes to the emergence of a hybrid tadpole from an egg, the percentage of specimens which live to metamorphose and, still more, that of metamorphosed specimens are extremely low. And there still remains a difficult task to do, namely, that of their identification as hybrids.

Table showing the morphological differentiation in hybrids in the direction of *R. temporaria* or that of *R. arvalis* (after CUKIERZYS)

Ser. No.	Character	R. arvalis	Hybrid „A“	Hybrid „B“	Hybrid „C“	Hybrid „D“	Hybrid „E“	R. temporaria
1	Two (+) or three (—) warts on toe III	—	±	+	±	+	—	+
2	Metatarsal tubercle well (—) or poorly (+) developed	—	—	±	—	+	+	+
3	Internasal space smaller (+) or larger (—) than interorbital space	—	±	±	—	—	—	+
4	Snout rounded (+) or pointed (—)	—	—	—	—	—	+	+
5	Belly spotted (+) or spotless (—)	—	±	+	+	+	—	+
6	Swimming webs weakly (+) or strongly (—) indented	—	—	—	+	±	+	+
7	Indistinct (—) or distinct (+) angle on back	—	+	+	+	+	—	+
8	Body length above (+) or below (—) 7 cm	—	—	—	—	—	+	+
9	Nuptial pad on finger of males partite (+) or non-partite (—)	—	—	—	±	±	±	+

CUKIERZYS has undoubtedly made a number of essential mistakes both in the assumptions of his study and in conclusions.

Thus, out of the nine characters selected by him as routinely used in discrimination of the two species of brown frogs (Table after CUKIERZYS), several

are not distinctive at all (number of warts on toe III, distinctness of angular spot) or are only partly distinctive and so unreliable (ratio of internasal space to interorbital space, development of swimming webs), whereas such a character as the maximum body size, actually different in these species, may be of importance in a general analysis of populations of these species but not in that of individuals, since it shows at the most that specimens with a length of body exceeding 8 cm belong to the species *R. temporaria*. After all, in amphibians the body size depends on the age of specimens.

Keeping these fundamental qualifications in mind and, thus, taking into account only the remaining criteria used by CUKIERZYS to determine the species of brown frogs, i. e., the development of the metatarsal tubercle, form of the snout, maculation of the belly — this character may also often be deceptive — and appearance of the nuptial pads [1], we can refer nearly all the specimens either to the grass frog or to the moor frog, almost beyond any doubt.

Thus, the problem of existence of hybrids between the grass frog and moor frog at liberty needs further studies, including cytogenetic studies (especially intermediate specimens found at liberty should be examined in this respect) and, I daresay, above all, serological and chromatographic ones.

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[1] It should be mentioned that in the light of my observations the nuptial pads of the grass frog differ in fact from those in the moor frog, but in another character from that usually given, i. e., that the nuptial pads are quadripartite in the grass frog and uniform in the moor frog, since in most cases they are also quadripartite in moor frogs. They differ in the basal portion of the pad, which in the grass frog is broader and more expanded.

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STRESZCZENIE

Pracę wykonano na 600 dorosłych okazach żaby trawnej i 292 dorosłych okazach żaby moczarowej, zebranych z obszaru płn.-wsch. Polski (okolice Torunia, Gdańska i Olsztyna). Badaniu poddano 29 cech morfologicznych i morfometrycznych, stosowanych przy rozróżnianiu żaby trawnej od żaby moczarowej, bądź takich, którym można by przypisać takie znaczenie taksonomiczne. Analizę niektórych cech przeprowadzono za pomocą metod statystycznych. Autor wykazał, że dla prawidłowego oznaczenia dorosłych osobników żab: trawnej i moczarowej nadają się tylko 4 cechy (stosunek długości wewnętrznej narośli „piętowej" do długości 1 palca stopy, wykształcenie wewnętrznej narośli „piętowej", kształt szczytu pyska, wykształcenie wzdłużnych fałdów grzbieto-bocznych). Użycie tylko tych 4 cech zmniejsza wyraźnie ilość osobników określanych jako trudne do oznaczenia, a traktowanych przez niektórych jako hybrydy. Dwie dalsze cechy (kształt ciemnych smug nosowych, kształt fałdów grzbieto-bocznych) zwykle istotnie też różnią badane gatunki, jednak z powodu małej wyrazistości mogą mieć tylko znaczenie przy diagnostyce. Nie mają natomiast praktycznego znaczenia w oznaczaniu tych żab, na skutek braku alternatywności, takie cechy, jak:1) obie próby „piętowe" (przy wyciągniętej kończynie tylnej wzdłuż tułowia — tzw. próba „piętowa" A i przy prostopadłym ułożeniu kończyn tylnych do długiej osi ciała — tzw. próba „piętowa" B); 2) szerokość górnej powieki do rozstępu międzyocznego; 3) występowanie zewnętrznej narośli „piętowej" i 4) barwa i wypłamienie brzucha. Autor miał możność też wykazać, że powyższe próby „piętowe", które dość często traktuje się jako równoważne sobie próby (tzw. indeks długonogości) w istocie nie stanowią prób jednoznacznych. Próba „piętowa" B w dużym przybliżeniu oddaje stosunek długości uda do goleni, natomiast właściwym odpowiednikiem wskaźnika długonogości jest próba „piętowa" A.

Autor ustosunkowuje się negatywnie do możliwości istnienia naturalnych mieszańców między obu badanymi gatunkami.

РЕЗЮМЕ

Произведено исследования на 600 взрослых особях лягушки травяной и 292 взрослых особях лягушки остромордной, собранных на территории северо-восточной Польши (окрестности Торуня, Гданска и Ольштына). Изучено 29 морфологических и морфометрических признаков, применяемых при различении лягушки травяной от лягушки остромордной, относительно которых можно было бы отне-

сти такое таксономическое значение. Анализ некоторых признаков произведено статистическими методами. Автор установил, что для правильного определения взрослых особей лягушек: травяной и остромордной подходят только 4 признака: отношение внутренней длины „пяточного" нароста к длине 1 пальца ступни, образование внутреннего „пяточного" нароста, форма вершины морды, образование продольных дорзально-латеральных складок. Употребление только этих 4 признаков, отчётливо уменьшает количество особей диагностируемых, как трудные к определению и трактованных за гибридов. Два следующих признака (форма тёмных носовых полос, форма дорзально-латеральных складок) обычно существенно отличают исследованные виды, однако по поводу малой отчётливости могут иметь значение только при диагностике. Зато практического значения при определении этих лягушек не имеют (в результате отсутствия альтернативности) такие признаки как: 1) обе „пяточные" пробы (при вытянутой задней конечности вдоль туловища — так называемая „пяточная" проба А и при перпендикулярном уложении задних конечностей к длинной оси тела, так называемая „пяточная" проба Б); 2) ширина верхнего века к расстоянию между глазами; 3) присутствие внешнего „пяточного" нароста, и 4) цвет и пятнистость живота. Автор имел возможность также доказать что выше указанные „пяточные" прбы, котор ые довольно часто трактуют, как равнозначные пробы (так называемый индекс длинноногости) по существу не являются однозначными. „Пяточная" проба Б с большим приближением отдаёт отношение бедра к голени, зато соответственным эквивалентом указателя длиннонгости является „пяточная" проба А.

Автор отрицательно относится к возможности существования естественных помесей между обоими исследованными видами.

TABLES

Table I

R. arvalis arvalis			*R. arvalis wolterstorffi*		
min	M	max	min	M	max
L. 47,0 —	(50,5) —	64,0	53,0 —	(61,7) —	72,0
F. 20,0 —	(24,0) —	30,0	27,0 —	(31,0) —	35,5
T. 25,0 —	(27,5) —	30,0	31,0 —	(32,6) —	36,5

After Fuhn (1960), in mm

Table II

R. arvalis wolterstorffi	*R. arvalis arvalis*	Author	Character
T. goes into L. less than twice ($\pm 1\frac{2}{3}$—$1\frac{3}{4}$ times)	T. goes into L. about twice (♂♂) or more than twice	Fejérváry (1919)	2T.: L.
T goes into L. less than twice ($1\frac{2}{3}$—$1\frac{3}{4}$)	T. goes into L. nearly twice (♂♂) or more times (♀♀)	Calinescu (1931)	
2T. always exceeding L.	2T. equal to or somewhat larger than L.	Fuhn (1960)	
2T. always exceeding L.	2T. somewhat smaller than or equal to L., or only slightly exceeding L.	Dely (1964a)	
"Heel" reaching at least nostrils or snout tip, in ♂♂ often beyond snout tip	"Heel" reaching eye, in ♂♂ approximately as far as nostrils	Fejérváry (1919)	"Heel" test A
"Heel" extending beyond nostrils, reaching snout tip or even, in ♂♂, beyond it	"Heel" reaching eye or coming near nostrils (♂♂)	Calinescu (1931)	
"Heel" reaching at least nostrils, often beyond snout tip	"Heel" reaching eye or even, in ♂♂, nostrils	Fuhn (1960)	
"Heel" reaching at least half-way between anterior margin of eye and nostril, mostly up to nostril or near snout tip, and sometimes just beyond snout tip (♀♀), and at least near snout tip, mostly as far as or beyond snout tip (♂♂)	"Heel" reaching anterior margin of eye (♀♀), nostril or somewhat farther (♂♂)	Dely (1964a)	
"Heels" overlapping markedly, but more so in ♂♂	"Heels" touching each other (♀♀) or overlapping slightly (♂♂)	Fejérváry (1919)	"Heel" test B
"Heels" overlapping markedly, but more so in ♂♂	"Heels" touching each other (♀♀) or overlapping slightly (♂♂)	Calinescu (1931)	

"Heels" always overlapping, but more markedly in ♂♂	"Heels" never touching each other	Fuhn (1960)	"Heel" test B
"Heels" always touching each other or overlapping (♀♀), still more so in ♂♂	"Heels" not touching each other at all, sometimes, in ♂♂, slightly overlapping	Dely (1964a)	
C. int. goes into T. 8½—9½ times or more in ♀♀ and 9½—12 times in ♂♂	C. int. goes into T. 6—8½ times in ♀♀ and 8.3—8.8 times in ♂♂	Fejérváry (1919)	C. int.: T.
C. int. goes into T. 8½—9½ times or more in ♀♀ and 9½—12 times in ♂♂	C. int. goes into T. 6—8½ times in ♀♀ and 8,3—8.8 times in ♂♂	Calinescu (1931)	
T. 8.5—8.9 times as long as C. int. in ♀♀ and 9.0—12 times in ♂♂		Dely (1953)	
T. 8—13 times as long as C. int. in ♀♀ and 8.8—13.2 times in ♂♂	T. 6—8 times as long as C. int. in ♀♀ and 7—8.8 times in ♂♂	Dely (1964a)	
D_4 as long as or somewhat shorter than T.	D_4 longer or, at least, as long as T.	Funh (1960)	D_4p.: T.
D_4 as long as or somewhat shorter than T., or only little exceeding it	D_4 longer or, at least, as long as T.	Dely (1964a)	
T. generally longer than Ext. a. or at least as long as Ext. a	T shorter than Ext. a.	Fejérváry (1919)	T.: Ext. a.
T. generally longer than Ext. a.	T. shorter than Ext. a.	Calinescu (1931)	
	T. shorter than Ext. a.	Puhn (1960)	
T. generally longer than Ext. a.	T. shorter than Ext. a.	Dely (1964a)	

Table III

	Toruń			Gdańsk			Olsztyn			Total		
	♂♂	♀♀	?	♂♂	♀♀	?	♂♂	♀♀	?	♂♂	♀♀	?
R. temporaria	42	38	3	110	104	4	171	122	6	323	264	13
R. arvalis	38	36	6	29	24	3	87	65	4	154	125	13

Table IV

The Occurrence of the Outer Metatarsal Tubercle (C. ext.)

Author	*R. temporaria temporaria*	*R. arvalis arvalis*
1	2	3
Angel (1946)	+ (hardly visible or lacking)	—
Bayger (1937)	+	—
Bedriaga (1889)	rarely + (poorly developed)	—
Berger (1957)	+ (often badly seen)	—
Berger and Michałowski (1963)	+ (often badly seen)	—
Born (1883)	— (but the skin at this place, with few exceptions, stained light)	— (the skin at this place rarely stained light)
Boulenger (1910)	rarely + (rather indistinct)	—
Dely (1964a)	+ (in the form of a light spot)	+ (only in 50% of the specimens in the form of a light spot, in the remaining specimens it is lacking)
Dürigen (1897)	+ (in the form of a lightstained elevated point)	—
Fejérváry (1923)	rarely +	
Freytag (1961) 0	+	—
Frommhold (1959a) 0	+	—
Fuhn (1956) 0		—
Gadov (1958)	+ (hardly visible)	
Gaupp (1904)	+ (sometimes indistinct and marked only by a white spot on the skin)	
Iskakova (1959) 0	+	—
Klingelhöffer (1955)	+	—

Table IV (continued)

Author	*R. temporaria temporaria*	*R. arvalis arvalis*
1	2	3
Koch (1872)	+	—
	—	—
Leydig (1877)	(but the skin at this place stained light)	
	+	—
Makushok (1926)	(often missing)	
Méhely (1894)	most often + (in the form of a light spot)	—
Nikolskiĭ (1918) 0	+	—
Pflüger and Smith (1883)		+
	+	—
Schreiber (1912)	(Usually small and rather indistinct, often marked only by a light dot)	
Serra and Albuquerque (1963)	rarely + (weakly marked)	
Tarashchuk (1959)		—
Terentev and Chernov (1949) 0	+	—
	rarely +	—
de Witte (1948)	(rather indistinct)	

Symbols:

\+ — present

— — missing

0 — authors who do not mention this character in the text but show it in the drawings included in their papers.

Table V

The Occurrence of the Outer Metatarsal Tubercle (C. ext.)

	Present		Absent
	on both feet	on one foot	
R. temporaria temporaria	437 (74,5%)	65 (11,0%)	84 (14,5%)
R. arvalis arvalis	107 (39,0%)	43 (15,5%)	126 (45,5%)

Table VI (in mm)

	R. temporaria temporaria (160 specimens — Olsztyn)		
	min	M	max
$D_1p.$	3,8	(6,89) $\delta = 1,02$	10,0
C. int.	1,8	(2,80) $\delta = 0,4$	3,9
$\frac{D_1p.}{C. int.}$	1,9	(2,47) $\delta = 0,35$	3,5

Table VII (in mm)

	R. temporaria temporaria					
	♂♂ (84 specimens) (Olsztyn)			♀♀ (74 specimens) (Olsztyn)		
	min	M	max	min	M	max
$D_1p.$	3,8	(7,14) $\delta = 1,05$	10,0	4,5	(6,62) $\delta = 0,96$	9,8
C. int.	2,0	(2,90) $\delta = 0,49$	3,9	1,8	(2,67) $\delta = 0,35$	3,6
$\frac{D_1p.}{C. int.}$	1,9	(2,47) $\delta = 0,31$	3,4	2,0	(2,49) $\delta = 0,33$	3,5

Table VIII (in mm)

	R. arvalis arvalis (63 specimens — Olsztyn)		
	min	M	max
$D_1p.$	3,6	(4,58) $\delta = 0,63$	6,4
C. int.	2,1	(3,11) $\delta = 0,41$	4,0
$\frac{D_1p.}{C. int.}$	1,1	(1,48) $\delta = 0,25$	2,1

The same data in sex groups: table IX

Table IX (in mm)

	R. arvalis arvalis					
	♂♂ (33 specimens) (Olsztyn)			♀♀ (24 specimens) (Olsztyn)		
	min	M	max	min	M	max
$D_1p.$	4,0	(4,87) $\delta = 0,65$	6,4	3,6	(4,24) $\delta = 0,43$	5,0
C. int.	2,3	(3,30) $\delta = 0,43$	4,0	2,1	(2,93) $\delta = 0,31$	3,6
$\frac{D_1p.}{C. int.}$	1,1	(1,46) $\delta = 0,39$	2,1	1,1	(1,44) $\delta = 0,21$	1,7

Table X

„Heel" test A

	„Heels" up to snout tip	„Heels" up to nostrils	„Heels" up to eye	„Heels" up to drum-membrane
	1	2	3	4
R. temporaria temporaria	ANGEL (1946) (rarely) ADOLPH (1927) BAYGER (1937) BERGER and MICHAŁOWSKI (1963) (often)-exceptionally extending beyond it	BERGER and MICHAŁOWSKI (1963) (often)	ANGEL (1946)	
	BEDRIAGA * (1898/1912) (hardly reaching it)	BEDRIAGA (1898/1912)	BEDRIAGA (1898/1912) (often)	BEDRIAGA (1898/1912) (often)
	BOETTGER (1885) (hardly or not reaching at all)			
	BOULENGER (1910 (very rarely)	BOULENGER (1910) (often) DELY (1964a) (or somewhat behind	BOULENGER (1910) (often)	BOULENGER (1910) (often)
	DÜRIGEN (1897) (rarely)	DÜRIGEN (1897) (often)	DÜRIGEN (1897) (often) — up to anterior angle)	DÜRIGEN (1897) (often)
		FATIO (1872)	FATIO (1872)	
	FROMMHOLD (1959a, 1965) (at most rarely)	FROMMHOLD (1959a, 1965) (rarely)	FROMMHOLD (1959a, 1965) (mostly)	

Table X (continued)

	1	2	3	4
R. temporaria temporaria		Fuhn (1960)	Fuhn (1960)	Fuhn (1960)
	Gadov (1958)	Gadov (1958)	Gadov (1958)	
			Kiritzescu (1903)	
	Klingelhöffer (1955) (exceptionally)		Klingelhöffer (1955) (mostly)	
	Lachmann (1890) (hardly reaching)			
			Lenz (1878) (or somewhat above)	
	Makushok (1926) (nearly reaching)			
		Méhely (1894)		
	Mertens (1960) (rarely)	Mertens (1960) (rarely)	Mertens (1960) (mostly)	
	Nikolskii (1918) (often) (nearly reaching)	Nikolskii (1918) (often)	Nikolskii (1918) (often) — up to eye centre)	
	Schreiber (1912) (exceptionally)	Schreiber (1912) (exceptionally)	Schreiber (1912) (often)	Schreiber (1912) (often)
	Serra and Albuquerque (1963) (rarely) — nearly reaching	Serra and Albuquerque (1963)		Serra and Albuquerque (1963)
				Štěpánek (1949) (rarely above)
	Sternfeld (1952) (not reaching)			
	Tarashchuk (1959) (rarely) — exceptionally extending beyond it)	Tarashchuk (1959) (mostly)		
	de Witte (1948) (rarely)	de Witte (1948)	de Witte (1948)	de Witte (1948)
	Wolterstorff (1921) (very rarely)		Wolterstorff (1921) (often)	Wolterstorff (1921) (often)
R. arvalis arvalis	Angel (1946) (rarely)	Angel (1946)	Angel (1946)	
	Bayger (1937) (rarely)	Bayger (1937) (often)	Bayger (1937) (often)	
		Bedriaga (1898/1912)	Bedriaga (1898/1912)	
		Berger and Michałowski (1963) (rarely)	Berger and Michałowski (1963) (often)	

* Only the characters of the typical form have been included. Bedriaga describes also var. asiatica, recently separated as *Rana chensinensis* David.

Table X (continued)

	1	2	3	4
R. arvalis arvalis	Boettger (1885) Boulenger (1910) (rarely)	Boulenger (1910) (often) Calinescu (1931) Dely (1964a) (or somewhat in front)	Boulenger (1910) (often) Calinescu (1931) Dely (1964a) (nearly reaching anterior margin of eye)	
	Dürigen (1897) (or nearer)			
		Fatio (1872) Fejérváry (1919)	Fatio (1872) Fejérváry (1919)	
	Frommhold (1959a) (rarely)	Frommhold (1959a) (often) Fuhn (1960)	Frommhold (1959a) (often) Fuhn (1960)	
	Klingelhöffer (1955) (or nearer) Lachmann (1890)			
		Lenz (1878) (at most)		
	Méhely (1894) * (sometimes somewhat it front)	Méhely (1894) (above)		
		Mertens (1960)	Mertens (1960) Nikolskii (1918) (up to centre or posterior margin of eye)	
	Schreiber ** (1912) (exceptionally) Sternfeld (1952) (or extending beyond it)	Schreiber (1912) (often)	Schreiber (1912) (often)	
	Tarashchuk (1959) (rarely)	Tarashchuk (1959) (rarely)	Tarashchuk (1959) (mostly)	
	de Witte (1948) (rarely)	de Witte (1948)	de Witte (1948)	

*, ** Describing the typical form the authors probably took into account specimens belonging to *Rana arvalis wolterstorffi*, now treated as a separate subspecies.

Table XI

	„Heels" up to snout	„Heels" up to nostrils	„Heels" up to eye
R. temporaria temporaria (494 specim.)	143 (29%)	268 (54%)	83 (17%)
R. arvalis arvalis (131 specimens)	7 (5,5%)	80 (61%)	44 (33,5%)

Table XII

„Heel" test B

	„Heels" overlap	„Heels" touch each other	„Heels" clear of each other
R. temporaria temporaria	BERGER and MICHAŁOWSKI (1963) (generally) FUHN (1960) SCHREIBER (1912) TARASHCHUK (1959) TERENTEV and CHERNOV (1949) DE WITTE (1948)	BERGER and MICHAŁOWSKI (1963) (rarely) FATIO (1872) TERENTEV and CHERNOV (1949) DE WITTE (1948)	
R. arvalis arvalis	CALINESCU (1931) (hardly) FEJÉRVÁRY (1919) (slightly) SCHREIBER (1912) DE WITTE (1948)	BERGER and MICHAŁOWSKI (1963) (most often) CALINESCU (1931) FATIO (1872) FEJÉRVÁRY (1919) TARASHCHUK (1959) TERENTEV and CHERNOV (1949)	DELY (1964a) FUHN (1960)

Table XIII

	„Heels" overlap	„Heels" touch each other	„Heels" clear of each other
R. temporaria temporaria (152 specimens)	62 (41%)	86 (56,5%)	4 (2,5%)
R. arvalis arvalis (34 specimens)	—	23 (67,5%)	11 (32,5%)

The same data in sex groups:

	„Heels" overlap		„Heels" touch each other		„Heels" clear of each other	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
R. temporaria temporaria (150 specimens)	43 (29%)	19 (13%)	44 (29,4%)	40 (26,5%)	—	4 (2,5%)
R. arvalis arvalis (31 specimens)	—	—	14 (45%)	8 (25,5%)	3 (10%)	6 (19,5%)

Table XIV

Ratio of Width of Upper Eyelid to Interorbital Space (Lt. p.: Sp. p.)

Author	*R. temporaria temporaria*	*R. arvalis arvalis*	
1	2	3	4
Bedriaga (1898/1912)	+ (often)		Lt. p. < Sp. p.
Nikolskii (1918)	+ (often) (slightly)		
Udziela (1910)	+ (often)		
Wałecki (1882)	+		
Werner (1929)	+ (often)		
Adolph (1927)	+		Lt. p. = Sp. p.
Angel (1946)	+		
Bedriaga (1898/1912)	+		
Boulenger (1910)	+ (often)		
Calinescu (1931)	+		
Dürigen (1897)	+		
Fuhn (1960)	+		
Makushok (1926)	+ (relatively nearly equal)		
Nikolskii (1918)	+ (often)		
Schreiber (1912)	+		
Serra and Albuquerque (1963)	+		
Udziela (1910)	+ (often)		
Wałecki (1882)	+	+	
Werner (1929)	+ (often)		
de Witte (1948)	+ (often)		
Adolph (1927)	+	+	Lt. p. > Sp. p.
Angel (1946)	+ (somewhat wider)		
Bedriaga (1889, 1889/1912)	+ (rarely — 1889)	— (only sometimes twice as long as interorbital space)	
Boulenger (1898, 1910)	+ (often) (somewhat wider — 1898 and 1910 — and only sometimes as 3 : 2 — 1898)	+ ($1\frac{1}{2}$— 2 times as large as interorbital space — 1898)	
Calinescu (1931)		+	
Dürigen (1897)		+	
Fuhn (1960)	+ (a little wider)	+ ($1\frac{1}{2}$ — 2 lenghts of interorbital space)	
Koch (1872)		+	
Makushok (1926)		+	
Méhely (1894)		+ (about twice as great)	

Table XIV (continued)

1	2	3	4
Schreiber (1912)	+ (rarely)	+	Lt. p > Sp. p.
Serra and Albuquerque (1963)	+ (somewhat wider)		
Udziela (1910)		+	
Wěrner (1929)		+	
de Witte (1948)	+ (often) (somewhat wider)	+ ($1\frac{1}{2}$ — 2 lenghts of interorbital space)	

Table XV

	R. temporaria (82 specimens — Olsztyn)			
	min	M	δ	max
Lt. p.	3,6	(4,5)	0,5	6,0
Sp. p.	3,0	(4,3)	0,59	5,6

The same data in sex groups:

	R. temporaria							
	♂♂ (35 specimens — Olsztyn)				♀♀ (45 specimens — Olsztyn)			
	min	M	δ	max	min	M	δ	max
Lt. p.	3,7	(4,5)	0,52	5,5	3,7	(4,6)	0,52	6,0
Sp. p.	3,3	(4,4)	0,70	5,5	3,0	(4,2)	0,54	5,6

Table XVI

	R. arvalis (61 specimens — Olsztyn)			
	min	M	δ	max
Lt. p.	2,5	(3,7)	0,46	4,6
Sp. p.	2,7	(3,3)	0,40	4,4

The same data in sex groups:

	R. arvalis							
	♂♂ (32 specimens — Olsztyn)				♀♀ (24 specimens — Olsztyn)			
	min	M	δ	max	min	M	δ	max
Lt. p.	3,1	(3,9)	0,43	4,6	2,5	(3,4)	0,44	4,0
Sp. p.	2,7	(3,4)	0,44	4,3	2,8	(3,2)	0,33	3,9

Table XVII

Ratio of Width of Upper Eyelid to Interorbital Space (Lt. p.: Sp. p.)

	min	M	δ	max
R. temporaria (82 specimens — Olsztyn)	0,7	(1,04)	0,17	1,4
R. arvalis (61 specimens — Olsztyn)	0,6	(1,11)	0,16	1,5

The same data in sex groups:

	♂♂				♀♀			
	min	M	δ	max	min	M	δ	max
♂♂ (35 specimens — Olsztyn) *R. temporaria* ♀♀ (45 specimens — Olsztyn)	0,7	(1,01)	0,15	1,4	0,8	(1,07)	0,16	1,4
♂♂ (32 specimens — Olsztyn) *R. arvalis* ♀♀ (24 specimens — Olsztyn)	0,9	(1,15)	0,15	1,5	0,6	(1,07)	0,19	1,4

Table XVIII

Ratio of Width of Upper Eyelid to Interorbital Space (Lt. p.: Sp. p.)

Author	*R. temporaria*	*R. arvalis*
Terentev and Chernov	0,81—1,81	0,78—1,61
Terentev	0,81—1,89	„
Tarashchuk	„	„

Table XIX

Ratio of Internasal Space to Interorbital Space (Sp. n.: Sp. p.)

Author	*R. temporaria temporaria*	*R. arvalis arvalis*	
Bedriaga (1898/1912)	+ (usually)		Sp. n. < Sp. p.
Cukierzys (1938)	+		
Schreiber (1912)	+		
Bedriaga (1899, 1898/1912)	+ (more rarely)		Sp. n. = Sp. p.
Boulenger (1910)	+		
Calinescu (1931)	+ (nearly equal)		
Fuhn (1960)	+		
Serra and Albuquerque (1963)	+		
Bedriaga (1889)		+	Sp. n. > Sp. p.
Boulenger (1910)	+ (somewhat larger)	+ (much larger)	
Calinescu (1931)		+	
Cukierzys (1938)		+	
Fuhn (1960)	+	+	
Schreiber (1912)		+	

Table XX

(Sp. n.)

	min	M	δ	max
R. temporaria (82 specimens — Olsztyn)	3,2	(4,5)	0,56	5,8
R. arvalis (59 specimens — Olsztyn)	3,1	(3,8)	0,36	4,6

The same data in sex groups:

	♂♂				♀♀			
	min	M	δ	max	min	M	δ	max
♂♂ (35 specimens — Olsztyn) *R. temporaria* ♀♀ (45 specimens — Olsztyn)	4,0	(4,6)	0,51	5,8	3,2	(4,4)	0,60	5,6
♂♂ (32 specimens — Olsztyn) *R. arvalis* ♀♀ (22 specimens — Olsztyn)	3,1	(3,9)	0,41	4,6	3,1	(3,6)	0,34	4,2

Table XXI

Ratio of Internasal Space to Interorbital Space (Sp. n.: Sp. p.)

	min	M	δ	max
R. temporaria (82 specimens — Olsztyn)	0,9	(1,05)	0,09	1,4
R. arvalis (59 specimens — Olsztyn)	1,0	(1,10)	0,16	1,5

The same data in sex groups:

	♂♂				♀♀			
	min	M	δ	max	min	M	δ	max
♂♂ (35 specimens — Olsztyn) *R. temporaria* ♀♀ (45 specimens — Olsztyn)	0,9	(1,05)	0,09	1,4	0,9	(1,05)	0,10	1,4
♂♂ (32 specimens — Olsztyn) *R. arvalis* ♀♀ (22 specimens — Olsztyn)	1,0	(1,20)	0,14	1,5	1,0	(1,10)	0,15	1,3

Table XXII

Occurrence of Light Dorsal Stripe in *R. arvalis arvalis*

Locality	Light Dorsal Stripe	
	Present	Missing
Toruń	116 (74,5%)	40 (25,5%)
Olsztyn	—	80 (100%)
Gdańsk	9 (16%)	47 (84%)

Table XXIII

Species	Single Stripe	Two Disconnected Stripes	Various Forms of Reduction and Deformation of Stripe	No Stripe
R. temporaria	103 (52,0%)	51 (25,5%)	21 (10,5%)	24 (12%)
R. arvalis	18 (35,5%)	22 (43%)	3 (6%)	8 (15,5%)

Table XXIV

Occurrence of Angular Spot in *R. temporaria*

Locality	No. of Specimens	Angular Spot	
		Present	Missing
Olsztyn	296	267	29
Toruń	83	81	2
Gdańsk	172	150	22

Table XXV

Occurrence of Angular Spot in *R. arvalis*

Locality	No. of Specimens	Angular Spot	
		Present	Missing
Olsztyn	156	39 (25%)	117 (75%)
Toruń	79	76 (96%)	3 (4%)

Table XXVI

Distance from Nostrils to Snout Tip and Eyes (D. n. r.: D. n. o.)

Author	*R. temporaria temporaria*	*R. arvalis arvalis*	
Bedriaga (1898/1912)	+ (most often)		D. n. r. = D. n. o.
Boulenger (1879)	+		
Fatio (1872)	+		
Fuhn (1960)	+	+	
Méhely (1894)	+		
Nikolskii (1918)	+	+	
Serra and Albuquerque (1963)	+		
Boulenger (1879)	+ (somewhat nearer)	+	D. n. r. > D. n. o.
Méhely (1894)	+ (somewhat nearer)	+ (somewhat nearer)	
Serra and Albuquerque (1963)	+		
Nikolskii (1918)	+		D. n. r. < D. n. o.
Fuhn (1960)		+	

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