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Studies on the Relationship of *Bombina bombina* (LINNAEUS) and *Bombina variegata* (LINNAEUS) III. Taxonomic Characters in Both Species from Laboratory and in Interspecific Hybrids

[Pp 173—202, pls XIX—XX and 2 text-figs.]

Badania nad pokrewieństwem *Bombina bombina* (LINNAEUS) i *Bombina variegata* (LINNAEUS) III. Cechy taksonomiczne obydwu gatunków pochodzących z hodowli i mieszańców międzygatunkowych

Исследования над родственностью *Bombina bombina* (LINNAEUS) и *Bombina variegata* (LINNAEUS) III. Таксономические признаки обеих видов, происходящих из разведения и межвидовых помесей

Abstract: Interspecific hybrids between *Bombina bombina* (LINNAEUS) and *Bombina variegata* (LINNAEUS) were reared under laboratory conditions. Taxonomic characters of laboratory and field specimens of the two species were subjected to a comparative analysis. A system of classification was worked out and on its basis the metamorphosed hybrids were classified. A description of the phenotype is given.

INTRODUCTION

The premature death of Jerzy MICHAŁOWSKI interrupted the actualization of his scheme of studies on the relationship between the two species of European *Bombina*. His last paper of this series, issued posthumously, includes the results of researches on the taxonomic characters of the tadpoles of *Bombina bombina*

and *Bombina variegata* as well as the tadpoles obtained by crossing these species under laboratory conditions (MICHAŁOWSKI, 1966).

The present paper is an elaboration of materials left by the late author. They concern metamorphosed forms of F1 hybrids. The materials were secured and next delivered to the co-author of this paper by Prof. Ryszard WRÓBLEWSKI, Head of the Department of General Biology, Silesian Academy of Medicine at Zabrze-Rokitnica, for which I owe him my heartfelt thanks.

The objective of the present paper has been 1) a comparative analysis of the most important taxonomic characters of the two species of *Bombina* obtained from laboratory rearing and those from the field and 2) a description of the characters of metamorphosed F1 hybrids.

This topic is closely connected with the still unexplained problem of the genesis of the well-known variation, characteristic of *Bombina* in the region where the ranges of the two species overlap. This variation is interpreted in two ways: some authors believe it to be a result of interspecific crossing, others regard it as a micro-evolutionary phenomenon independent of crosses (STUGREN and POPOWIČ, 1961). This problem has recently become still more interesting in the light of the results of investigations on *Bombina bombina* living in complete isolation from *Bombina variegata* (MADEJ, 1967) and showing similar variation even under such conditions. In this situation the crossing of the two forms and selection of characters which will allow the distinction of the true hybrid from other atypical specimens of either species becomes indispensable for the further progress of study of these intricate genetico-evolutionary problems.

Although HERON-ROYER crossed the two species of European *Bombina* as early as 1891, it should be kept in mind that his description of the phenotype of hybrids was based on 4 young specimens, hardly 22 mm long. Moreover, at that time there were no systems of classification of *Bombina* and genetics, as a branch of science, did not exist at all. It was, therefore, difficult to give a right interpretation of hybrids. For this reason, it became necessary to repeat HERON-ROYER'S experiment.

I owe my sincere thanks to Prof. Zygmunt GRODZIŃSKI for reading the typescript and his valuable criticism.

MATERIAL AND METHOD

1. The Origin of Parental Forms

The parental material used to produce interspecific hybrids and control specimens was collected in areas which are known on the basis of the previous studies by MICHAŁOWSKI (1958) and MADEJ (1964a) to be inhabited exclusively by pure forms of one of these species. Yellow-bellied toads were taken at Biertowice (Myślenice District, 270 m.a.s.l.) and Mogilany (Kraków District,

380 m.a s.l.) and fire-bellied toads at Katowice (region of the Kościuszko Park).

Catching was done just before or at the beginning of the mating season (the end of April and beginning of May). Out of the large number of specimens caught only the most typical representatives were used for study. Experiments were made in 1961, 1962, and 1963, those in 1961, being preliminary, served to master the technique of rearing. The material used in the present study comes exclusively from the years 1962 and 1963.

2. Combinations of Parental Pairs

The following combinations of pure forms were used to obtain interspecific hybrids and control specimens:

a) *Bombina bombina* (LINNAEUS) ♀ × *Bombina bombina* (LINNAEUS) ♂
b) *Bombina bombina* (LINNAEUS) ♀ × *Bombina variegata* (LINNAEUS) ♂
c) *Bombina variegata* (LINNAEUS) ♀ × *Bombina bombina* (LINNAEUS) ♂
d) *Bombina variegata* (LINNAEUS) ♀ × *Bombina variegata* (LINNAEUS) ♂

The manner of obtainment of spawn and rearing animals was described in detail in the previous paper of MICHAŁOWSKI (1966). We should only mention here that prompt and spontaneous amplex always occurred in the „b" combination, whereas in the other cases an injection of gonadotropin became necessary. The larval development took 2 months in *B. variegata*, 3 months in *B. bombina*, and had intermediate values for hybrids. This period was followed by the metamorphosis and fairly fast growth of specimens.

Only part of the rich material obtained in this way was used for the present study, whereas the rest was left in the laboratory for further experiments, the purpose of which was to examine the fertility of hybrids, to backcross them and to investigate the influence of lighting upon the number of coloured patches on the ventral side of body in *Bombina*. Unfortunately, these last experiments were conducted during the prolonged disease of their author and next, directed by his collaborators, for more than one year after his death. The results obtained are known to the co-author of this paper in outlines, but it is hard to foresee whether it will be possible to work them out definitively, since some data, especially the methodical ones, are wanting.

The specimens for the present study were taken successively from particular rearing aquaria, when the animals had reached about 30 mm in length. Their age ranged from 13 to 25 months. After a careful scrutiny and the recording of needed data, the material was fixed in the form of skins by the method described by JUSZCZYK (1952). The quantitative results are as follows: a) *Bombina bombina* — 18 specimens, b) Hybrids I (female *B. bombina* × male *B. variegata*) — 22 specimens, c) Hybrids II (female *B. variegata* × male *B. bombina*) — 18 specimens, and d) *Bombina variegata* — 20 specimens.

CLASSIFICATION

The description of the phenotype of hybrids demands references to the typical parental forms of both the species crossed. However, as the parental forms were taken in the field and the hybrids went through individual development under laboratory conditions, one must allow for modifications induced in the course of ontogenesis by the environmental circumstances of rearing, different from those in the wild. Hence it has become necessary to carry out keen comparisons of laboratory specimens (combinations „a" and „d") with pure forms caught in the field and, basing oneself on their results, to establish distinct diagnoses of particular characters used for the classification of either form. It is only then that it will be possible to classify the hybrids according to the diagnoses made for the laboratory specimens and to compare them with the parental forms derived from the field.

1. Comparative Analysis of Taxonomic Characters in Wild and Laboratory Specimens

I. Dorsal Papillae

Various authors regard the appearance of the dorsal papillae as a taxonomic character of *Bombina*, though they assume different diagnoses of these papillae and ascribe different taxonomic values to them. MICHAŁOWSKI (1958) observed the presence of papillules disposed concentrically round the main papilla (in *B. variegata*) or their lack (in *B. bombina*) and considered them to be a primary character (marked with 3 points). MADEJ (1964a) gives a similar diagnosis, but he believes that the dorsal papillae are of lower taxonomic value and, consequently, a secondary character (2 points). STUGREN (1959) and STUGREN and POPOWIČ (1961) emphasize, above all, the conical shape of the papillae in *B. variegata* and their flatness in *B. bombina*. LÁC (1961) gives attention

Table 1

Development of Dorsal Papillae

Species	Number of Specimens	*v*	*vb*	*b*
B. bombina from the field	30	—	2%	98%
B. bombina from the laboratory	18	—	7%	93%
B. variegata from the field	30	93%	2%	5%
B. variegata from the laboratory	20	56%	44%	—

to the arrangement of the papillae as well as to their endings and roughness, which qualities, according to him, constitute a primary character (3 points). In some regions of the range of the yellow-bellied toad MADEJ (1964b, 1966) found the prevalence of specimens with intermediate papillae and some dependence of the papillae on sex in respect of their development.

a) Own material: Composed of field and laboratory specimens, the material was examined for appearance of the dorsal papillae. The comparative data obtained are presented in Table 1. The symbol „vb" denotes very poorly marked concentrical systems of papillules.

It will be seen from this table that the development of the papillae, especially in the yellow-bellied toad, is to a great extent subject to modifications dependent on environmental circumstances.

b) Conclusions: The appearance of the dorsal papillae may be assumed as a taxonomic character, formulated for field specimens in the following manner: dorsal papillae surrounded by a large number of small papillules arranged concentrically — *B. variageta*; single dorsal papillae — *B. bombina*; secondary character — 1 point *. For laboratory specimens: dorsal papillae surrounded by a large number of small papillules, which form more or less distinct concentrical systems — *B. variegata*; single dorsal papillae — *B. bombina*; primary character — 2 points.

II. Degree to Which Orange and Yellow Patches Cover the Belly

In taxonomic practice the estimation of this character, as often as not made by eye, has hitherto been rather inexact. Diagnoses were also formulated in different ways. MICHAŁOWSKI (1958), LÁC (1961) and MADEJ (1964a) observed the degree to which the belly was covered with coloured patches, assuming 50 per cent as a limit value (patches occupying less than 50% of the belly area were treated as a character of *B. bombina* and those covering 50% and more of the belly area as a character of *B. variegata*). STUGREN (1959) and STUGREN and POPOWIČ (1961) pay attention to the fact whether the patches merge into each other (*B. variegata*) or whether they are isolated and the black colour prevails (*B. bombina*).

a) Own material: In the present study the term „belly" has been defined precisely and restricted to a definite area, and, in addition, the surface area of the patches has been measured exactly (the outlines of the belly area and those of the patches were traced on a sheet of paper by means of an episcope, then cut out, weighed and their percentage value was calculated). For this reason the results obtained cannot be compared with the previous findings concerning the less precisely defined and probably larger area. Forty per cent has been assumed to be the demarcating value. Specimens with 40% of the belly

* Two grades of the taxonomic value of characters are distinguished in this study, and they are marked witch 1 or 2 points, respectively.

area or more occupied by yellow patches were numbered among the yellow-bellied toads. A similar value for laboratory specimens is 30 per cent. The results of comparisons are presented in Tables 2 and 3.

Table 2

Area Covered by Coloured Patches on the Belly

Material	n	$x \pm s$	m	v
B. bombina 20—29 mm	7	27·3 ±6·3	2·39	23·0%
B. bombina 30—29 mm	31	29·9 ±7·27	1·31	24·3%
B. bombina ♂♂ 40 mm —	32	27·0 ±9·3	1·65	34·4%
B. bombina ♀♀ 40 mm —	20	26·0 ±6·21	1·39	23·9%
B. bombina from the laboratory	18	15·2 ±4·74	1·12	31·1%
B. bombina — Katowice	6	20·6 ±5·49	2·24	26·6%
Hybrids I	22	29·7 ±3·58	0·76	12·1%
Hybrids II	18	31·6 ±4·07	0·96	12·9%
B. variegata 20—29 mm	7	62·6 ±13·4	5·08	21·4%
B. variegata ♂♂ 30—39 mm	26	60·2 ±0·93	1·72	15·0%
B. variegata ♀♀ 30—39 mm	3	50·1 ±1·64	0·48	2·9%c
B. variegata ♂♂ 40 mm —	30	59·0 ±6·37	1·16	10·8%
B. variegata ♀♀ 40 mm —	31	52·7 ±7·11	1·28	13·5%
B. variegata from the laboratory ♂♂	7	48·0 ±8·21	3·12	17·2 ±
B. variegata — Mogilany	5	48·5 ±4·62	2·06	9·5%
B. variegata — Biertowice	10	44·2 ±6·85	2·17	15·5%

Abbreviations: n — number of specimens examined; x — mean percentage area of patches; s — standard deviation; m — standard error; v — coefficient of variation.

Table 3

Coloured Patches on the Belly

Species	v	b
B. bombina from the field	10%	90%
B. bombina from the laboratory	—	100%
B. variegata from the field	97%	3%
B. variegata from the laboratory	95%	5%

It will be seen from these tables that

1. both the *Bombina* species lack ontogenetic differences in the number of coloured patches on the belly,

2. the number of coloured patches undergoes a remarkable reduction both in the yellow-bellied toad and in the fire-bellied toad under laboratory conditions,

3. sexual differences occur in the yellow-bellied toad,

4. in spite of the existence of sexual dimorphism in the yellow-bellied toad, one can distinguish the two species from each other by the number of these patches to a great, over 90 per cent, certainty, if the species-demarcating value is established fairly low (40 or 30%).

b) Conslusions: the degree to which coloured patches cover the belly may be used as a taxonomic character and, what is more, as a primary one — 2 points. It can be defined as follows: yellow patches occupy 40 (30) or more per cent of the belly area — *B. variegata*; orange and yellow patches cover less than 40 (30) per cent of the belly area — *B. bombina*.

Since in everyday practice the determination of the number of patches on the belly by the method described above would be very laborious, a series of photographs showing the skins of yellow-and fire-bellied toads, with their areas of coloured patches specified is, offered. These photographs may be used as standards for comparison and determination of approximate areas of the patches in specimens examined.

III. Breast Patches

MICHAŁOWSKI (1958) and LÁC (1961) used this character, defined as follows: On the breast there are two yellow patches connected by an arch with the yellow patches on the ventral side of the arm — *B. variegata*; on the breast there are two isolated orange patches — *B. bombina*; secondary character — 2 points. MADEJ (1964a) applied this character, similarly defined, but as primary (3 points), laying stress on the fact that only in the fire-bellied toad it is not subject to significant variation. STUGREN (1959) has not introduced this character at all.

Table 4

Breast Patches

Species	*v*	*vb*	*b*
B. bombina from the field	—	—	100%
B. bombina from the laboratory	—	—	100%
B. variegata from the field	95%	4%	1%
B. variegata from the laboratory	50%	50%	—

a) Own material: Data obtained from our material are presented in Table 4. The symbol „vb" is used for specimens in which the patches are isolated unilaterally only. Although the presence or lack of isolation of these patches refers, as a rule, both to the arm pathes and to the ventral ones, it should be emphasized that in the estimation of specimens we have taken into consideration the isolation of the breast pathes, or its lack, from the arm pathes.

Table 4 shows that this character undergoes great modifying changes in the yellow-bellied toad, which fact, however, does not prevent its application, because it is absolutely stabilized in the fire-bellied toad.

b) Conclusions: The appearance of the breast patches may be accepted as a primary taxonomic character — 2 points. The definition of this character for field specimens is as follows: breast patches connected with arm patches bilaterally — *B. variegata*; breast patches isolated from arm patches on both sides — *B. bombina*. For laboratory specimens: breast patches connected with arm patches at least unilaterally — *B. variegata*; breast patches isolated from arm patches on both sides — *B. bombina*.

IV. Patches on the Boundary of the Belly with the Thighs

Stugren (1959) does not mention these patches. Michałowski (1958) Láć (1961) and Madej (1964a) emphasize the presence of discrete inguinal patches in the fire-bellied toad and their connection with other patches in the yelow-bellied toad. However, Láć (op. cit.) and Madej (op. cit.) lay stress on the connection of these patches with or their isolation from the patches on the thigs, whereas Michałowski (1958) considers them in relation to the patches on the belly. On the other hand, Michałowski (op. cit.) and Láć (op. cit.) treat these patches as a secondary character and Madej as a primary character.

a) Own material: Preliminary observations of our own material indicate that the classification of specimens according to either alternative leads to

Table 5

Inguinal Patches

Species	*v*	*vb*	*b*
B. bombina from the field	—	1%	99%
B. bombina from the laboratory	—	—	100%
B. variegata from the field	97%	3%	—
B. variegata from the laboratory	82%	14%	4%

similar results. Nevertheless, a somewhat better criterion for distinction will be attained by using the alternative put forward by Láć (op. cit.) and Madej (op. cit). Table 5 has been made on the basis of this criterion.

b) Conclusions: The appearance of inguinal patches may by used as a primary character for distinction between the *Bombina* species — 2 points. For field specimens this character presents itself as follows: patches on the boundary of the belly and thighs (inguinal patches) connected with thigh patches bilaterally — *B. variegata*; inguinal patches isolated from thigh patches on both sides — *B. bombina*. For laboratory specimens: inguinal patches connected with thigh patches at least unilaterally — *B. variegata*; inguinal patches isolated from thigh patches on both sides — *B. bombina*.

V. Arcuate Black Patches over the Scapulae

Michałowski (1958) and Madej (1964a) found this character useful for taxonomy and described it as follows: no distinct arcuate patches between the scapulae on the back — *B. variegata*; two dark arcuate patches between the scapulae on the back — *B. bombina*. It is a third-grade character — 1 point. Stugren (1959) and Lác (1961) do not use this character in classification.

a) Own material: Results obtained are presented in Table 6. The designation „vb" indicates specimens in which a distinct arcuate patch occurs on one side of the body and on the other side is completely lacking or disrupted in the middle.

Table 6 shows that

Table 6

Dark Arcuate Patches on the Back

Species	*v*	*vb*	*b*
B. bombina from the field	18%	29%	53%
B. bombina from the laboratory	—	2%	53%
B. variegata from the field	64%	22%	14%
B. variegata from the laboratory	23%	41%	36%

1) the typical development of this character is observed in the slight majority of field specimen, whereas about a quarter of the population have the same appearance of patches in both species;

2) in laboratory specimens an evident shift towards the development of „b" — type arcuate patches can be seen in both species.

b) Conclusions: The character under discussion is not fit to be used in the classification of *Bombina*, which agrees with the opinions of Lác (1961) and Stugren (1959).

VI. White Spots on the Ventral Side of the Body

Michałowski (op. cit.) defines this character as follows: no white spots or only very few ones on the body flanks — *B. variegata*; white spots visible on the black-blue ground-colour of the ventral side and particularly numerous

on the flanks — *B. bombina*. Third-grade character — 1 point. LÁC (1961) and MADEJ (1964a) accept this character and give very similar definitions. STUGREN (1959) does not introduce it at all.

a) Our own material is summarized in Table 7, which shows that

1) this character is found in nearly all field specimens in the form described above;

Table 7

White Spots on the Venter and Flanks of Body

Species	*v*	*vb*	*b*
B. bombina from the field	—	5%	95%
B. bombina from the laboratory	—	—	100%
B. variegata from the field	96%	4%	—
B. variegata from the laboratory	95%	5%	—

2) in laboratory specimens a fairly large number of white spots occur in the yellow-bellied toad.

b) Conclusions:

1) This character may be regarded as significant in the taxonomy of *Bombina*.

2) Its definition for field specimens may be formulated as follows: lack of white spots or occurrence of only single ones on the ventral and lateral sides of the body — *B. variegata*; white spots on the venter and flanks occur in large numbers and great density — *B. bombina*. Primary character — 2 points.

3) In the case of laboratory specimens this definition runs in these words: white spots on the ventral side and on the flanks few or absent — *B. variegata*; large numbers of white spots densely disposed on the ventral side and on the flanks — *B. bombina*. Secondary character — 1 point.

VII. Colour of Belly Patches

This character has been introduced into the taxonomy of *Bombina* by STUGREN (1959), who expressed the specific differences in the following way: yellow patches on the belly — *B. variegata*; fiery-red, orange-red or orange-yellow patches on the belly — *B. bombina*. LÁC (1961) also used this character, ascribing a third-grade value to it — 1 point. He defined it as follows: coloration of the belly in all tints from yellow to orange — *B. variegata*; orange-red, orange and fiery-red colour of the patches — *B. bombina*.

a) Own material: The taxonomic value of this character has not been analysed on our own material, for though in general one must admit its occurrence, yet it cannot find any fairly wide application for practical purposes. It cannot be applied for skins or fixed specimens and thus to any kind of dead material, the advantage of which is that it allows the repetition of comparisons. Classi-

fication of *Bombina* on the basis of the coloration of patches, being less precise and more rarely used, is possible only with living specimens. But even then there are some contraindications. For example, in accordance with the actual situation and the data given by other authors, STUGREN (1959) writes about the possibility of occurrence of yellow patches also in the fire-bellied toad. Besides, the belly patches of very young specimens of the fire-bellied toad are always yellow, which also restricts the application of this character.

VIII. Patches on the Ventral Side of the Thighs

Table 8

Patches on the Ventral Side of the Thigh

Species	*v*	*vb*	*b*
B. bombina from the field	13%	41%	46%
B. bombina from the laboratory	—	39%	61%
B. variegata from the field	97%	3%	—
B. variegata from the laboratory	95%	5%	—

STUGREN (1959) directs attention to the significance of the appearance of these patches, giving the following description: patches of the ventral side of the thigh large and connected with each other — *B. variegata*; patches of the ventral side of the thigh small and isolated — *B. bombina*.

a) Own material: presented in Table 8.

This Table shows that

1) In field specimens of the yellow-bellied toad the pattern of thigh patches corresponds to the description given by STUGREN (1959). The fire-bellied toad is fairly often represented by specimens of the intermediate, „vb", type which have yellow-bellied toad type patches on one thigh and those of the fire-bellied toad type on the other.

2) In laboratory specimens of both species the situation is similar only that the patches of the yellow-belliad toad type are never observed on both thighs of the fire-bellied toad.

b) Conclusions: The appearance of thigh patches may be assumed as a taxonomic character, but it is seconary for field specimens — 1 point — and primary for laboratory animals — 2 points. Their description is as follows: patches of either thigh connected with each other — *B. variegata*; patches of at least one thigh disrupted into several smaller ones — *B. bombina*.

IX. Colour of Finger Tips

Out of the above-mentioned authors, the creators of classificatory systems, only STUGREN (1959) and, marginally, MADEJ (1964a) have dealt with this character. STUGREN (op. cit.) actually distinguishes two characters here: colour of the upper side of thumbs and the colour of toe tips. In both cases the colour

is light in the yellow-bellied toad and dark in the fire-bellied toad. MADEJ (op. cit.) considers the colour of finger tips in combination with the degree to which the belly is covered by yellow or orange patches. He gives the following description of this character: all finger tips yellow — *B. variegata*; lack of orange spots on the tips of fingers III and IV — *B. bombina*.

a) Own material: Irrespective of the colour of the tips of fingers and toes when seen from above, it can be found in both species that it is the darker, the closer to the outer side a given digit is positioned on the limb. This is usually the reason why it is impossible to establish one colour for all the digits; moreover, there is great individual variation in this respect and, finally, in genetically indubitable yellow-bellied toads living under laboratory conditions the digit tips show no yellow shades, and yet they are light. As a result, the digit tips are defined only as light or dark. The light colour includes such tints as light-grey, grey-yellow, yellowish, yellow, yellow-orange and orange, and the shades regarded as dark are dark-grey, grey, blackish and black.

Summary 1

B. bombina (field specimens) — at least fingers III and IV dark — 100%
B. bombina (laboratory specimens) — at least finger IV dark — 89%
B. variegata (field specimens) — fingers I—IV light — 100%
B. variegata (laboratory specimens) — fingers I—IV light — 100%

b) Conslusions:

1) The colour of finger tips is fit to be used as a taxonomic character: primary for field specimens — 2 points, secondary for laboratory specimens — 1 point.

2) The colour of finger tips in field specimens presents itself as follows: tips of all fingers seen from above light — *B. variegata*; tips of at least fingers III and IV seen from above dark — *B. bombina*.

3) The colour of finger tips in laboratory specimens: tips of all fingers seen from above light — *B. variegata*; at least the tip of finger IV is dark when seen from above — *B. bombina*.

X. Colour of Toe Tips

a) The discussion and description of the character on the basis of our own material as in Section IX.

Summary 2

B. bombina (field) — toes III—V dark — 100%
B. bombina (laboratory) — toes III—V dark — 94%
B. variegata (field) — toes I—V light — 97%
B. variegata (labolatory) — toes I—V light — 100%

b) Conclusions: The colour of toe tips may be applied as a primary taxonomic character (2 points) for both field and laboratory specimens. The description is also the same for both these groups of material: all toe tips seen from above light — *B. variegata*; tips of at least toes III, IV and V dark when seen from above — *B. bombina*.

XI. Connection of Tarsal and Plantar Patches

STUGREN (1959) treats the occurrence or lack of connections between the tarsal and plantar patches as a taxonomic character, which he defines as follows: tarsal and plantar patches connected bilaterally — *B. variegata*; tarsal and plantar patches isolated bilaterally — *B. bombina*.

a) Own material: The results of examination of this character are given in Table 9. The designation „vb" indicates the state where the patches of one leg are connected and those of the other leg separated. It will be seen from the Table that

Table 9

Tarsal and Plantar Patches

Species	*v*	*vb*	*b*
B. bombina from the field	—	12%	88%
B. bombina from the laboratory	—	—	100%
B. variegata from the field	60%	29%	11%
B. variegata from the laboratory	—	53%	47%

1) a high proportion of field specimens have this character developed intermediately (vb);

2) the proportion of specimens with isolated — even bilaterally — patches increases remarkably among the laboratory specimens of the yellow-bellied toad and none of them has connected patches on both legs (v).

b) Conclusions: The taxonomic value of the character under discussion is not very high. It may be used only for the determination of field specimens and even then as a secondary character — 1 point. Its description goes as follows: yellow patches of the tarsal and plantar portions of the hind limb connected at least on one leg — *B. variegata*; orange patches of the tarsal and plantar portions of the hind limb isolated on both legs — *B. bombina*.

XII. Colour of the Black

This character has been adopted as a taxonomic one only by STUGREN (1959), according to whom the ground colour of the back of the yellow-bellied toad resembles that of clay or earth and in the fire-bellied toad is black. MADEJ (1964a) raised reservations as to the taxonomic value of this character, referring to the fact found by him that the colour of the back depends to a great extent on environmental conditions. However, in view of the uniform environment in which the laboratory specimens of both species livied, the character has been reanalysed.

Table 10

Colour of the Back

Species	*v*	*vb*	*b*
B. bombina from the field	3%	23%	74%
B. bombina from the laboratory	—	—	100%
B. variegata from the field	64%	33%	3%
B. variegata from the laboratory	50%	32%	18%

Table 11

Classification Table for *Bombina* Specimens Derived from the Field

Species / Character	*Bombina variegata*	*Bombina bombina*
Primary	A. All finger tips seen from above light — 2 points	Tips of at least fingers III and IV dark when seen from above — no points
	B. All toe tips seen from above light 2 points	Tips of at least toes III, IV and V dark when seen from above — no points
	C. Breast patches connected with arm patches on both sides — 2 points	Breast patches isolated from arm patches on both sides — no points
	D. Yellow patches cover 40 and more per cent of the belly area — 2 points	Orange patches cover less than 40 per cent of the belly area — no points
	E. Want of white spots on the venter and flanks of body or, if present, they are single — 2 points	White spots present in large numbers on the venter and flanks of body — no points
	F. Yellow patches (inguinal) on the boundary of the belly with the thighs connected with thigh patches on both sides — 2 points	Orange patches on the boundary of the belly with the thighs isolated from thigh patches on both sides — no points
Secondary	G. Dorsal papillae surrounded by numerous, concentrically arranged papillules — 1 point	Dorsal papillae single — no points
	H. On both thighs yellow patches connected with each other — 1 point	Orange patches of at least one thigh disrupted into several smaller ones — no points
	I. Yellow tarsal and plantar patches connected with each other on at least one hind-limb — 1 point	Orange tarsal and plantar patches isolated from each other on both hind-limbs — no points

a) Own material: Application of the colour of the back as a taxonomic criterion seems to be very difficult in the case of fixed specimens and not quite truthful for skins, whose colour undergoes modifications after the animal has been killed and its skin dried. Some differences can, however, be observed. Therefore, one specimen of either species was chosen such as to correspond in its colour of the back to the description given by STUGREN (1959) and these specimens were regarded as standards. The coloration that was intermediate in relation to these specimens was marked with the symbol „vb". The results are presented in Table 10, which shows that

Table 12

Classification Table for *Bombina* Specimens Derived from the Laboratory

Character \ Specimens	*Bombina variegata*	*Bombina bombina*
Primary	A. Dorsal papillae surrounded by numerous small papillules which form more or less distinctly marked concentrical systems — 2 points	Dorsal papillae single — no points
	B. All toe tips seen from above light — 2 points	Tips of at leats toes III, IV and V dark when seen from above — no points
	C. Yellow breast patches connected with arm patches at least on one side — 2 points	Orange breast patches isolated from arm patches on both sides — no points
	D. Yellow patches occupy 30 or more per cent of the belly area — 2 points	Orange patches occupy less than 30 per cent of the belly area — no points
	E. Yellow (inguinal) patches on the boundary between the belly and the thighs connected with thigh patches at least on one side — 2 points	Orange patches on the boundary between the belly and thighs isolated from thigh patches on both sides — no points
	F. Thigh patches connected with each other on either side — 2 points	Thigh patches divided into several smaller ones at least on one thigh — no points
Secondary	G. Back in light or brown shades — 1 point	Back in black shades — no points
	H. All finger tips seen from above light — 1 point	At least the tip of finger IV dark when seen from above — no points
	I. White spots on the venter and flanks of body not numerous or absent — 1 point	White spots on the venter and flanks of body numerous — no points

1) the „vb" group, and so that of specimens which cannot be classidied on the basis of this character, is fairly numerous among the specimens of both species, especially the field ones;

2) in laboratory specimens of both species the back is evidently darker (a higher proportion of specimens with a dark back).

b) Conclusions: The character „colour of the back" may be applied exclusively for laboratory specimens and even then as a secondary character — 1 point. The species are distinguished like this: back in light or brown shades — *B. variegata*; back in dark or black shades — *B. bombina*.

A summary of the analysis of the taxonomic characters presented above is shown in Tables 11 and 12. It can be seen from these tables that the maximum number of points that a specimen can receive comes to 15, the minimum to 0. Specimens with 8—15 points, therefore, belong to *Bombina variegata* and those with 0—7 points to *Bombina bombina*.

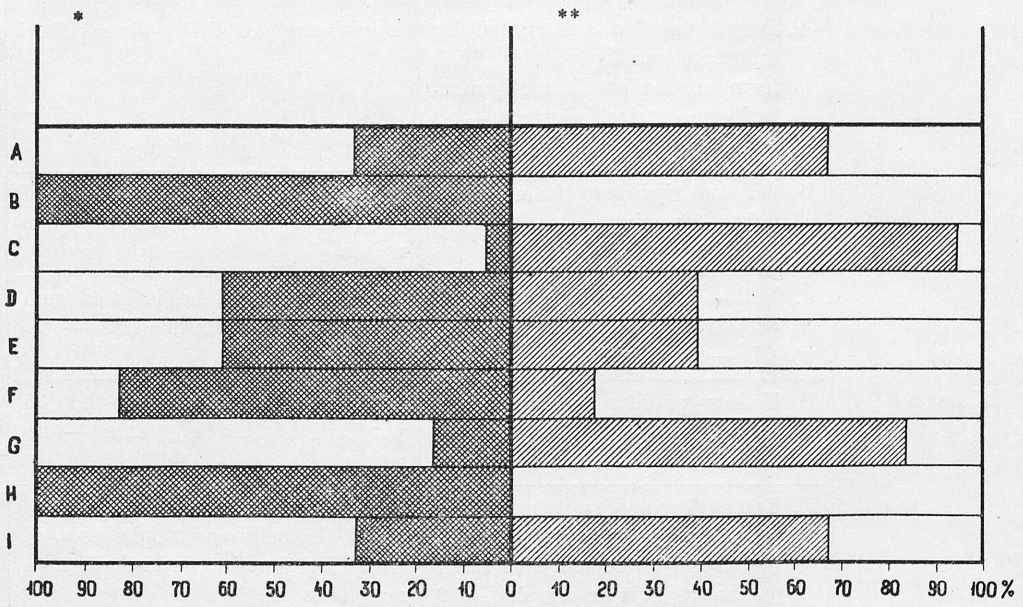

Fig. 1. Freguency of Particular Characters in Hybrids I
* Characters developed as in *Bombina variegata*
** Characters developed as in *Bombina bombina*

2. Results of Classification of Hybrids

The classification of hybrids was performed on the basis of Table 12, and its results are presented in Tables 13 and 14. The symbols A — I correspond with those in Table 12. The data from Tables 13 and 14 were used to construct

Table 13

A Survey of the Results from Classification for Hybrids I (*B. variegata* ♀ × *Bombina bombina* ♂)

Nr	A	B	C	D	E	F	G	H	I	Total	Sex
1	0	2	0	2	2	0	0	1	0	7	♂
2	2	2	0	2	0	1	0	1	0	8	♀
3	0	2	2	2	2	2	1	1	0	12	♀
4	2	2	0	0	0	2	0	1	1	8	♀
5	0	2	0	2	0	2	0	1	0	7	♂
6	2	2	0	0	0	2	0	1	0	7	♂
7	0	2	0	0	2	2	0	1	0	7	♀
8	0	2	0	0	2	2	0	1	0	7	♂
9	2	2	0	0	0	1	0	1	1	7	♀
10	2	2	0	0	2	2	0	1	1	10	♂
11	0	2	0	0	2	2	0	1	1	8	♀
12	0	2	0	0	1	2	0	1	0	7	♀
13	0	2	0	2	0	2	1	1	0	8	♀
14	0	2	0	0	0	2	0	1	1	6	♀
15	0	2	0	2	2	2	1	1	0	10	♂
16	2	2	0	0	0	2	0	1	0	7	♂
17	0	2	0	2	2	2	0	1	0	9	♀
18	0	2	2	2	0	2	1	1	0	10	♀
19	2	2	0	2	2	2	0	1	1	12	♂
20	2	2	0	0	2	0	0	1	0	7	♂
21	0	2	0	0	2	2	0	1	1	8	♀
22	2	2	0	2	0	2	0	1	1	10	♂

Table 15, which illustrates the membership of the hybrids in the particular species, whereas the frequency of characters of either species in the hybrids is presented graphically in Figs. 1 and 2. Finally, in order to obtain general data on the nature of both hybrid populations, the mean sums of points of these populations were calculated and amounted in both cases to 7.8 and so they lie exactly on the boundary between the species. These data constitute a basis for the characterization of the hybrids.

Table 14

A Survey of the Results from Classification for Hybrids II (*B. bombina* ♀ × *B. variegata* ♂)

Nr	A	B	C	D	E	F	G	H	I	Total	Sex
1	0	2	0	2	2	2	0	1	1	10	♂
2	2	2	0	2	0	2	0	1	1	10	♂
3	0	2	0	0	2	1	0	1	0	6	♀
4	0	2	0	0	0	2	0	1	0	5	♂
5	0	2	2	2	2	1	0	1	1	11	♂
6	2	2	0	0	0	2	0	1	0	7	♂
7	0	2	0	2	2	2	0	1	0	9	♂
8	0	2	0	0	0	0	0	1	1	4	♂
9	2	2	0	2	2	2	0	1	1	12	♂
10	2	2	0	2	2	2	0	1	1	12	♂
11	0	2	0	0	2	1	1	1	0	7	♀
12	0	2	0	0	0	1	0	1	0	4	♂
13	0	2	0	2	0	2	1	1	0	8	♀
14	2	2	0	0	2	2	0	1	0	9	♂
15	2	2	0	2	2	2	0	1	0	11	♂
16	0	2	0	2	2	0	1	1	0	8	♀
17	0	2	0	2	2	0	0	1	0	7	♀
18	0	2	0	2	0	2	0	1	0	7	♂

PHENOTYPE OF HYBRIDS

1. General Characteristics

The two types of hybrids (MI and MII) do not, as a rule, differ from each other. The huge majority of specimens resemble one of the parental species, the number of characters of the given species being different in particular individuals. In the whole population of hybrids the specimens with predominating characters of yellow-bellied toad somewhat outnumber those in which the characters of fire-bellied toad predominate.

Table 15

Membership of Hybrids in Species

Species	Number of Points	Number of Specimens		Total	%
		M I	M II		
Bombina variegata	15	—	—	22	55
	14	—	—		
	13	—	—		
	12	2	2		
	11	—	2		
	10	4	2		
	9	1	2		
	8	5	2		
Bombina bombina	7	9	4	18	45
	6	1	1		
	5	—	1		
	4	—	2		
	3	—	—		
	2	—	—		
	1	—	—		
	0	—	—		

2. Characters of Hybrids

Hybrids of both types (MI and MII) show a coincidence in respect of 8 out of the 9 characters considered and for these characters they can be analysed all together. The only differences occur in the size of the area covered by yellow patches on the belly, in which most of the MI hybrids resemble the fire-bellied toad and, *vice versa*, most of the MII hybrids are similar to the yellow-bellied toad. The other characters present themselves as follows:

a) characters developed in all or nearly all specimens as in the yellow-bellied toad: thigh patches, colour of finger tips and that of toe tips;

b) characters developed in most specimens as in the yellow-bellied toad: mutual relation between inguinal and thigh patches;

c) characters developed in most specimens as in the fire-bellied toad: distribution and number of white spots on the venter and flanks of body, appearance of dorsal papillae, colour of the back;

d) characters developed in all or nearly all specimens as in the fire-bellied toad: appearance of breast patches.

As a result, these of the above-mentioned characters which have the same quality in all or nearly all specimens may be used as diagnostic ones. A typical hybrid of either type (MI or MII) has therefore the colour of the tips of fingers

and toes like that in the yellow-bellied toad (light), the yellow thigh patches connected at least on one thigh, and the yellow breast patches bilaterally isolated (Table 15).

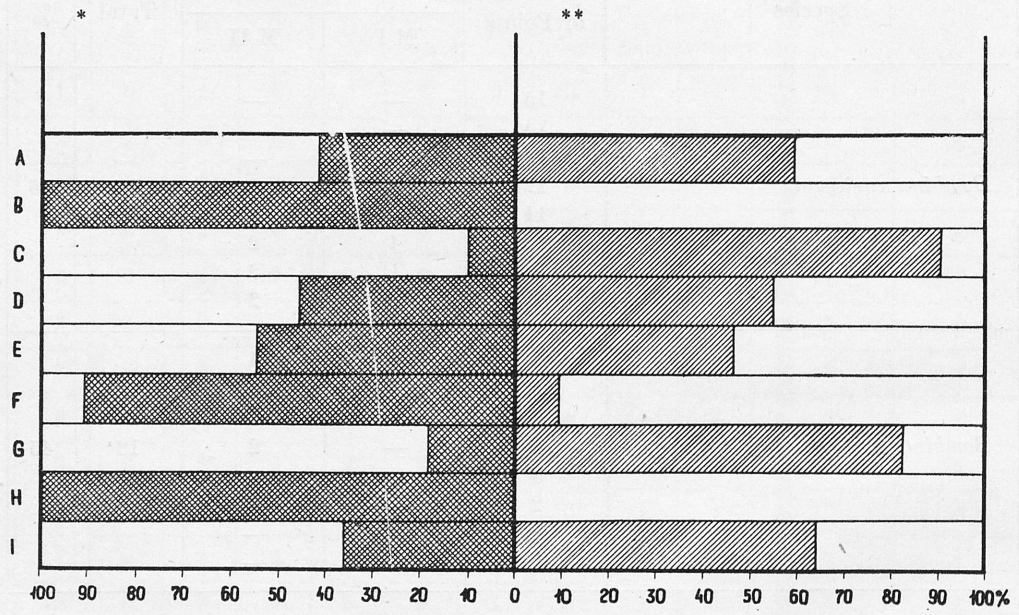

Fig. 2. Frequency of Particular Characters in Hybrids II
* Characters developed as in *Bombina variegata*
** Characters developed as in *Bombina bombina*

3. Explanation of Similarities

As has been mentioned above, specimens with characters of both *Bombina* species occur among the hybrids, though those similar to the yellow-bellied toad predominate. This evidently disagrees with the data presented by HERON-ROYER (1891) and the opinions of many other authors. In the light of the present study there is no doubt that this one-sided attribution of predominance to the characters of fire-bellied toad was due to the lack of close analysis of specimens described, whose appearance, at first sight, seems to indicate their indubitable greater similarity to the fire-bellied toad. Out of the eight characters under discussion, in respect of which the hybrids commonly show uniformity irrespective of the direction of crossing, four represent a more or less distinct predominance of the elements of *Bombina variegata* and four others the predominance of the *Bombina bombina* elements, which seemingly points to the perfect balance of these characters. It has, however, appeared that there are three obviously predominating characters of yellow-bellied toad and only one of fire-bellied toad. The yellow-bellied toad type has generally three pri-

mary characters in four hereditary ones, whereas the fire-bellied toad type has only two in five hereditary characters. On that account, though at first sight a specimen under study may more resemble *B. bombina*, a close examination with special attention given to the systematic value of the characters included does not always confirm those observations. Perfunctory analysis of the coloration of the belly and, in general, of the ventral side of the body greatly contributes to the subsistence of the wrong supposition about the absolute and regular similarity of hybrids to the fire-bellied toad. As can be seen from Table 2, in hybrids the amount of the yellow colour on the belly (arithmetic mean) is almost exactly intermediate between those in the parental species. In view of the fact that in the yellow-bellied toad the yellow patches on the belly occupy most of its area but, none the less, only slightly more than 50% of it, and in the fire-bellied toad the orange patches cover a markedly smaller area of the belly (twenty odd per cent), in a hybrid with an intermediate amount of maculation the greater part of the area of the belly will naturally be dark and void of patches. Consequently, a perfunctory analysis of the colour of the belly in such hybrids shows their similarity to the fire-bellied toad. On the other hand, inasmuch as, for instance, the colour of the belly or the presence of isolated patches on the breast readily strikes the eye, the determination of the colour of the digit tips needs a closer analysis. At the same time, it should be kept in mind that the items so important to the characterization of hybrids as the appearance of thigh patches and the colour of oligit tips were virtually left out by most authors, to receive attention, and justly, from STUGREN (1959) only.

DISCUSSION

The comparative analysis of the taxonomic characters of *Bombina* obtained both from the field and from laboratory breeding shows that each of them is subject to smaller or larger modifications induced by environmental factors. The number of coloured patches on the belly and the colour of the back belong to the characters which are modified to the same extent in both of the species. The inguinal and breast patches and the spots on the venter and flanks of the body represent the characters which more often undergo modifications in the yellow-bellied toad, whereas the patches of the ventral side of the thigh and the colour of the tips of fingers and toes are modified in an essential manner in the fire-bellied toad. Naturally, only these modifications were evaluated which change the character in the direction appropriate to the other species. A comparison of the distribution of these characters in hybrids with that in controls, however, allows the statement that their development is influenced to a mush higher degree by the hereditary factor. There are therefore no obstacles to apply the characters in question in taxonomy, though when estimating materials obtained from the field, one should allow for modifications caused

by different living conditions of the specimens examined. However, the simultaneous application of many characters in classification reduced the posibility of making errors to an insignificant minimum.

The characteristics of hybrids presented above show that they do not differ from the so-called atypical forms encountered in the zone where the ranges of these two species overlap. In this way the impediments to accept the opinion that variation of *Bombina* in this zone is due to interspecific crosses have been definitively removed. Moreover, it must be added that, though it has not been published formally, J. MICHAŁOWSKI carried out backcross experiments with positive results, which indicates the fertility of hybrids, and thus the possibility of the free passage of genes between the two *Bombina* species under favourable geographical and ecological conditions has been confirmed decidedly.

It may therefore be stated that there are no genetic isolating mechanisms between both *Bombina* species. It is, however, hard to decide whether there are any ethological and ecological mechanisms of this kind and, if so, how effective they are. At any rate, it is certain that interspecific crosses of the *Bombina* species occur in nature and that the hybrids are viable. Nevertheless, it is not known whether they are adapted better or worse than the parental forms and thus whether they undergo positive or negative selection.

A comparison of interspecific hybrid populations obtained by laboratory crossing with populations of the so-called atypical forms which occur in the zone where the ranges of both species overlap shows a difference in the frequency of particular forms, for if the hybrids obtained are classified according

Table 16

Results of Classification of Hybrids by the Method Used for the Zone of Overlap of the Ranges of Both Species

	N	*Bombina bombina*			Intermediate Form	*Bombina variegata*		
		Cl. I.	Cl. II.	Cl. III.	Cl. IV.	Cl. I.	Cl. II.	Cl. III.
M I	22	3	10	4	5	—	—	—
M II	18	3	5	4	5	—	—	1
Total	40	6	15	8	10	—	—	1
%	100	15	37·5	20·0	25·0	—	—	2·5

to the system used for classification of material from the zone of overlap of the ranges, it will appear that the characters of fire-bellied toad are decidedly predominant in the hybrids, whereas the so-called atypical forms of this zone include both the specimens that show the predominance of the characters of *B. bombina* and those with the predominant characters of *B. variegata* and, what is more, the latter specimens slightly outnumber the former ones (MICHAŁOWSKI, 1958, 1961; MADEJ, 1964a). The results of this classification are given in Table 16.

A striking thing in this table is the fact that on the basis of this classification some hybrids were numbered in Class I of *B. bombina*, which shows that so far the classificational systems are not sufficiently precise. None the less, it remains an unaltered fact that such atypical forms with the definitive predominance of the characters of *B. variegata* are much more often met with in the field than among authentic hybrids.

The causes of this state of things may be numerous. Firstly, the backcrosses in the direction of the yellow-bellied toad may be more frequent than those in the direction of the fire-bellied toad. This statement is grounded on the fact that at the time of mating pairs in different combinations spontaneous amplexus always and almost immediately takes place between male yellow-bellied toads and female fire-bellied toads and between male yellow-bellied toads and female hybrids. In all the other combinations amplexus must be stimulated by injections of gonadotropin. It may therefore be assumed that similarly at liberty male yellow-bellied toads prefer females of hybrids to those of their own species and, on the contratry, males of the fire-bellied toad, as in the laboratory, show aversion to enter into amplexus with females not belonging to their species. It is due to this very fact that the introgression of genes from *B. bombina* to *B. variegata* can be seen more frequently than that in the opposite direction.

Secondly, the more frequent introgresion of genes in the direction of *B. variegata* may also be caused by the well-known fact that the yellow-bellied toad has a stronger inclination to undertake migrations than the fire-bellied toad, the genetic effect of which may be that there are more heterozygotes in the populations of the yellow-bellied toad than in those of the fire-bellied toad, where inbreeding prevails.

Thirdly, some micro-evolutionary phenomena, discussed by STUGREN and POPOWIČ (1961), may come to be independently of crosses. This opinion has been confirmed by the results of the study on variation in the fire-bellied toad carried out in the Suwałki Lake District (MADEJ, 1967), where the possibility of interspecific crosses is excluded and yet there is variation like that in the zone of overlap of the ranges of both species.

Finally, it may result from modifications or other paragenetic phenomena about which we do not know anything at present.

As can be seen, the determination of the causes of such characteristic variation in *Bombina* appears to be much more intricate than it may have looked to be. Some further studies will be needed to draw an exact distinction between a cross and micro-evolutionary phenomena and between these last and modifications, which perhaps will eventually allow the definitive solution of the problem.

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STRESZCZENIE

W latach 1961—1966 Jerzy Michałowski przeprowadził w laboratorium międzygatunkową krzyżówkę obu europejskich gatunków kumaków *Bombina bombina* i *Bombina variegata*. Wyniki zamierzał ogłosić w kilku kolejnych publikacjach. Pierwsza z nich została opracowana przez autora (Michałowski, 1966) i dotyczyła wyników badań nad cechami taksonomicznymi kijanek obu gatunków kumaków oraz kijanek otrzymanych ze skrzyżowania z sobą tych gatunków zwierząt. Druga miała dotyczyć przeobrażonych form, znów następne miały być poświęcone płodności mieszańców i krzyżówkom wstecznym. Niestety, długa choroba zakończona śmiercią uniemożliwiła mu kontynuację tych prac. Ponieważ jednak jeszcze w początkach choroby zdążył on skompletować materiał do drugiej publikacji, przeto stało się możliwe jego opracowanie przez współautora.

Tak więc celem niniejszej publikacji jest: (1) analiza porównawcza cech taksonomicznych obu gatunków kumaków pochodzących z hodowli i z terenu, oraz (2) opis cech przeobrażonych mieszańców pokolenia F1.

Pozostaje to w ścisłym związku z nie wyjaśnionym dotąd problemem przyczyn charakterystycznej zmienności kumaków w strefie nakrywania się zasięgów obu gatunków. Zmienność ta interpretowana jest dwojako: jedni uważają ją za rezultat krzyżówek międzygatunkowych, inni jako zjawisko mikroewolucyjne, niezależne od krzyżówek. W tej sytuacji przeprowadzenie krzyżówki w laboratorium i uchwycenie cech pozwalających odróżnić autentycznego mieszańca od innych nietypowych osobników każdego gatunku było rzeczą nieodzowną dla postępu dalszych badań tych zawiłych problemów genetyczno-ewolucyjnych.

Materiał rodzicielski użyty do krzyżówek pochodził z terenów, o których wiedziano, że występują tam wyłącznie formy typowe. Tak więc kumak górski został odłowiony w Biertowicach, powiat myślenicki i Mogilanach, powiat krakowski, kumak nizinny w Katowicach.

Dla otrzymania mieszańców międzygatunkowych i okazów kontrolnych użyto następujących kombinacji par rodzicielskich:

a) *Bombina bombina* (L) ♀ × *Bombina bombina* (L) ♂
b) *Bombina bombina* (L) ♀ × *Bombina variegata* (L) ♂
c) *Bombina variegata* (L) ♀ × *Bombina bombina* (L) ♂
d) *Bombina variegata* (L) ♀ × *Bombina variegata* (L) ♂

Do ampleksu, w razie potrzeby, zmuszano okazy rodzicielskie zastrzykami gonadotropiny. W rezultacie otrzymano bogaty materiał skrzeku, kijanek, a następnie form przeobrażonych. Do niniejszej pracy odławiano okazy po osiągnięciu przez nie około 30 mm długości ciała. Liczbowo przedstawiały się następująco: a) *B. bombina* — 18 okazów, b) Mieszańce I (*B. b.* ♀ × *B. v.* ♂) — 22 okazy, c) Mieszańce II (*B. v.* ♀ × *B. b.* ♂) — 18 okazów, d) *B. variegata* — 20 okazów.

Opis fenotypu mieszańców wymagał odniesienia do typowych form rodzicielskich obu krzyżowanych z sobą gatunków. Ponieważ jednak te ostatnie pochodziły z terenu, zaś mieszańce przeszły rozwój osobniczy w warunkach laboratoryjnych, przeto trzeba było się liczyć z modyfikacjami wywołanymi wpływem odmiennych warunków środowiska hodowlanego. Dlatego konieczne było dokonanie wnikliwej analizy okazów hodowlanych (kombinacja „a" i „d") z formami odłowionymi w terenie i na tej podstawie ustalenie odrębnych diagnoz poszczególnych cech u jednych i drugich. Wyniki tej analizy przedstawiają tabele 11 i 12. W oparciu o tabelę 12, zawierającą diagnozy dla okazów hodowlanych, dokonano klasyfikacji mieszańców.

Rezultaty przedstawiają się następująco: 1) obydwa typy mieszańców (MI i MII) nie różnią się zasadniczo między sobą, 2) ogromna większość upodabnia się do jednego z gatunków rodzicielskich, przy czym nieco więcej jest osobników o przewadze cech kumaka górskiego, 3) typowy mieszaniec posiada kolor palców przednich i tylnych łap taki jak kumak górski (jasny), połączone

przynajmniej na jednym udzie żółte plamy udowe w jedną całość, oraz żółte plamy piersiowe obustronnie izolowane od plam ramienia (vide ilustr. Tabl. XIX, XX).

Mieszańce na pierwszy rzut oka zdecydowanie wydają się być podobne do kumaka nizinnego. Jednakże dokładna analiza poszczególnych cech nie potwierdza takiego mniemania. Okazuje się bowiem, że wyraźnie dominujących cech kumaka górskiego jest trzy, a nizinnego tylko jedna. Ponadto na powstanie błędnego mniemania o podobieństwie mieszańców do kumaka nizinnego ma duży wpływ powierzchowna ocena ubarwienia brzucha. Jak wykazują dane tabeli 2, ilość barwy żółtej na brzuchu jest u mieszańców dokładnie pośrednia w stosunku do gatunków rodzicielskich i wynosi około 30 procent, co skłania do zaliczenia ich do kumaka nizinnego.

Wykazano również, że każda z cech taksonomicznych kumaków podlega w mniejszym lub większym stopniu modyfikacjom wywołanym czynnikami środowiska, chociaż w niejednakowym stopniu u obu gatunków. Niemniej jednak zdecydowanie przeważający wpływ na ich ukształtowanie się ma czynnik dziedziczny i dlatego nie ma przeszkód w stosowaniu ich w taksonomii, pod warunkiem jednakże stosowania jednocześnie wielu cech.

Uzyskane wyniki pozwalają stwierdzić, że krzyżówki międzygatunkowe kumaków europejskich są możliwe i mogą zachodzić nawet spontanicznie oraz że autentyczne mieszańce nie różnią się od tzw. nietypowych form spotykanych w strefie nakrywania się zasięgów obu gatunków. Ponadto autor powołując się na znane mu a nie opublikowane dotąd pozytywne wyniki krzyżówki wstecznej podkreśla, że i mieszańce są płodne, co definitywnie potwierdza możliwość swobodnego przepływu genów między obydwoma gatunkami kumaków, jeśli tylko warunki geograficzne i ekologiczne na to pozwalają. Wszystko to zdaniem autora nie zaprzecza możliwości zachodzenia zjawisk mikroewolucyjnych, dających podobne efekty w naturze, na co istnieją oczywiste dowody.

W pracy porównano również populację otrzymanych mieszańców z populacjami tzw. nietypowych form występujących w strefach nakrywania się zasięgów obu gatunków i stwierdzono różnice w częstości występowania poszczególnych form. Mianowicie wśród tzw. nietypowych form tej strefy częściej występują okazy o przewadze cech kumaka górskiego niż to ma miejsce wśród otrzymanych mieszańców. Praca kończy się próbą interpretacji tego zjawiska i sugestiami odnośnie do dalszych badań w jego zakresie.

РЕЗЮМЕ

В 1961—1966 годах Ежи Михаловски провёл в лаборатории межвидовое скрещивание обоих европейских видов жерлянок *Bombina bombina* и *Bombina variegata*. Результаты намеревался опубликовать в нескольких очередных публикациях. Первая из них, разработанная автором (Михаловски, 1966), касалась результатов исследований над таксономическими признаками у головастиков обоих видов

жерлянок, а также головастиков, полученных путём скрещивания между собой этих видов животных. Вторая публикация должна была рассмотреть метаморфические формы; — и затем следующие были бы посвящены плодовитости гибридов и возвратным скрещиваниям. К сожалению, длительная болезнь, законченная смертью воспрепятствовала ему дальнейшее продолжение этих работ. Так как ещё в начале болезни он успел укомплектовать материал ко второй публикации, сделалась возможной его обработка соавтором.

Итак, целью настоящей публикации является: (1) сравнительный анализ таксономических признаков обоих видов жерлянок, происходящих из разведения и из полевых условий, а также (2) описание признаков гибридов из поколения F_1, прошедших метаморфоз.

Это остаётся в тесной связи с неразъяснённой до сих пор проблемой причин характеристической изменчивости жерлянок в зоне захождения друг на друга пределов распространения обоих видов. Эта изменчивость интерпретируется двояко: одни исследователи полагают, что она является результатом межвидовых скрещиваний, другие, что это микроэволюционное явление, независимое от скрещиваний. В такой обстановке, для дальнейшего прогресса исследований этих сложных генетическо-эволюционных проблем, возникла необходимость проведения лабораторного скрещивания и находки признаков, позволяющих отличать подлинный гибрид от других нетипичных особей каждого вида.

Родительский материал происходил из местности, о которой было известно, что там выступают исключительно типичные формы. Итак жёлтобрюхая жерлянка была поймана в Бертовицах, Мысленицкого уезда и в Могилянах, Краковского уезда, а краснобрюхая жерлянка — в Катовицах.

Для получения межвидовых гибридов и контрольных экземпляров употреблено следующие комбинации родителей:

а) *Bombina bombina* (L) ♀ × *Bombina bombina* (L) ♂
б) *Bombina bombina* (L) ♀ × *Bombina variegata* (L) ♂
в) *Bombina variegata* (L) ♀ × *Bombina bombina* (L) ♂
г) *Bombina variegata* (L) ♀ × *Bombina variegata* (L) ♂

К амплексу, в случае необходимости, заставляли родительские особи уколами гонадотропина. В результате получено богатый материал икры, головастиков, а затем форм, прошедших метаморфоз. К настоящей работе отлавливались жерланки, имеющие длину тела около 30 мм. Пойманный материал, выраженный в цифрах, представлялся следующим образом: а) *B. bombina* — 18 особей, б) Гибриды I (*B. b.* ♀ × *B. v.* ♂) — особи, в) Гибриды II (*B. v.* ♀ × *B. b.* ♂) — 18 особей, г) *B. variegata* — 20 особей.

Опись фенотипа гибридов требовала отнесения к типичным родительским формам обоих, скрещиваемых между собой видов. Так как эти последние взято из природных условий, а помеси прошли индивидуальное развитие в лабораторных условиях, поэтому надо было учесть модификации, вызванные влиянием иных условий среды разведения. Поэтому было необходимо проделать тщательный анализ особей, полученных из разведения (комбинация „а“ и „г“) с пойманными формами в природных условиях и на этом основании установить особые диагнозы

отдельных признаков у одних и других. Итоги этого анализа показано в 11 и 12 таблицах. Опираясь на данные 12 таблицы, содержащие диагнозы для особей, полученных из разведения, произведено классификацию гибридов.

Результаты представляются следующим образом: 1) Оба типа гибридов (M I и M II) принципиально не отличаются между собой, 2) огромное большинство уподобляется к одному из родительских видов, причём немного больше особей имеет признаки жёлтобрюхой жерлянки, 3) типичный гибрид имеет окраску концов пальцев, передних и задних ног такую же, как жёлтобрюхая жерлянка (светлая), соединены хотя бы на одном бедре жёлтые бедренные пятна в единое целое, а также грудные жёлтые пятна с обеих сторон изолированы от пятен плеча (см. иллюстрация, табл. XIX, XX).

Гибриды на первый взгляд кажутся похожими на краснобрюхую жерлянку. Однако тщательный анализ отдельных признаков не подтверждает этого мнения. Оказывается, что жёлтобрюхая жерлянка имеет три резко доминирующие признаки, а краснобрюхая жерлянка только один. Кроме того, на ошибочное мнение о подобии гибридов к краснобрюхой жерлянке имеет большое влияние поверхностная оценка окраски живота. Как видно из данных таблицы 2 количество жёлтой окраски на животе у гибридов является точно промежуточным по отношении к отцовским видам и составляет около 30%, что склоняет к зачислению их к краснобрюхим жерлянкам.

Обнаружено также, что каждый таксономический признак жерлянок подлежит в большей или в меньшей степени модификациям, вызванным факторами окружающей среды, но не в одинаковой степени у обоих видов. Тем не менее, однако, решительно преимущественное влияние на их сформирование имеет наследственный фактор и, поэтому нет препятствий в применении их в таксономии, при условии применения одновременно многих признаков.

Полученные результаты позволяют констатировать, что межвидовые скрещивания европейских жерлянок возможны и могут происходить даже самопроизвольно и что подлинные гибриды не отличаются от т. н. нетипичных форм, встречаемых в зоне захождения пределов обоих видов. Кроме того, автор, опираясь на ему известные, но не опубликованные положительные результаты возвратного скрещивания, подчёркивает, что гибриды также являются плодовитыми, что окончательно подтверждает возможность свободного перехода генов между обоими видами жерлянок, если только географические и экологические условия на это позволяют. Всё это по мнению автора не отрицает возможности возникновения микроэволюционных явлений, дающих подобные эфекты в природе, на что имеются явные доводы.

В работе сравнено также популяцию полученных гибридов из популяциями т. н. нетипичных форм, находящихся в зонах захождения пределов обоих видов, и констатировано разницы в частоте появления отдельных форм. Среди т. н. нетипичных форм этой зоны чаще появляются особи с преимущественными признаками жёлтобрюхой жерлянки, чем это имеет место среди полученных гибридов. Работа заканчивается попыткой интерпретации этого явления и предложениями относительно дальнейших исследований в его объёме.

PLATE

Plate XIX

Photographs of Skins of *Bombina*

Phot. 1. *Bombina variegata* (L.) — parental form from the field; yellow patches occupy 61% of the belly area

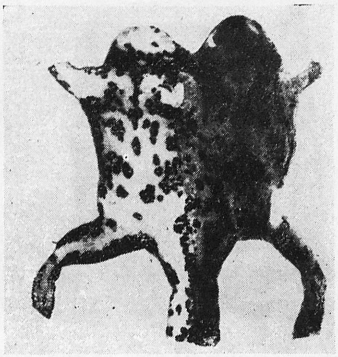
Phot. 2. Hybrid I from the laboratory; yellow patches occupy 34·0% of the belly area

Phot. 3. *Bombina variegata* (L.) — control specimen from the laboratory; yellow patches occupy 52% of the belly area

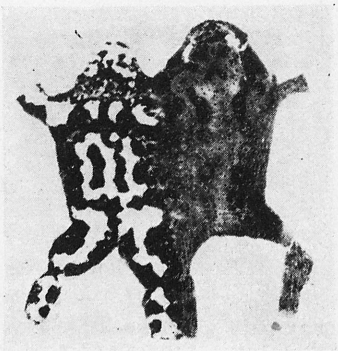
Phot. 4. *Bombina bombina* (L.) — parental form from the field; orange patches occupy 12·2% of the belly area

Phot. 5. Hybrid II from the laboratory; yellow patches occupy 26·0% of the belly area

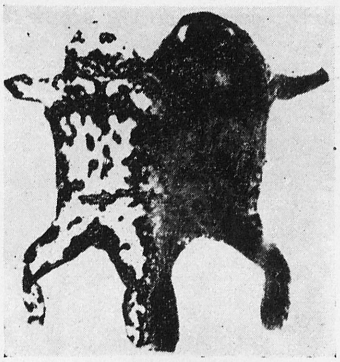
Phot. 6. *Bombina bombina* (L.) — control specimen from the laboratory; orange patches occupy 23·0% of the belly area



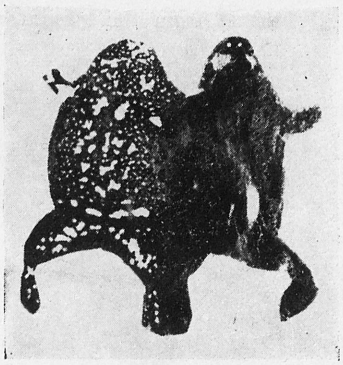
Phot. 1



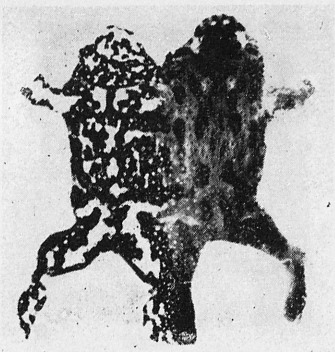
Phot. 2



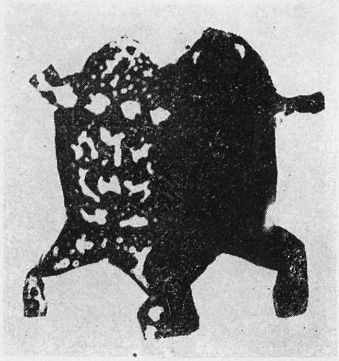
Phot. 3



Phot. 4



Phot. 5



Phot. 6

J. Michalowski, Z. Madej

Plate XX

Photographs of Skins of *Bombina*

Phot. 7. *Bombina variegata* (L.) — control specimen from the laboratory; yellow patches occupy 38·6% of the belly area

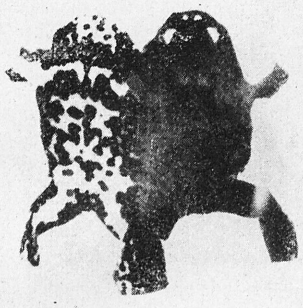
Phot. 8. Hybrid I from the laboratory; yellow patches occupy 31·6% of the belly area

Phot. 9. *Bombina bombina* (L.) — control specimen from the laboratory; orange patches occupy 10·9% of the belly area

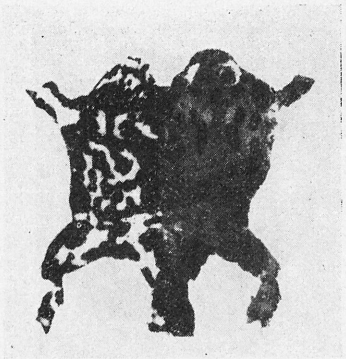
Phot. 10. Hybrid II from the laboratory; yellow patches occupy 31·6% of the belly area

Phot. 11. Hybrid II from the laboratory; yellow patches occupy 28·6% of the belly area

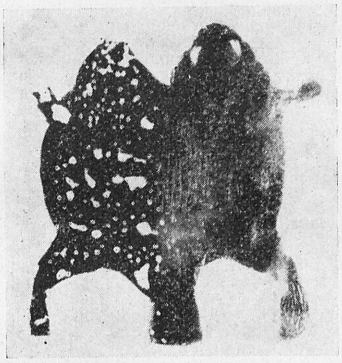
Phot. 12. Hybrid II from the laboratory; yellow patches occupy 40·1% of the belly area



Phot. 7

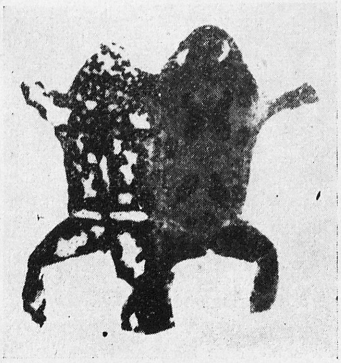


Phot. 8



Phot. 9

Phot. 10



Phot. 11

Phot. 12

J. Michałowski, Z. Madej

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