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Studies on the Fire Bellied Toad (*Bombina bombina* (LINNAEUS, 1761)) and Yellow Bellied Toad (*Bombina variegata* (LINNAEUS, 1758)) of Upper Silesia and Moravian Gate

[4 maps and 8 text-figures]

Studia nad kumakami (*Bombina bombina* (LINNAEUS, 1761) i *Bombina variegata* (LINNAEUS, 1758)) Górnego Śląska i Bramy Morawskiej

Исследования по жерлянкам (*Bombina bombina* (LINNAEUS, 1761), *Bombina variegata* (LINNAEUS, 1758)) Верхней Силезии и Моравских Ворот

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PREFACE

The field study and collection of material for the present paper were carried out in 1959—1961: in the Polish territory in 1959—1960 and in Czechoslovakia in 1960—1961. A total of over 2000 specimens were collected from 251 localities. As the material included both of the European species of *Bombina* and was sufficiently abundant, it was used not only for a physiographic study but also to analyse specific characters statistically. Thus, two parts of the paper sprang up, each on a different subject: the taxonomic part and the physiographic one. This division into two parts seems to have been necessary considering the dissimilarity of the problems dealt with as well as the fact that the reader is not always interested in both questions.

I wish to express my hearty gratitude to Prof. Z. GRODZIŃSKI, who suggested and guided the study, for his valuable information and advice, which he never spared me during my work, and for his help with arranging my journey to Czechoslovakia and obtaining a financial grant from the Polish Academy of Sciences.

During my field study in the territory of Czechoslovakia I enjoyed the hospitality and help afforded me by Dr Z. TESAR, Head of the Zoological Division of the Silesian Museum at Opava, who, among other things, put the Biological Station at Jeseník at my disposal for the period of my work in that region. Dr Z. KUX, Head of the Zoological Division of the Moravian Museum at Brno, was very helpful in working out the Moravian and Slovakian regions, rendering the whole material possessed in the Museum accessible and helping with the field work in many other ways, not to mention his hospitality. I am also indebted for aid, among others, to Mr J. LÁC of the Slovakian Academy of Sciences and Dr O. OLIVA of the Prague University.

I give my heartfelt thanks to all the naturalists mentioned above as well as to Mr H. SKRZYŃSKI, who accompanied me and assisted on my numerous excursions into the country, and to all unnamed who offered aid during my work.

Part I

TAXONOMY

1. INTRODUCTION

C. L. Bonaparte (1832) was the first to give attention to the differences among the European members of *Bombina*. The essential morphological differences between both species, *Bombina bombina* (LINNAEUS, 1761) and *Bombina variegata* (LINNAEUS, 1738), were described by G. A. BOULENGER (1898), then by E. SCHREIBER (1912), and others. Though the specific characters of Bombina have been precisely defined, the matter of their taxonomy has not been explained as yet. It is so mainly because there occur frequent forms unconformable to the classical diagnoses of the species. Such forms are met with over the area extending from the North Sea to the lower Danube, where the ranges of both the species overlap (R. MERTENS, 1928). Great variation characterizing the *Bombina* populations of this area is interesting on account of its causes; on the other hand, it presents difficulties in physiographic work of all kinds. The exact determination of specific characters and of their taxonomic value is a problem of great importance.

The opinions on the nature of variation in *Bombina* disagree: is it hereditary and then does it result from specific crosses, or is it of the nature of modifications dependent on environment (B. STUGREN and N. POPOWIC, 1961)? The question may be answered by experimenting, which no one has been doing recently. The only publication on an interspecific hybrid obtained in captivity was issued in the XIX century (HERON-ROYER, 1891) and is still waiting for confirmation. In the latest times P. V. TERENTYEV and S. H. CHERNOW (1947), J. MICHAŁOWSKI (1958, 1961), B. STUGREN (1959), and others have been working at the determination of specific characters of both species of *Bombina*. It seems that so far only J. MICHAŁOWSKI (1958) has dealt with establishing the taxonomic value of characters. The aim of this part of the paper is to analyse the characters of both species by statistical methods so as to determine their taxonomic value.

2. METHOD AND MATERIAL

a. Collection and Preparation of Material

The areas from which the material has been collected are very varied as far as both their hypsometry and the make-up of *Bombina* taken in them are concerned (see Part II—Physiography). Table 1 shows exact numerical results of collections in the particular years and months. These results, however, are not only an exponent of intensity of the field work in the given period, as they depend also on the occurence of *Bombina* in or their absence from the region

Table 1

Number and sex of *Bombina* specimens collected in particular years and months

Species	*Bombina variegata*						*Bombina bombina*					
	1959		1960		1961		1959		1960		1961	
Month	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
May	—	—	—	1	—	—	33	22	43	58	4	3
June	3	1	19	8	16	13	70	54	41	32	64	78
July	43	11	37	31	—	—	147	109	3	6	—	—
August	254	210	351	276	—	—	27	38	12	5	—	—
Total	300	222	407	316	16	13	277	223	99	101	68	81

The table does not include intermediate forms.

searched. Specimens were collected wherever they were come across, but the region was searched carefully at 3-kilometre intervals. These intervals were reduced only where the hypsometric and ecological differences or the differences in characters of *Bombina* were considerable. Collection of 10 specimens at each locality was made the rule, though, of course, it was not always possible. At particularly abundant localities in the regions where the ranges of both species of *Bombina* overlapped more specimens were taken, but the number never exceeded 20.

The animals having been put to death, the lengths of their bodies, thighs, shins, and feet, the width of eyelids, and the distance between the inner eye angles were measured by means of dividers. The coloration of the digit tips of the forelimbs and the state of the nuptial pads and vocal pouches were noted. The specimens were stripped of skin and the skins dried by the method of W. Juszczyk (1951, 1952). The specimens being stripped, their bodies were cut open to determine the sex and to note the colour of the testes in males and the stage of maturity of the ovaries in females. The dried skins were stuck on pieces of white cardboard, 14·5 cm long by 9·5 cm wide. The stamp, made for this purpose, with blank spaces for the number of locality, the number of specimen at the given locality, the time and place of collection, the nature of environment, all the other data noted previously, and after identification the specific name and class of the individual, was impressed at the side of the skin on the cardboard. The skins thus prepared were placed in separate envelopes and arranged in the form of a card-index, which made the finding and comparing of specimens from any locality very easy. The whole material has been deposited in the Institute of Systematic Zoology of the Polish Academy of Sciences in Kraków.

b. Classification of Material

The distinction of the species presents no difficulties, if the specimens come from typical localities, for the differences in appearance between the two species of *Bombina* are very characteristic and never raise doubt. This is not the case, if the specimens under study are from the so-called transition zones, where they show a considerable confusion of characters, or such characters as have not developed fully. A reliable method of classification is then necessary to identify the species and to determine the admixture of characters of the other species. The application of such a method is also important because except the morphological characters no other particulars such as type of water reservoir, the altitude and relief of terrain, or the kind of voice uttered, can be used for this purpose, since some pure populations of the fire-bellied toad were found at an altitude of 600 m. a. s. l. and those of the yellow-bellied toad in lowlands (190 m), and there was a whole population of the fire-bellied toad the males of which had not vocal pouches (Ćmok near Mysłowice).

There are many characters discriminating the two species, both in their appearance, body proportions and in their internal structure. Not all of them, however, are suitable for being used as a basis for classification, because they are difficult in mass application, e. g., the thickness of skin, or are partly or completely connected with sex, e. g., vocal pouches, horny growths on the hindlimbs of males, colour of the testes, etc. Therefore, the number of characters used for classification must necessarily be limited. The unequal value of particular characters seen clearly in atypical individuals presents another difficulty, for some characters never or very seldom occur in atypical individuals of the opposite species, while others are very often present in them. All the characters are generally well developed in all the specimens from typical localities, and so the value of characters cannot be considered on the basis of typical populations.

The large number of characters differentiating the two species and the difficulties mentioned above probably caused the fact that almost every author dealing with the European species of *Bombina* applied a different system of classification. The system of L. Horbulewicz (1927) was based on subjective estimation without using any closely measurable values, and for this reason it cannot be taken into account nowadays. P. V. Terentyev and S. A. Chernov (1947) as well as J. Michałowski (1961) suggest the application of some biometric indices. However, as my preliminary study has shown, these, too, are associated at least partly with sex. The system adopted by B. Stugren (1959) and B. Stugren and N. Popowic (1961) in their works makes it possible not only to distinguish the species but also to determine the admixture of characters of the other species in a measurable manner. The weak point of this system is that the value of characters is not differentiated and the colour of the back of the body is treated as a character equivalent to the others. It is well-known that this character varies with environment. The most purposeful and practical

Table 2

Classification of Bombina according to the external characters of coloration and the type of skin papillae

Species / Character	*Bombina variegata*	*Bombina bombina*	Conventional value of character
Category I	Two yellow patches on the breast with arcuate conexions to yellow patches on the ventral side of the arms.	Two isolated orange patches on the breast.	3 points
	Yellow patches of the abdomen connected with yellow patches on the ventral side of the thighs.	Orange patches of the abdomen without connexions to orange patches on the ventral side of the thighs. Two transverse isolated patches on the border of the abdomen with the thighs. They are continuous or broken into several smaller spots.	
Category II	Dorsal papillae surrounded by a large number of concentrically arranged tiny papillae.	Dorsal papillae single.	2 points
	Yellow patches occupy over 50% of the surface area of the ventral side of body. Tips of all digits of the hand yellow on the palmar side.	Orange patches occupy less than 50% of the surface area of the ventral side of body. No orange spots on tips of digits III and IV on the palmar side of the hand.	
Category III	Lack of distinct arcuate patches between the scapulae on the dorsum.	Two dark arcuate patches between the scapulae on the dorsum.	1 point
	White spots on the flanks of body lacking or very few.	White spots on the blackblue background of the ventral side of body, particularly numerous on the flanks.	

in application seems to be the system of J. Michałowski (1958). It is based only on essential characters and introduces the differentiation of the value of characters. For this reason, I apply it with slight modifications in the present study.

The alterations made in this system consist in ascribing different values to some characters. In addition, a new character has been introduced in it (colour of the tips of digits III and IV of the forelimb); however, it is not treated separately, only as a support of another character partly linked with it.

The frequency of the particular characters typical of one species but present in atypical individuals of the opposite species and the frequency of the particular characters in relation to sex were chosen as criteria of the value of characters. It was realized that the more rarely a character occurs in atypical individuals of the opposite species and the more loosely it is connected with sex, the greater is the value of this character. In order to determine the value of characters in this way I used the results of the classification of J. Michałowski (1958), and on this basis the characters occurring in the members of the opposite species most rarely were ascribed the highest value — 3 points, the characters occurring most often — 1 point, and those of intermediate frequency — 2 points. It must be admitted that even such estimation was not free from difficulties, for some pairs of characters appeared to have different values for either of the species: if, for instance, the isolated patches occurring on the border of the abdomen with the thighs are hardly ever present in atypical members of the yellow-bellied toad and consequently on the basis of this one character a specimen can be classified in the species *Bombina bombina*, the lack of such isolated patches is rather often met with in atypical members of this species and so it cannot be used to prove that a specimen belongs to the species *Bombina variegata*. This is also true of the other pairs of characters. At any rate, I succeeded in determining the value of at least one character of each pair in each category. Besides, estimating the value of the characters I took into consideration their usefulness, that is to say, whether they can be recognized easily, for not all of them have this quality. Dealing, for instance, with the skin papillae or with the number of yellow patches occupying the ventral side of body in atypical specimens (for which, first of all, this method has been worked out) it is sometimes hard to decide how to treat them and mistakes are possible. If their value is then established as low, the possible error will be less important. The values of characters thus determined are shown in Table 2.

As can be seen from the foregoing considerations, the alterations introduced into the adopted method of classification do not concern the very manner of classifying. Nevertheless it will be purposeful to present the principles of this method here. They are based on Table 2, which offers 6 pairs of characters and their values expressed in points. The maximum score of a skin is 12 points, the minimum 6. The skins thus appraised are divided into 4 classes:

Class I: 11—12 points. Typical form.

Class II: 9—10 points. Atypical form with small admixture of characters of the other species.

Class III: 7—8 points. Atypical form with large admixture of characters of the other species.

Class IV: 6 points. Intermediate form with equivalent characters of both species.

Although the method offered above is based on a small number of characters, which is its weak point as its author has already stated, it renders a fairly

Table 3

Numerical indices of characters of particular classes of *Bombina* and numbers of specimens examined within classes

Name of form	Numerical indices	Number of specimens		
		Total	♂	♀
Bombina variegata	3v3v 2v2v 1v1v	683	437	246
Class I	3v3v 2v2v 1b1v	328	183	145
Points: 11—12	3v3v 2v2v 1v1b	59	35	24
Bombina bombina	3b3b 2b2b 1b1b	502	257	245
Class I	3b3b 2b2b 1v1b	207	118	89
Points: 11—12	3b3b 2b2b 1b1v	40	16	24
Bombina variegata	3v3v 2v2v 1b1b	31	16	15
Class II	3v3v 2v2b 1v1v	15	6	9
Points: 9—10	3v3v 2b2v 1v1v	59	5	54
	3v3v 2v2b 1v1b	1	0	1
	3v3v 2v2b 1b1v	6	6	0
	3v3v 2b2v 1v1b	5	2	3
	3v3v 2b2v 1b1v	44	6	38
Bombina bombina	3b3b 2b2b 1v1v	16	8	8
Class II	3b3b 2b2v 1b1b	20	8	12
Points: 9—10	3b3b 2v2b 1b1b	1	1	0
	3b3b 2b2v 1b1v	7	0	7
	3b3b 2b2v 1v1b	14	9	5
	3b3b 2v2b 1v1b	1	1	0
	3b3v 2b2b 1b1b	15	7	8
Bombina variegata	3v3v 2v2b 1b1b	4	1	3
Class III	3v3v 2b2v 1b1b	6	1	5
Points: 7—8	3v3v 2b2b 1v1v	3	1	2
	3v3v 2b2b 1v1b	1	1	0
	3v3v 2b2b 1b1v	1	0	1
	3b3v 2v2v 1v1b	7	2	5
	3b3v 2v2v 1b1v	7	6	1
	3b3v 2v2v 1b1b	6	5	1
	3b3v 2v2b 1v1v	7	6	1
	3b3v 2b2v 1v1v	2	0	2
Bombina bombina	3b3b 2b2v 1v1v	2	0	2
Class III	3b3b 2v2v 1b1b	2	1	1
Points: 7—8	3b3v 2b2b 1b1v	3	3	0
	3b3v 2b2b 1v1b	8	7	1
	3b3v 2b2b 1v1v	2	1	1
	3b3v 2b2v 1b1b	9	5	4
Intermediate form from	3v3b 2b2v 1v1b	1	1	0
highland locality	3v3b 2v2b 1v1b	2	1	1
Class IV	3b3v 2v2b 1v1b	5	4	1
Points: 6	3b3v 2v2b 1b1v	4	2	2
	3b3v 2b2v 1b1v	10	6	4
Intermediate form from	3b3v 2b2v 1v1b	11	3	8
lowland locality	3v3b 2b2v 1b1v	2	1	1
Class IV				
Points: 6				

accurate and objective appraisal of skins possible. First of all, it is very convenient in use, which is not without significance in mass application.

Table 4

Dependence of variation upon species and sex

Species / Number / Class	*Bombina variegata*			*Bombina bombina*		
	Total	♂	♀	Total	♂	♀
Class I	1070	655	415	479	391	358
Class II	161	41	120	74	34	40
Class III	44	23	21	26	17	9
Total	1275	719	556	849	442	407
Class IV	35	18	17			

Table 5

General comparison of material

Species	Total number of specimens	% of total number of specimens of all forms	Number of specimens in particular classes and % of total number of specimens of given species		
			Class I	Class II	Class III
Bombina variegata	1275	60.0%	1070/84%	161/13%	44/3%
Bombina bombina	849	38.4%	749/88%	74/9%	26/3%
Intermediate form Class IV	35	1.6%			
Total	2159	100.0%			

3. RESULTS OF CLASSIFICATION

The numerical results of classification are shown in Tables 3, 4, and 5. Of these only Table 3 needs explanation. The letters b and v placed at the side of the numerical values indicate the origin of the character. The letter b points to the characters proper to *Bombina bombina* and v those proper to *Bombina variegata*. The order of figures in the horizontal rows corresponds to the order of the characters in the vertical columns for either species in Table 2. Tables 4 and 5 were made on the basis of the data from Table 3.

It will be seen from these tables that:

a. The yellow-bellied toad outnumbers the fire-bellied toad in the study area.

b. Males outnumber females in both species. They form 56 % of the total of yellow-bellied toads and 52 % of fire-bellied toads.

c. The fire-bellied toad shows a greater stability of characters (88 % specimens in Class I) than the yellow-bellied toad (84 % of specimens in Class I).

d. Out of the typical individuals (Class I) of both species, a majority (on the average 65 %) are specimens showing no essential divergencies under the classification adopted. The variation of the remaining specimens includes mainly dark arcuate patches occurring between the scapulae on the back (on the average 30 %) and, to a considerably lower degree (on the average 5 %), white spots on the ventral side and on the flanks of the body.

e. Among the atypical individuals Class II is the most numerous (averaging 11 %), Class III is remarkably less abundant (3 % in each species), while the intermediate forms (Class IV) occur occasionally (1·6 %).

f. Females of *Bombina variegata* show the greatest variability so far as the characters used for classification are concerned. The specimens of *Bombina bombina* and intermediate forms of both sexes show nearly the same degree of variability.

g. The variation of individuals of Class II concerns, first of all, the characters of the second and third categories (see Table 2). The variation of individuals of Classes III and IV includes the characters of all categories.

The detailed description of the external characters in the typical individuals of both species has been given by J. MICHAŁOWSKI (1958).

Frequency of particular characters in atypical member

Character	Species	*Bombina variegata*					
		♂		♀		Total	
		Number	%	Number	%	Number	%
Patches on breast	(v) A (b) a	19	30	10	7	29	14
Patches on border of abdomen with thighs	(v) B (b) b	0	0	0	0	0	0
Skin papillae	(v) C (b) c	16	25	105	74	121	59
Patches covering ventral side of body	(v) D (b) d	21	33	17	12	38	18.5
Dark arcuate patches on dorsum	(v) E (b) e	41	64	64	45	105	51.2
White spots on flanks and on ventral side	(v) F (b) f	28	44	33	23	61	29.7

4. STATISTIC ANALYSIS OF SPECIFIC CHARACTERS

a. Skin Coloration and Papillae

The aim of the analysis is to determine the taxonomic significance of the particular characters and to examine whether the qualification of the value of the characters carried out provisionally on the basis of the data obtained by Michałowski (op. cit.) and adopted for classification of material in the present study is correct. The criterion of the value of characters was discussed in detail in the section entitled „Classification of Material". For the practical purposes the particular characters proper to *Bombina variegata* are marked by the capital letters A, B, C, D, E, F, and the corresponding characters proper to *Bombina bombina* by the small letters a, b, c, d, e, f. Their order in Table 6 corresponds to the order in which they are arranged in Table 2. The numerical data are those of Table 3. The results obtained are presented graphically in Figs. 1 and 2.

It will be seen from Table 6 and Figs. 1 and 2 that the particular characters used as a basis for classification are not equivalent so far as taxonomy is concerned. This is apparent both in the distribution itself and in the correspondence of the distribution of characters in the particular species to the distribution of these characters in the intermediate forms. The characters a and c of the fire-bellied toad occur most rarely in atypical members of the yellow-

Table 6

of the opposite species and in intermediate forms

Bombina bombina						Intermediate form					
♂		♀		Total		♂		♀		Total	
Number	%	Number	%	Number	%	Number	%	Number	%	Number	%
0	0	0	0	0	0	3	17	2	11	5	14.3
						15	83	15	89	30	84.3
23	45	14	29	37	37	15	83	15	89	30	84.3
						3	17	2	11	5	14.2
3	6	1	2	4	4	7	39	4	23.5	11	31.0
						11	61	13	76.5	24	68.5
23	45	31	21	54	54	11	61	13	76.5	24	68.5
						7	39	4	23.5	11	31.0
26	51	17	35	43	43	9	50	10	59	19	54.0
						9	50	7	41	16	45.0
12	23	18	37	30	30	9	50	7	41	16	45.0
						9	50	10	59	19	54.0

bellied toad and consequently they have the highest taxonomic value for the fire-bellied toad, while the characters B and D have the highest value for the yellow-bellied toad. The characters Ee and Ff are equivalent for both species. However, occurring rather frequently in atypical specimens and also in the typical members of the opposite species, they have a comparatively low taxo-

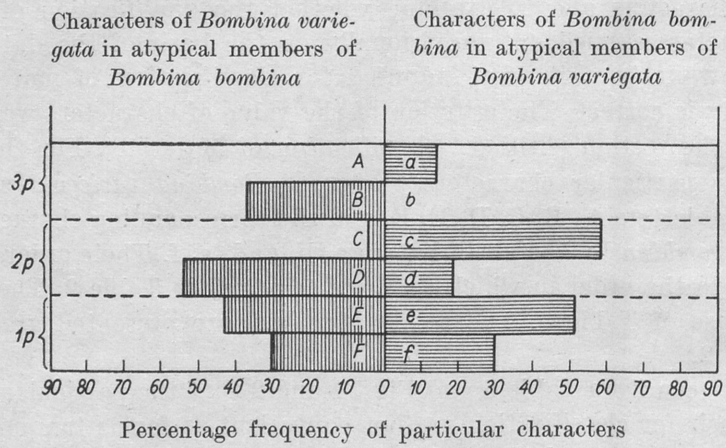

Fig. 1. Diagram showing occurrence of particular characters of *Bombina* in typical members of the opposite species

nomic value for both species. As Table 6 shows, the characters Cc and Dd display the closest correlation with sex. Thus, the warts typical of the yellow-bellied toad (C) occur in the atypical males of the fire-bellied toad three times as often as in the females and, vice versa, the warts typical of the fire-bellied

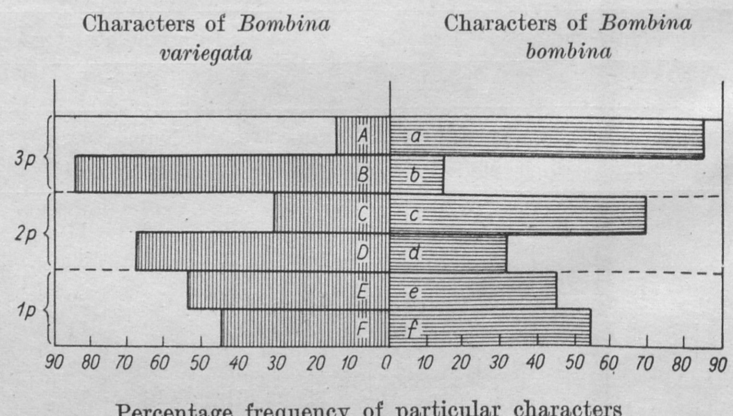

Fig. 2. Frequency of particular characters in intermediate forms

toad (c) occur in the atypical females of the yellow-bellied toad three times as often as in the males. The case is somewhat different when we deal with the number of yellow patches on the ventral side of the body. These patches, covering over 50% of the ventral surface of the body (character D distinctive of the yellow-bellied toad), occur in the atypical males of the fire-bellied toad twice as often as in the females. A smaller number of patches, occupying less than 50% of the surface area of the abdomen (character d distinctive of the fire-bellied toad), also occur nearly three times as often in the atypical males of the yellow-bellied toad. In the first case the correlation is, therefore, bilateral, in the second unilateral. In both cases, however, such a correlation of characters with sex depreciates their taxonomic value. Considering the foregoing, the discrimination of the particular characters according to their value for classification must be regarded as correct.

b. Biometric Indices: T: L, F: L, P: L

The biometric indices of *Bombina* have already been analysed many a time. There were, however, weak points in these analyses, such as the poor material the authors had at their disposal and their disregard of sexual differences, which have inclined me to take the work up once again. The abundant material available for this study makes it possible to obtain reliable results, to divide the specimens into groups according to their body length, and to treat sexes separately.

Only the material from typical localities (Cl. I) was used for study. The measurements were taken in millimetres on fresh specimens, adopting the measuring points established by P. V. Terentyev and S. A. Chernov (1947). The indices were calculated as percentages of the body length; thus expressed they are easier to compare. The results obtained have been presented not in tables but graphically as smoothed curves based on averages, thanks to which the picture gains in clarity. To check the accuracy of measurements taken on fresh material, they were made additionally on skeletons. Since these measurements were treated as control ones, they were restricted to the T : L index in the skeletons with L exceeding 39 mm. After working up the results and drawing the curves I found that the results obtained in both ways as a rule agreed with each other (Fig. 3A). Then it may be supposed that the remaining results are adequately accurate as well.

The relation of the length of the shin to that of the body (T : L) is given in Fig. 3 B, C, D. It shows that there is a difference in shin length between *Bombina bombina* and *Bombina variegata*. It is noteworthy that the T : L ratio changes when the body length reaches about 40 mm. The difference between males and females of the yellow-bellied toad is also distinctive. The graph and the arithmetic means show that the mature females of the yellow-bellied toad, exceeding 40 mm in body length (L), stand right midway between the male fire-bellied toad and the male yellow-bellied toad. The difference, being smaller in immature individuals (less than 40 mm long), must be regarded as a typical sexual character. It makes the determination of the limit value of the index impossible, and thus this index cannot be used for taxonomy of *Bombina*.

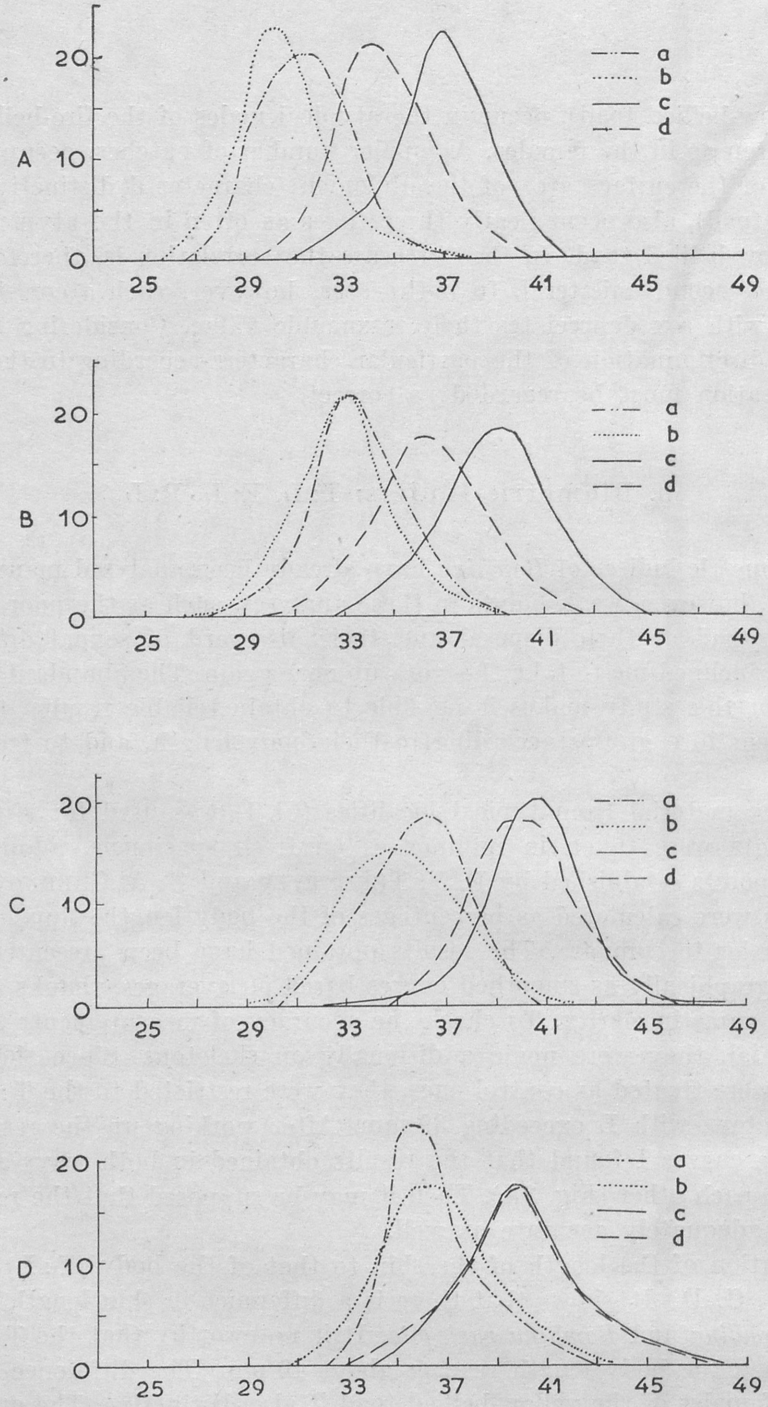

Fig. 3. Smoothed curve showing the distribution of the index T : L, calculated from the formula $\frac{T \times 100}{L}$; A — based on the measurements taken on skeletons, B, C, D — based on the measurements taken on the whole animal. A — with L over 39 mm., B — with L over 40 mm., C — with L from 30 to 39 mm., D — with L up to 29 mm. a-♂♂ *Bombina bombina*, b-♀♀ *Bombina bombina*, c-♂♂ *Bombina variegata*, d-♀♀ *Bombina variegata*. N — quantity, M — arithmetic mean, δ — standard deviation based on the formula: $\delta = \frac{1}{N} \sqrt{N\ fX^2 - (fX)^2}$

The relation of thigh length to body length (F : L) is shown in Fig. 4A, B, C. It indicates that the two species differ also in this respect, though by 30 % less than in the case of the T : L index. As the body grows the proportions change, but gradually during the whole period of growth. The sexual differences are like those in the T: L index.

Fig. 5A, B, C shows the relation of foot length to body length (P: L). The differences between males and females of *Bombina variegata* are here remarkable, but only in individuals more than 40 mm long. The fire-bellied toad takes an intermediate position between them. It may be stated that excepting sexual differences there are no interspecific differences in this respect. It is, however, interesting that in both species the P : L ratio is the highest when the body length ranges between 30 and 40 mm. It may be connected with the ways of living of these animals in this period of life. A very high standard deviation (δ) indicates that the foot length is various in particular specimens.

To find the correlation, if there is any, between body proportions and altitude, the indices T : L and F : L were calculated for adult specimens of the typical forms of the fire-bellied toad from the lowest and the highest localities. The mean altitude of the lowest localities from which the specimens were taken was 176 m a. s. l. (the valley of the upper Odra and the Danube Lowlands), that of the highest localities 490 m (the Bohemian-Moravian Highlands). Unluckily, the material at my disposal was poor, for it consisted of 47 specimens from the lowest localities and 43 from the highest. For this reason the results presented in Fig. 6A and B are to be treated only as approximate. Nevertheless, they show that there are differences between the specimens of the same species but coming from various altitudes, though they are not so distinct as the differences between the species. On the other hand, the sexual differences in the specimens from the highest localities are nearly the same as in the yellow-bellied toad.

c. Colour of Testes

It was noticed during the collection of material that there was a difference in coloration of testes between the males of *Bombina bombina* and those of *Bombina variegata*. This character does not seem to have been recorded in

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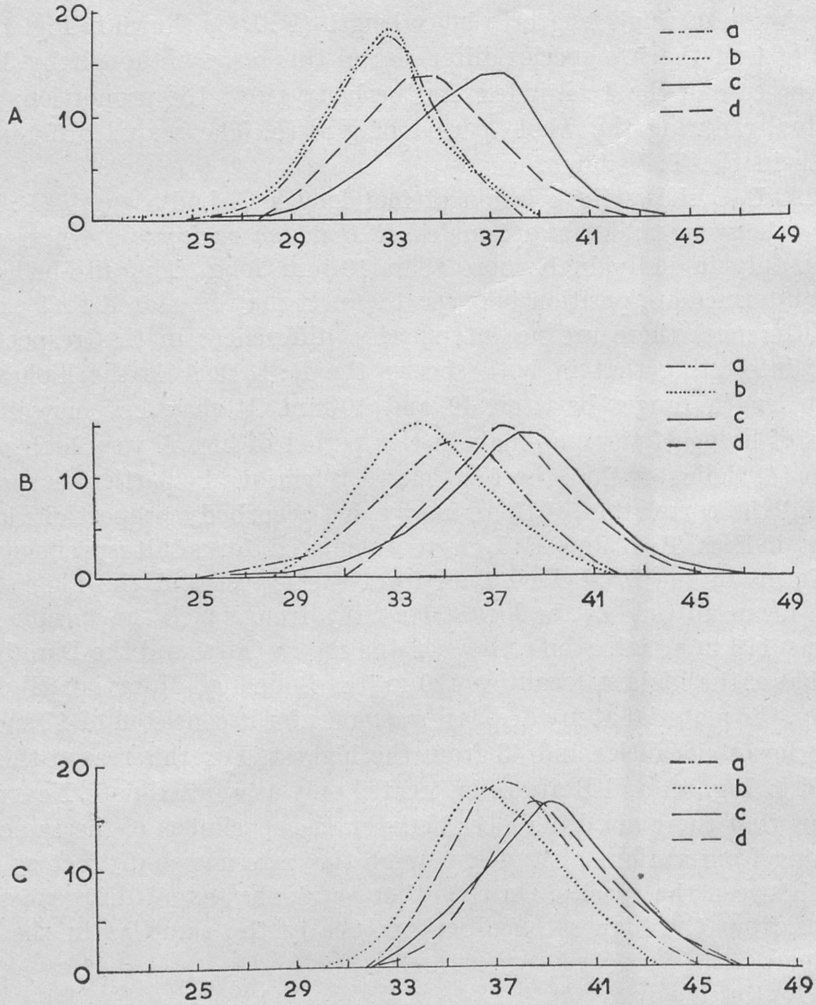
A. a —	N = 119	M = 31.45	$\delta = \pm$ 1.93		B. a —	N = 227	M = 33.50	$\delta = \pm$ 2.21
b —	N = 106	M = 30.71	$\delta = \pm$ 2.09		b —	N = 207	M = 32.90	$\delta = \pm$ 2.06
c —	N = 72	M = 36.91	$\delta = \pm$ 1.66		c —	N = 265	M = 39.14	$\delta = \pm$ 2.27
d —	N = 101	M = 34.66	$\delta = \pm$ 1.81		d —	N = 170	M = 36.27	$\delta = \pm$ 2.32
C. a —	N = 102	M = 35.72	$\delta = \pm$ 2.09		D. a —	N = 61	M = 36.71	$\delta = \pm$ 2.28
b —	N = 93	M = 35.28	$\delta = \pm$ 2.35		b —	N = 58	M = 36.89	$\delta = \pm$ 2.51
c —	N = 231	M = 40.41	$\delta = \pm$ 1.40		c —	N = 159	M = 40.44	$\delta = \pm$ 2.12
d —	N = 126	M = 40.05	$\delta = \pm$ 2.24		d —	N = 119	M = 40.01	$\delta = \pm$ 2.43



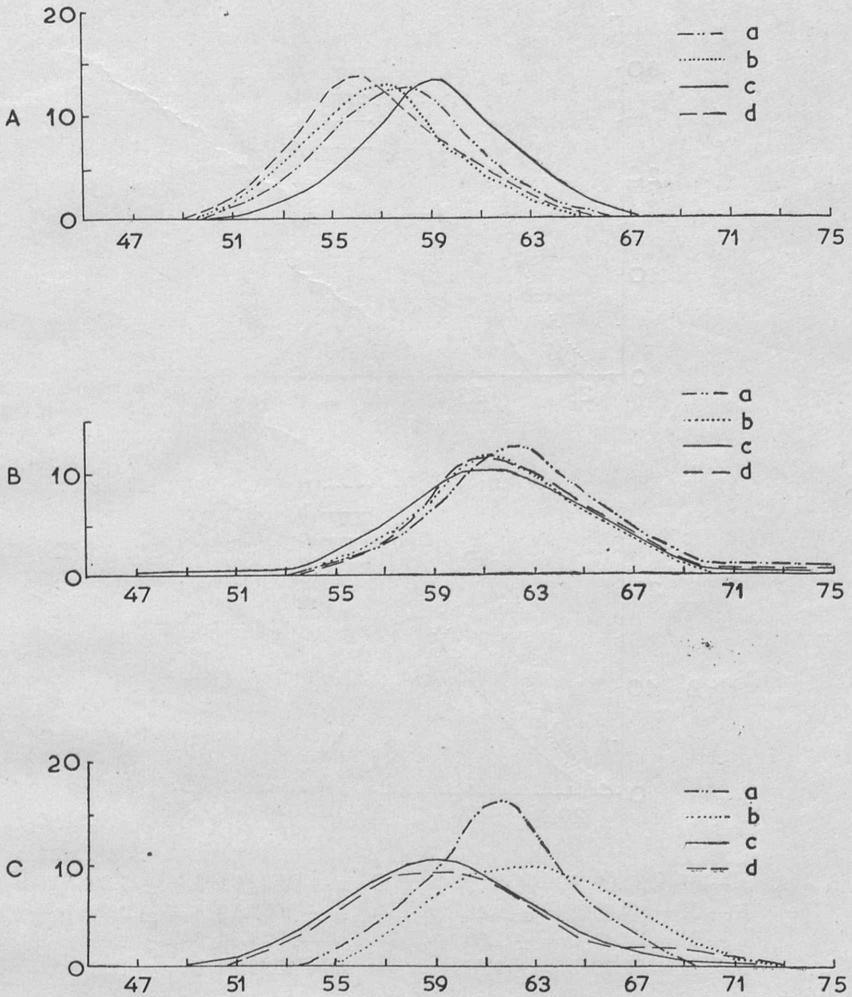
A. a — N = 227 M = 32.08 δ = ± 2.32
b — N = 207 M = 32.16 δ = ± 2.50
c — N = 265 M = 35.97 δ = ± 11.40
d — N = 170 M = 34.38 δ = ± 2.76

B. a — N = 102 M = 34.71 δ = ± 2.15
b — N = 93 M = 34.43 δ = ± 2.66
c — N = 231 M = 37.91 δ = ± 3.24
d — N = 126 M = 37.40 δ = ± 1.08

C. a — N = 61 M = 37.45 δ = ± 2.86
b — N = 58 M = 36.85 δ = ± 2.53
c — N = 159 M = 39.27 δ = ± 2.87
d — N = 119 M = 39.01 δ = ± 3.00

Fig. 4. Smoothed curve showing the distribution of the index F : L

literature hitherto. It is noteworthy that the coloration of testes does not depend on the age of specimens. Unfortunately, this phenomenon was noticed relatively late, when a half of the material had already been collected. None the less, it was observed carefully from that time forth. The results obtained are shown in Table 7.



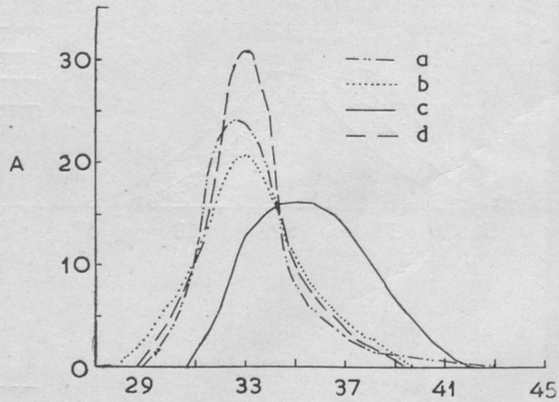
A. a — N = 227 M = 57.74 δ = ± 5.71
b — N = 207 M = 56.65 δ = ± 4.55
c — N = 265 M = 59.23 δ = ± 7.27
d — N = 170 M = 56.61 δ = ± 3.04

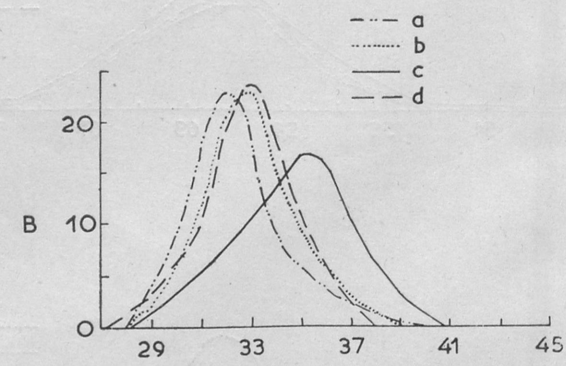
B. a — N = 102 M = 62.25 δ = ± 10.13
b — N = 93 M = 61.98 δ = ± 9.63
c — N = 231 M = 61.64 δ = ± 3.91
d — N = 126 M = 62.09 δ = ± 3.02

C. a — N = 61 M = 61.09 δ = ± 3.74
b — N = 58 M = 63.60 δ = ± 3.75
c — N = 159 M = 59.85 δ = ± 27.07
d — M = 119 M = 59.35 δ = ± 29.36

Fig. 5. Smoothed curve showing the distribution of the index P : L

Instead of symbolic designations, testes with their colour marked have been drawn in the spaces for „Colour" in the caption of Table 7. The differentiation of the testes is characteristic and permits the distinction of 6 groups among them: from both testes quite black, through one testis black and one grey, one black and one colourless, both grey, one grey and one colourless, to both colourless.





A. a — M = 33.00 $\delta = \pm 2.84$
b — M = 33.29 $\delta = \pm 2.40$
c — M = 35.47 $\delta = \pm 1.98$
d — M = 33.45 $\delta = \pm 1.67$

B. a — M 32.71 $\delta = \pm 3.20$
b — M 33.11 $\delta = \pm 2.29$
c — M 34.62 $\delta = \pm 2.46$
d — M 32.96 $\delta = \pm 1.48$

Fig. 6A. Smoothed curve showing the distribution of the index T : L in *Bombina bombina* from the highest and the lowest localities

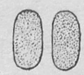
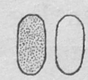
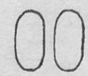
Fig. 6B. Smoothed curve showing the distribution of the index F : L in *Bombina bombina* from the highest and the lowest localities

a, b — ♂♂ ♀♀ from localities of a mean altitude of 176 m a. s. l.; c, d — ♂♂ ♀♀ from localities of a mean altitude of 490 m a. s. l.

It will be seen from Table 7 that the black coloration of testes evidently prevails in *Bombina bombina*, while the lack or a small amount of pigment in the testes is characteristic of *Bombina variegata*. The results concerning the distribution of the amounts of pigment in atypical and intermediate individuals are not significant, because the material is too scanty. At any rate, attention should be given to this phenomenon in the future, particulary so when carrying out interspecific crosses. For this reason it is worth notice in further studies on *Bombina*.

Table 7

Correlation of testis colour with species

Species	Colour / Number						
Bombina variegata Class I	382	5.7	0.4	5.2	11.0	5.9	71.8
Bombina variegata Class II	29	3.4	—	3.4	10.4	10.3	72.5
Bombina variegata Class III	7	14.3	—	—	14.3	14.3	57.1
Intermediate form Class IV	5	20.0	20.0	—	20·0	—	40.0
Bombina bombina Class III	6	16.3	—	16.7	17·0	—	50.0
Bombina bombina Class II	15	33.3	20.3	19.3	6.0	—	21.1
Bombina bombina Class I	135	57.0	7.5	15.6	6.5	3.3	10.1

d. Arriving at Sexual Maturity

The determination of the age at which *Bombina* matures sexually under natural conditions is impossible, because no age indices, such as are known for many other animals, have been found for it so far. It necessitated the use of body length for this purpose. However, even such comparison seems interesting, since the body proportions change as an individual grows, and these changes vary with sex. Thus, there is a chance to grasp a correlation between these phenomena if there is any.

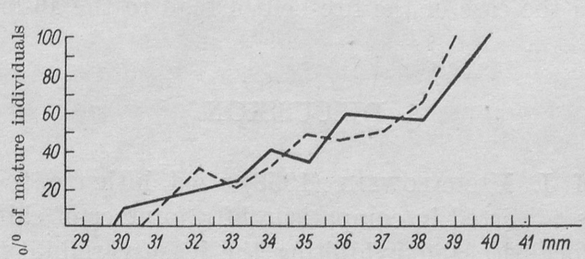


Fig. 7. Relationship between sexual maturity and body length: —— *Bombina variegata*, N=492; - - - - - *Bombina bombina*. N=326.

The maturity of specimens was determined on the basis of the ripeness of their ovaries and, in males, of nuptial pads. The use of nuptial pads for this aim is possible, as they are present in the males of *Bombina* all the time of their breeding activity, which lasts from spring to autumn. The results are offered in Fig. 7.

The graph shows that the process of maturing runs alike in both species and falls in the period of life when they reach a length of 30—40 mm. The percentage of mature individuals increases continuously but very slowly up to 38 mm. There is an obvious rise between 38 and 40 mm. Hence it may be supposed that the regularity falls within these limits of body length.

e. Body Length in Both Species

In order to establish whether there is any difference in body length between the two species of *Bombina*, the whole material of typical individuals (Class I) was tabulated according to body length at group intervals of 3 mm. Next the

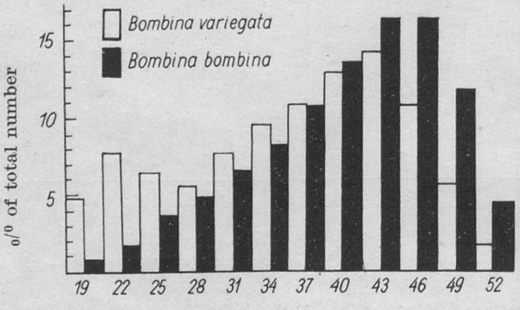


Fig. 8. Comparison of body lengths classified in groups at a group interval of 3 mm

abundance of each group was calculated in percentages and the results were used to make the histogram presented in Fig. 8. It shows that, although the maximum length of body is the same in both *Bombina* species (it amounts to 53 mm), the mean body length is greater in the fire-bellied toad. A majority of specimens of the yellow-bellied toad collected belong to the 43-millimetre group and in the case of the fire-bellied toad to the 46-millimetre group.

5. DISCUSSION

The method of J. MICHAŁOWSKI (1958) used hitherto to determine the value of characters consisted in comparison of a number of skins derived from the most typical localities and exhibiting the least variability. Then the frequency was established for each character, which undoubtedly rendered it possible to grasp the most distinctive characters of both species but little spoke of their taxonomic value, because in typical specimens all the characters are generally present and well developed. The principal difference between this method and the method adopted in the present work depends on the fact that in this work the value of characters was analysed on the material of atypical specimens and the determination of frequency of the particular characters was based not on the specimens of the species whose character was being considered but on those of the opposite species. Such an inversion is admissible, since the variation of *Bombina* for taxonomic characters, with which we are concerned here, always regards the admixture of characters of the other species. It was far easier to determine the degree of stability of the particular characters in this way and, first of all, this method made it possible to base oneself on the comparative statistical material. The rarer the occurrence of a character of a given species in the atypical individuals of the opposite species, the greater its taxonomic value. On the other hand, the character which is equally frequent in atypical specimens of both species speaks very little of the specific membership of a given individual.

A lack of differentiation in the value of characters or the incorrect definition of this value leads to serious consequences in the taxonomy of *Bombina*. The comparison of the results concerning variation obtained during the present study with the data that could be obtained by applying the values of characters as they were established hitherto — such a comparison is possible on the basis of Table 3 — will show considerable differences. They consist in changes in the classification of atypical specimens of the yellow-bellied toad in 70 cases and of the fire-bellied toad in 33 cases. Moreover, the general pattern of variation is different: the number of specimens in Class III and that of intermediate forms increase, in the latter case from 35 to 46, while the number of specimens in Class II decreases. It may be expected that the pattern of variation would be similar, if all the characters were treated uniformly, e. g., the number of intermediate individuals would increase by 50%. In general, it may be stated that the pattern of variation in the same population of *Bombina bombina* changes according to the value given to the characters. The results obtained in our case indicate a narrower range of variation than it was judged by the results of classifications carried out by other methods. However, it should be emphasized that these differences do not concern typical forms, their number being always the same irrespective of the method of classification used. It is why these differences do not undermine the main results of the physiographic studies carried out on the basis of other classifications.

The distribution of characters in both species and its accordance with the distribution of the same characters in the intermediate forms prove unequivocally, as will be seen from Figs 1 and 2, that the particular specific characters of *Bombina* differ in degree of stability. This suggests the genetic interpretation of the phenomenon. The genetic methods would provide the taxonomy of *Bombina* with solid foundations and contribute to the solution of many obscure problems.

The biometric indices T: L, F: L, and P: L were analysed in *Bombina* by P. V. Terentyev and S. H. Chernow (1949), B. Stugren (1959), J. Michałowski (1961), J. Lác (1961), and B. Stugren and N. Popowic (1961). They are also presented in an anonymous work entitled Fauna Republici Populare Romîne (1960). In this last case the number of specimens examined was not mentioned. The results obtained by all these authors and those of the present work agree in the fact that the two species of *Bombina* differ in body proportions, that is to say, the thighs and shins of the yellow-bellied toad are longer than those of the fire-bellied toad. However, the authors disagree as to the taxonomic value of these differences probably because they have not applied the classification in groups according to body length, or the group intervals used by them are not the same. Moreover, not all of them treat each sex separately. It appers that the body proportions vary with age, the changes being particularly clear in the period of sexual maturation. There are also apparent sexual differences in the yellow-bellied toad. These differences have been confirmed by the results obtained by J. Lác (1961), who treats each sex separately, and by the data from the above-mentioned anonymous study. The sexual differences have not allowed the determination of the limit value of indices between the two species. Besides, as the comparison of the indices T: L and F: L in the fire-bellied toad from the lowest and the highest localities shows, they presumably have the nature of modifications dependent on environment. Consequently, it is doubtful whether they have any major taxonomic value in *Bombina*. B. Stugren and N. Popowic (1961) came to similar conclusions, stating that most of the *Bombina* populations are from the statistical point of view divergent for L, T, and F. The indices discussed may, however, be of some importance in the interpretation of ecological and zoogeographical problems concerning *Bombina*.

6. CONCLUSIONS

1. The external characters of coloration and the skin papillae of *Bombina* have unequal taxonomic values. The character which permits the unambiguous determination of the specific membership of a given specimen in *Bombina bombina* is the isolated orange patches on the border of the abdomen with the thigh. Two yellow patches on the breast with arcuate connexions to the yellow patches on the ventral side of the arms are a similar character in *Bombina variegata*. The remaining characters do not constitute unequivocal criteria of the specific membership of a given individual.

2. There are differences in body proportions between the two species of *Bombina*. The thigh and shin of the yellow-bellied toad are longer than the corresponding body parts of the fire-bellied toad. In addition, the yellow-bellied toad shows sexual differences in lengths of thigh and those of shin: they are larger in males than in females. This last difference makes the determination

of the limit value of indices impossible and, consequently, they cannot be applied for the taxonomy of *Bombina* without reserve.

3. There are differences in coloration of testes in the males of both species of *Bombina*. Black coloration of the testes prevails in the fire-bellied toad, while in most specimens of the yellow-bellied toad the testes are colourless.

4. Both species of *Bombina* reach sexual maturity when their body length ranges between 30 and 40 mm, but most frequently between 38 and 40 mm.

5. The maximum body length of both species is 53 mm, but the average length of the fire-bellied toad is larger than that of the yellow-bellied toad.

Part II

PHYSIOGRAPHY

1. INTRODUCTION

The fire-bellied toad *Bombina bombina* and the yellow-bellied toad *Bombina variegata* differ in their environmental demands and for this reason dwell different areas. The fire-bellied toad is very closely associated with water environment and inhabits lowlands up to an altitude of 250 m. above sea level, abounding in permanent water reservoirs, which are situated mostly in river valleys. The yellow-bellied toad lives in highlands and mountains up to an altitude of 2000 m. (M. Radovanović, 1951), in small water reservoirs, seasonally drying pools, ditches filled with water, but obviously avoiding large reservoirs. Thus, this species is a little less closely associated with water environment. In areas where the ranges of both species overlap there occur individuals or whole populations showing characters of both species mixed up. In the opinions of most authors (L. Méhely, 1905; E. Schreiber, 1912; L. Horbulewicz, 1927, H. Szarski, 1939, J. Michałowski, 1958, and others) this state is due to interspecific crossings, which doubtless prove a close kinship of these species. Such a geographic distribution and close relationship of the two species made some authors regard the Ice Age as a factor bringing about their differentiation. A general conception of the splitting of original species in isolated refuges was set forth by B. Stresemann (1919). It was developed in detail and based on ecological data for *Bombina* by R. Mertens (1928), whose opinion has been maintained up to the present time (Z. Grodziński, 1954). According to this opinion the population of the Pliocene form of *Bombina* *, which probably inhabited the plains throughout Europe, was severed owing

* Fossil materials, so far known only from the „pregacial layers“ of Hungary and Rumania, are unreliable (M. Młynarski, 1961).

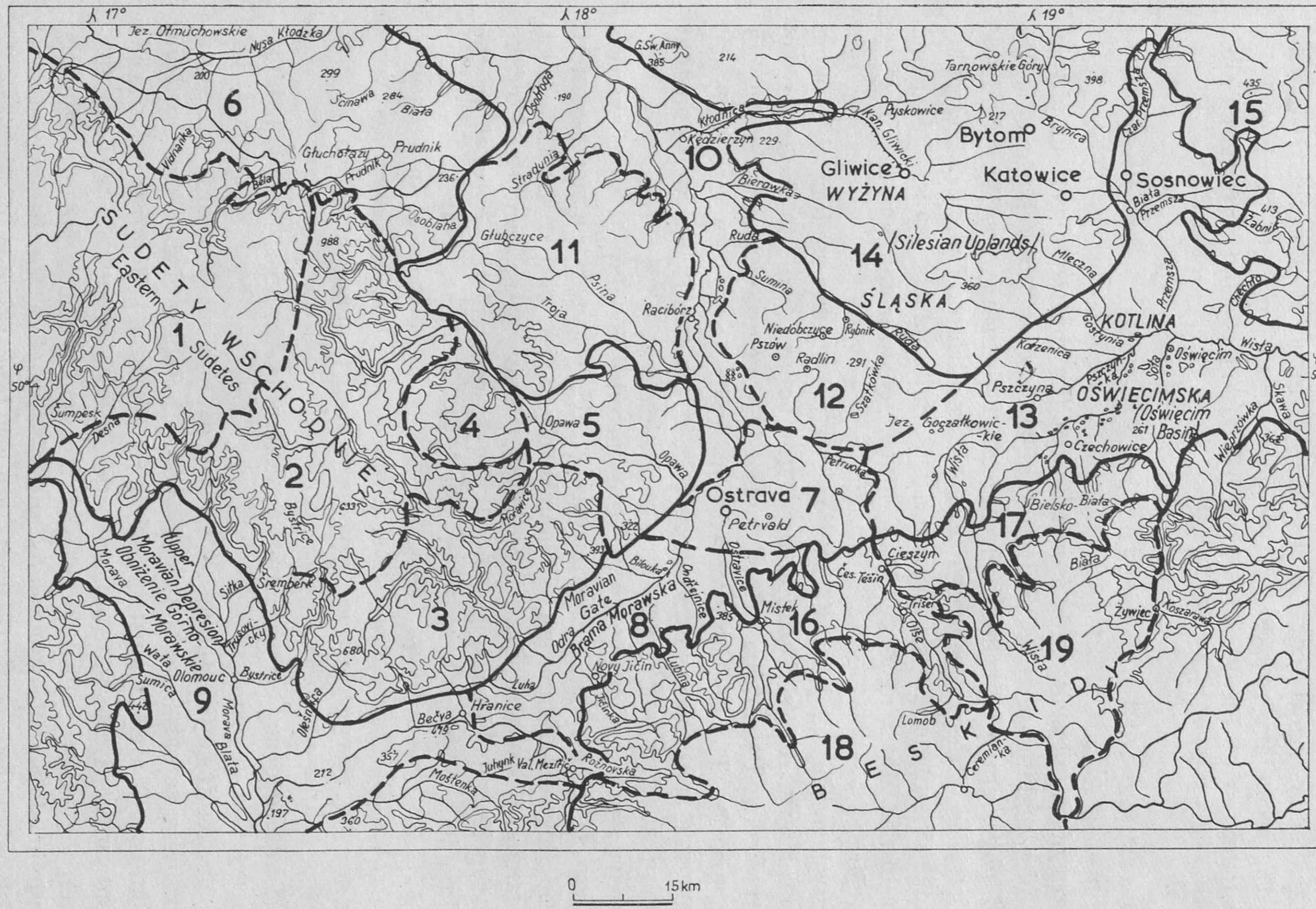
to the transgression of the glacier and compelled to move away from the glacier, eastwards and westwards. The eastern group found a refuge in the southern part of the East-European steppes on the Black Sea. The western group retreated to South and Central France, leaving the plains for the elevated area of the Central Massif. It is believed that in these new and dissimilar conditions *Bombina* developed different adaptations to the lowland and highland environments. J. Lác (1961) has recently put forward a supposition that the Pannonian Lowlands, especially their southern part, or the steppe areas of the southern part of the European U. S. S. R., may have been such a refuge as well. The shrinking and expanding of the ranges of both species are supposed to have taken place in the particular glacial and interglacial periods. It may also be assumed that these shifts were the main factor of selection. The final expansion of both species followed the disappearance of the glacier in the Holocene, the eastern form moving north-westwards and the western one north-eastwards.

The fire-bellied toad (E. Frommhold, 1959) occupies the lowlands of Central Europe, reaching as far as Oldenburg and the Weser to the west, Denmark and southern Sweden to the north, and the Ural Mts. to the east. On the south it borders upon the northern range of the yellow-bellied toad, and its boundary runs from the Vienna region across Hungary, northern Yugoslavia, Rumania, Bulgaria, the Ukraine up to the Caucasus. The yellow-bellied toad dwells in the uplands and mountains from France (except the Pyrenees) through Belgium, Holland, western and southern Germany, Alpine countries, Italy (north of the Po) to the Balkans (north of Dalmatia, Albania and Macedonia). On the north its range includes the Carpathians, Czechoslovakia, Thuringia, Harz Mts., Brunswick, and Hannover.

The data concerning the geographic distribution of *Bombina* obtained from the herpetological literature are general in many cases and often based on casual observations or fragmentary collections. On the other hand, there are few detailed works recording all the localities or their lack in particular areas. Basing on this material it is, therefore, difficult to say anything strict about one or the other direction of the postglacial migrations of *Bombina*. The aim of this part, which also governed the selection of the study area, was to check R. Mertens's hypothesis (1928) of the postglacial migration of the yellow-bellied toad in the region of the Moravian Gate, assuming its passage from the Alps to the Carpathians.

In the foreland of the Carpathians (Podkarpacie) the distribution of both *Bombina* species was carefully studied between Stryj and Sambor and between Dobromil and Jarosław (L. Horbulewicz, 1927, 1933), as well as in the Kraków region bordered by the Vistula, the Skawa, the Raba, and the Kraków-Chrzanów Ridge (J. Michałowski, 1958, 1961). The occurrence of *Bombina* in the adjoining regions was recorded fragmentarily and information obtained rather casually.

This is also true of the knowledge of the distribution of *Bombina* in Czechoslovakia. The territory of Slovakia has been an exception since it was fairly



Map 1. Physiographic regions of the study area

Legend: 1. Jeseník hrubý, 2. Jeseník nýzký, 3. Odřanske Mts., 4. Opavske Mts., 5. Hlučinské Highland, 6. Foothills of the Sudeten Mts., 7. Ostrava-Karviná Basin, 8. Moravian Gate, 9. Upper Moravian Depresion, 10. Racibórz Basin, 11. Głubczyce Plateau, 12. Rybnik Plateau, 13. Oświęcim Basin, 14. Silesian Uplands, 15. Kraków-Częstochowa Uplands, 16. Silesian and Moravian Highland, 17. Silesian Highland, 18. Silesian and Moravian Beskids Mts., 19. Silesian Beskidy Mts.

well explored by J. Lác (1961). O. Štěpánek (1949) deals with the distribution of *Bombina* in Bohemia and Moravia. He discusses the problem in general, mentioning scarcely some dozen of localities of the fire-bellied toad and several ones of the yellow-bellied toad on the basis of museum collections.

Thus, the secondary purpose of this paper is to complete the knowledge of the distribution of *Bombina* in this very interesting but unexplored area.

2. STUDY AREA

The area of the present study is situated at the contact of various physiographic units making up the territories of Poland and Czechoslovakia. In respect of physiography the most prominent of them are the West Sudetes, part of the West Beskids, southern part of the Silesian Uplands, the valley of the upper Vistula and its tributaries, the valley of the upper Odra, and the region of the Moravian Gate. These units include a number of subregions shown on Map 1.

The physiographic division of the area into subregions used in this paper is rather arbitrary. It is so because there is no agreement as to the criteria of division applied in Poland and those applied in Czechoslovakia, as well as for practical purposes. The division worked out by M. Klimaszewski (1946) and S. Lencewicz (1959) has been taken as a basis for the Polish area and that published by A. Wrzosek (1960) for Czechoslovakia.

The areas studied additionally are not included in Map 1, as they were explored less carefully and unsystematically. They cover the north-western part of the Bohemian-Moravian Highlands, the region of Usti on the Orlici, and the regions of Brno and Bratislava. The remaining areas, from the Kłodzko Basin to the Danube Lowlands (Gabčikovo) were explored only along the main highroads.

3. ENVIRONMENTS DWELT BY BOTH SPECIES

Table 8 has been made up in order to determine the most typical habitats of both species of *Bombina*.

It will be seen from this table that fish ponds, clay pits and different contaminated water reservoirs are the most typical habitats of *Bombina bombina*. Clay pits and pools are the most suitable habitats for *Bombina variegata*, while greatly contaminated reservoirs suit this species less. In contrast with the fire-bellied toad, the yellow-bellied toad rather frequently comes out on to the dry land. It obviously avoids fish ponds and oftener than the fire-bellied toad dwells in slow-flowing waters. Clay pits are a habitat suitable for both species of *Bombina*, which is also evidenced by the fact that they form mixed localities, very frequently inhabited by intermediate forms.

Table 8

Occurrence of *Bombina* in various habitats

Habitat	Localities of *Bombina bombina*		Localities of *Bombina variegata*		Mixed localities	
	Number	%	Number	%	Number	%
Fish ponds	27	30·7	—	—	2	4·5
Clay pits and ditches with water	27	30·7	73	57·9	21	56·7
Pits with dungwater and other similarly contaminated reservoirs	19	21·6	14	11·1	5	13·5
Muddy pools and marshes	11	12·5	2	1·6	1	2·7
Seasonal drying pools	2	2·3	24	19·0	7	19·0
Slow-flowing water	1	1·1	3	2·4	1	2·7
Damp meadows, furrows of cultivated fields, and other land environments	1	1·1	10	8·0	—	—

To comlete the characteristics of habitats of *Bombina* it is necessary to add some explanations based on field studies. It has been found beyond doubt that if in a given area a fire-bellied toad has different habitats to choose, it always chooses clay pits, other pits, and muddy pools with strongly contaminated water, and not fish ponds or clay pits with clean water. And above all, it lives in sites best protected against enemy, strewn with branches, rubbish, rumble etc. The fire-bellied toad very rarely inhabits all the ponds of a system, but most frequently chooses one pond, usually the smallest, often fishless, contaminated and shallow, and even then occupies only a part of it. In general, out of the 27 localities of that kind examined, only in 6 the occurrence of *Bombina* in medium or large numbers was ascertained.

The foregoing observations on the environment preference in the fire-bellied toad do not refute the opinion that it chooses fairly large reservoirs of clean water for nuptial season. In several cases, tadpoles and very young specimens of this species were found in such reservoirs, while adult specimens were completely lacking in them. In other cases, spawn and tadpoles at various stages of development occurred in clean clay pits and pools of rain water in the close vicinity of the extremely contaminated muddy pools inhabited by large numbers of adults. Finally, tadpoles and very young individuals were found accumulated in the cleanest parts of reservoirs, abounding in algae and other vegetation.

The yellow-bellied toad leaves water reservoirs in masses after showers and occupies all kinds of pools. In July and August it was often met out of water reservoirs. If the ground was uneven, adults occurred in elevated places and the young of that year in damper places, mostly in holes left in the ground by cattle hooves and filled with water.

4. GEOGRAPHIC DISTRIBUTION

The area being very extensive and diverse in respect both of its geographic aspect and of *Bombina* present in it, I decided to divide it into several regions and subregions so as to make the description of geographic distribution as clear as possible and to render it easier for the reader to find the data on the particular parts of the area. A list of localities showing the species and classes of *Bombina* occurring in them was made for each region. The numbers given in brackets in the text are the serial numbers of localities in the lists and are also used to mark these localities on Map 2. The lists together with the whole material have been deposited in the Institute of Systematic Zoology of the Polish Academy of Sciences in Kraków. Map 2 shows the distribution of localities. The occurrence of *Bombina* in the area covered by Map 2 is discussed in the Section entitled Ranges of Both Species. Additional areas, examined perfunctorily, are dealt with in the Section on the postglacial migrations of *Bombina*.

a. East Sudetes

Jeseník Hrubý. No specimens of *Bombina* were found in this area with a mean altitude of about 1000 m above sea level, nearly completely wooded and uninhabited except for the deep valleys of the rivers Bělá and Starič at altitudes of 400—600 m. Its main town is Jesenîk and the highest summit Praděd (1491 m.). As can be seen from this short description, the area is lacking in habitats suitable for *Bombina*. The two above-mentioned river valleys make an exception, but they provide only a few poor localities at Domašov, Adolfovice, and Dolna Lipová. Besides, in the region of Rejviz at an altitude of 769 m. there are marshes and a small lake, which could possibly constitute a habitat suitable for *Bombina*. The western part, in the region of Stare Město and Branná, has more places in which one might expect to find the yellow-bellied toad, but even there it has not been seen. The situation presents itself similarly on the south-western slopes, in the region of Šumperk and Šternberk. But coming down farther towards the Upper Moravian Depression, I met pure forms of *Bombina bombina* (59).

The Jesenîk Nizký is a relatively flat upland with a few summits reaching 750—800 m. above sea level, sloping steeply southwards and south-westwards to the Upper Moravian Depression and the Moravian Gate. It slopes more gently eastwards and north-eastwards, towards the Ostrava-Karvina Basin and the Lowlands of the Upper Odra. This area is drained by many streams, such as the Podolský, Mlýnský, Bělokamenný, Černý, Bukový, all emptying into the Moravice, and on the south by the tributaries of the Morava: Bystrice, Silka, and others. The soils prevailing here are clay loams overlying the Upper

Carbonian rocks. The region is poorly wooded, with spruce woods predominating. Bombina occurs in insular localities, of which I managed to find only three: at Jelenia near Bruntál (1) and at Dětrichov (2) with *Bombina variegata* in its pure form, and at Štablovice (3), where intermediate forms accompanied *Bombina variegata.*

The Oderske Mountains constitute the south-eastern border of the East Sudetes. The relief of this area is very varied. The country abounds here in elevations of medium altitude (360—680 m.), cut by the valleys of rivers flowing to the upper Odra, especially in the middle and northern parts, in the region of Suchdol, Mošnov, and Studénka. As in Jesenîk Nizký, clay loams predominate in this area. It is moderately wooded, more densely only in the south-western part, by spruce forests. *Bombina variegata* occurs here in its pure form in modest numbers (4—17), in the south-eastern part of this region it is seen more rarely.

Opava Hills (350—650 m.). This is a strongly undulating and poorly wooded area, mostly under cultivated fields. The soil in its south-western part is clay loam, in the north-eastern part clay. The main rivers are the Čižina, Hořyna, and Hvozdnice, flowing into the Opava and Moravice. No specimens of *Bombina* were found in this region. Environments suitable for *Bombina* are also very scarce. Some were observed at Heřmanice, Vel. Heraltice, Nepalovice and in the Krnov region.

Hlučin Hills. This very poorly wooded and mostly agricultural, wavy area is covered with loess soils on the sandy substratum. It abounds in pits, for the most part sandy pits, which do not often contain water owing to this permiable substratum. Specimens of *Bombina* were found only on the border with the Jesenîk Nizký at Otice (18), on the border with the Oderske Mts. at Lhota Dolna (19), and at Hlučin itself (20). In addition to the pure forms of *Bombina variegata*, intermediate forms and *Bombina bombina* of Class II appeared in all these localities. In the remaining parts of this area, from the river Opava up to the Polish-Czechoslovakian frontier, no specimens of *Bombina* were found. Environments suitable for *Bombina* were recorded from Chuchelnia, Bolatice, and Dolny Benešov.

The Foreland of the Sudetes was explored superficially, because it transcended the scope of the present work. None the less it may be stated that Bombina do not generally occur in this region. Only two localities were found: a mixed one at Niemysłowice (21) near Prudnik and the other at Niewnica (22) near Nysa. The last-mentioned locality was not examined because of difficulties in catching specimens. Judging from the field observations and the sonorous voice of animals, they were pure forms of the fire-bellied toad.

b. Region of the Moravian Gate

The Ostrava-Karvina Basin (200—300 m.) is very varied as far as its relief is concerned and poorly wooded, with clay soils prevailing. The effect of industrial activity of man, manifesting itself in an increasing number of barren areas, is here striking. All this forms suitable conditions for *Bombina* to spread. The localities of both species of *Bombina* are present throughout this region: *Bombina bombina* (25, 31) or mixed populations (24, 27) were met on the Odra in the western part, *Bombina variegata*, not always in its pure form, in the other parts (23, 26, 28, 29, 30, 32—38).

The Moravian Gate (250—310 m.) is a narrow and long basin crossed in the middle by the river Odra. It rises to its greatest altitude (310 m.) where the Bečva comes near the Odra in the region of Bělotin. As regards the distribution of *Bombina*, large marshes and fish ponds, extending along the Odra from the Mošnov region to Klimkovice, deserve special attention. The soil is here mostly clay loam and, in the southern part, clay. It is almost woodless farmland. *Bombina variegata*, for the most part in its pure form, occurs in this area (39—58) except the above-mentioned fishpond region, in which no specimens of *Bombina* were found at all. The occurrence of *Bombina bombina* cannot, however, be ruled out definitely, as the area was to a great extent inaccessible owing to the flood at the time of study. People living in this region do not know this species.

Upper Moravian Depression. Only the northern part of the Upper Moravian Depression, between Olomouc and Šumperk was explored. This is a flat, woodless, eminently agricultural country lacking in environments proper to *Bombina*. I succeeded in finding only one locality of the pure form of *Bombina bombina* at Uničov (59). *Bombina bombina* appears also in the central and southern parts of the area, as can be seen from literature.

c. Racibórz-Oświęcim Basin

The Racibórz Basin (190—250 m.) is a narrow wedge pressed between the Głubczyce Plateau and the Rybnik Plateau. All along the basin there are numerous meadows and pastures and in the regions of Lubomia and Syrynia as well as at Książęca Zawada there are large fish ponds. Another basin, Niecka Kozielska (180—220 m.), stretching from Głógówek eastwards to the region of Gliwice, is included in this area. A layer of dune sand is spread over its bottom drained by the Kłodnica. *Bombina bombina* predominates decidedly in the Odra Valley (60—66). At Racibórz and farther to the south, in the regions of Krzyżanów (68) and Chałupki (69), mixed localities are present. No localities of *Bombina* were found in Niecka Kozielska, which is probably due to its sandy substratum and, consequently, the lack of water reservoirs.

The Głubczyce Plateau (250—280 m.) constitutes a higher western bank of the valley of the upper Odra. This area is built of Miocene clays covered by a thick layer of diluvial formations (moraine, sands, loess). It is wavy, cut up by tributaries of the Odra, and abounds in claypits and sandpits, though only some of them holding water. The only locality of *Bombina variegata* found was at Lewice (70).

The Rybnik Plateau (260—370 m.) lies between the upper Odra and the upper Vistula. The highest places of this area are the hills of Wodzisław and Pszów (300—368 m.), which slope gently towards the Vistula until they reach the level of the sandy region of Pszczyna (250—270 m.). The western part of the plateau is heavily dismembered by tributaries of the Odra. It is where *Bombina bombina* in its pure form reaches sporadically. Its localities were found at Szymocice (71) and Rzuchów (72). At the latter locality catching failed and it was recognized only on the basis of field watching. In the remaining parts of this area, in spite of careful and repeated explorations, no specimens of *Bombina* were found.

The Oświęcim Basin extends between the Rybnik Plateau, the Silesian Uplands and the Silesian Highlands. On the south-west it borders on the Ostrava-Karvina Basin in the region of Zebrzydowice, on the north-east on the Przemsza Valley and the Kraków Gate. Two levels can be distinguished in this valley: the lower terrace, 2—4 m. high, accompanying the meandering Vistula and its tributaries and the higher terrace spreading widely 6—8 m. above the level of the river (Klimaszewski, 1946). Extensive bogs, marshes and a large number of fish ponds together with the Goczałkowickie Lake and the Paprocańskie Lake form the most distinctive characteristic of this area. A broad zone of fish-ponds ranges from Zebrzydowice through Ochaby, Pierściec, Iłownica, Ligota, Goczałkowice, Czechowice, Bestwina, Kaniów, Przecieszyn, Góra, Harmęże to Oświęcim. In this area the pure form of *Bombina bombina* occurs almost exclusively, and its localities are most densely accumulated in the regions of Oświęcim, Wilamowice, and Czechowice (73—114). The western boundary of its range runs from Kostuchna through Tychy, Goczałkowickie Lake up to Skoczów. On the border with the Ostrava-Karvina Basin there are localities of incompletely pure forms of *Bombina variegata* at Zebrzydowice (115), Pogwizdów (116), and Hażlach (117). Moreover, mixed localities and localities of *Bombina bombina* with a remarkable admixture of characters of the yellow-bellied toad occur all along the boundary with the Silesian Highlands (118—130).

The valley of the Przemsza and its tributaries lies in the north-eastern part of this area. The region has natural connexions with the Oświęcim Basin and so is discussed together with it. It extends on the border of the Silesian Uplands with the Jurassic Questa. The pure form of *Bombina bombina* occurs here (131—135), especially at the junction of the rivers Biała Przemsza, Czarna Przemsza, and Brynica.

d. Silesian Uplands

The Southern Part of the Silesian Uplands displays a scenery of plateaux and rounded hills with sides cut off by faults, as well as numerous tectonic and denudational basins. Industrial activity of man apparently dominates this scenery of the whole coal basin. The highest elevations are here the Łaziska Hills ranging between Czerwionka Orzesze and Mikołów, reaching an altitude of 360 m., and their eastern extension, the Murckie Hills with an altitude of 350 m. Another range of hills runs north of the above-metioned ones, on the right bank of the upper Kłodnica near Halemba (300 m.) and then forms the so-called Katowice Hills (335 m.) south of Katowice. Finally, the third group, called the Chorzów Hills, reaches an altitude of 320 m. north of Katowice (J. SZAFLARSKI, 1955). As can be seen from the foregoing data, most of the area exceeds the upper boudary of the normal range of *Bombina bombina*, and this is probably the reason for its uncommonly rare occurrence and even then mostly in river valleys. On the other hand, it is difficult to explain the complete lack of the yellow-bellied toad, as the area provides very suitable conditions for this form. The localities of the pure form of *Bombina bombina* are most numerous in the Katowice region (137—139), occasional and very poor localities were found in the Murcki region, at Giszowiec (140), Kostuchna (141), and at Borowa Wieś between Mikołów and Gliwice (142). The last three localities were so poor that I gave up collecting material and let the specimens go after identification. A rich locality, but obviously insular, was encountered at Łabędy (143).

Kraków-Częstochowa Jurassic Ridge. Only part of this unit, namely the south-western part between Krzeszowice, Trzebinia and Olkusz, was searched, but then very carefully. This territory is characterized by a complete lack of habitats suitable for *Bombina*. Favourable conditions were found at Olkusz and Trzebinia. At Trzebinia the pure form of *Bombina bombina* occurs in a brickyard (144).

e. West Beskids

The Silesian-Moravian Highlands stretch from Valašské Meziřiči on the west to Třinec on the east. The 400 m. contour line has been assumed to be the southern boundary separating this area from the Silesian-Moravian Beskids. It forms a zigzag line running from Frenštát through Kozlowice, Frydlant on the Ostrava, Roškowice, Komorna Lhotka, Oldřichovice to Třinec. The north-western boundary is the 300 m. contour, running through Novy Jičin, Rychaltice, Stařic, Frydek-Mistek and Terlicko near Tešin. The scenery of this area is greatly diversified by lime rocks of the so-called „External Klippen Belt". Some of them can be seen in a few places in the regions of Novy Jičin and Štamberk (WRZOSEK, 1961). In the eastern part isolated elevations, of which the most outstanding ones are Ondřejnik and

Palkovicke Hůrki, range between 550 and 690 m. above sea level. All these hills are mostly wooded, the remaining portions of the area are woodless and their soil is clay loam. The basin is drained by very many streams flowing into the Odra and Olza. The whole area is inhabited by the yellow-bellied toad in its pure form (145—148, 150—152, 154—161, 164—168), or with a slight admixture of characters of the fire-bellied toad (149, 153, 163). The intermediate form found at Palkovice (153) is an exception. No *Bombina* were ascertained in the wooded regions of the hills mentioned above.

The Silesian Highlands range from the Olza to the Soła. There is no distinct piedmont scarp here, so I use the 400 m. and 300 m. contour lines to mark out the area. The 400 m. contour line, separating the Highlands from the Silesian Beskids, runs through Leszna Górna, Cisownica, Ustroń, Lipowiec, then it cuts into the Beskids up to Brenna to continue its further course through Górki Wielkie, Jaworze Górne, Wapiennica Górna, Kamienica, Mikuszowice Śląskie, and Porąbka. The northern boundary (300 m. contour line) ranges through Pogwizdów, Hażlach, Dębowiec, Rudzica, Międzyrzecze, Komorowice, Bestwina, Janowice, Kęty, and Kobiernice. The whole area is inclined northwards, and consequently the rivers flow in the same direction, the country being divided into drainage basins with meridional courses (Klimaszewski, 1946). As regards the distribution of *Bombina*, attention should be given to numerous fish ponds cutting in between the watersheds and connected with the complex of ponds in the Oświęcim Basin. The zone of ponds in the Dębowiec-Dolny Dwór region, that in the Mała Rudzica-Jasienica region and the ponds at Skoczów Pogórze are the most significant.

The relief of the area described above has a very great effect on the distribution of *Bombina*. Besides not very numerous localities of the pure form of *Bombina variegata* (171, 172, 174, 175, 185, 192, 196), there are localities of *Bombina variegata* with various, usually considerable, admixtures of characters of *Bombina bombina* (169, 170, 173, 181, 187, 190), those of intermediate forms (189, 191, 194, 195, 197) and only a few of *Bombina bombina* (183, 193). The fire-bellied toad undoubtedly came here by way of those systems of ponds. As will be seen from the foregoing, the Silesian Highlands are a typical zone of overlapping of the ranges of both *Bombina* species.

Silesian-Moravian Beskids are exactly like the Silesian Beskids in their character. They do not bring anything new regarding the distribution of *Bombina*. It is known from literature that *Bombina variegata* occurs here frequently, and for this reason no collection was done.

The Silesian Beskids extend from the Jablunkov Pass to the Soła. This area is characterized by wooded steep slopes and the highest rainfall in the Beskids. The northern slopes are drained by the Vistula, Brenica and Biała, the eastern by numerous tributaries of the Soła, of which the Bystra and Żylica are the most important. The valleys of these rivers together with the Żywiec Basin are the main peopled regions in the Silesian Beskids, which doubtless has exerted an influence upon the distribution of *Bombina*, for they are admittedly synanthropic animals. The pure form of *Bombina variegata* is common in the higher-lying regions (205—211, 214, 217—231), while in the river valleys it loses its purity, especially in the valleys of the Vistula and the Biała (199—204, 212, 213, 215). I even found one specimen of *Bombina bombina* of Class III at Łodygowice near Żywiec (216).

Table 9

Localities of *Bombina* in the particular regions of the study area

	Region	No. of localities	*Bombina variegata*			*Bombina bombina*			Intermediate form
			Class						
			I	II	III	I	II	III	IV
1.	Jesenîk Hrubý	—	—	—	—	—	—	—	—
2.	Jesenîk Nizký	4	3	—	—	—	—	—	1
3.	Oderske Mts.	14	14	—	—	—	—	—	—
4.	Opava Hills	—	—	—	—	—	—	—	—
5.	Hlučin Hills	5	1	2	—	—	1	—	1
6.	Foreland of the Sudetes	3	—	1	—	—	—	1	1
7.	Ostrava-Karvina Basin	22	9	7	—	2	—	1	3
8.	Moravian Gate	21	19	1	—	—	—	—	1
9.	Upper Moravian Depression	1	—	—	—	1	—	—	—
10.	Racibórz Basin	12	—	2	—	9	1	—	—
11.	Głubczyce Plateau	1	1	—	—	—	—	—	—
12.	Rybnik Plateau	2	—	—	—	2	—	—	—
13.	Oświęcim Basin	70	2	4	3	49	5	1	6
	Przemsza Valley	5	—	—	—	5	—	—	—
14.	Silesian Uplands	8	—	—	—	8	—	—	—
15.	Kraków-Częstochowa Jurassic Ridge	1	—	—	—	1	—	—	—
16.	Silesian-Moravian Highlands	25	21	3	—	—	—	—	1
17.	Silesian Highlands	48	11	14	2	10	1	1	9
18.	Silesian Beskids	36	30	4	—	—	—	1	1
19.									
	Total	278	111	38	5	87	8	5	24

5. RANGES OF BOTH SPECIES OF *BOMBINA*

Map 2, on which all the localities mentioned are plotted, shows the distribution of *Bombina* in the study area. It can be seen from this map and from the destailed description that the range of the yellow-bellied toad includes

Map 2. Localities of *Bombina*

1 — Localities of *Bombina bombina* cl. I, 2 — Localities of *Bombina bombina* cl. II, 3 — Localities of *Bombina bombina* cl. III, 4 — Localities of *intermediate form* cl. IV, 5 — Localities of *Bombina variegata* cl. III, 6 — Localities of *Bombina variegata* cl. II, 7 — Localities of *Bombina variegata* cl. I, 8 — Not investigated localities of *Bombina bombina*, 9 — Typical habitats examined in which no *Bombina* were found, 10 — Towns, 11 — Rivers and lakes, — Contour line

the West Beskids, the Silesian-Moravian Highlands with a part of the Ostrava-Karvina Basin, the Moravian Gate and the adjoining part of the East Sudetes, the Oderske Mts., and the Jesenîk Nizký. The fire-bellied toad appears only in the valleys of the Vistula and Przemsza on the east and in the valley of the Odra on the west. Between the ranges of the two species there is a transitional zone including the Silesian Highłands (except the Cieszyn region) and the region of Ostrava. Both species, mostly impure or intermediate forms, occur in this zone. As the range of the fire-bellied toad in the study area is broken by the Silesian Uplands and the Rybnik Plateau, the transitional zone also shows a distinct break in the region of Cieszyn and Karvina, where the yellow-bellied toad occurs.

6. POSTGLACIAL MIGRATIONS OF *BOMBINA*

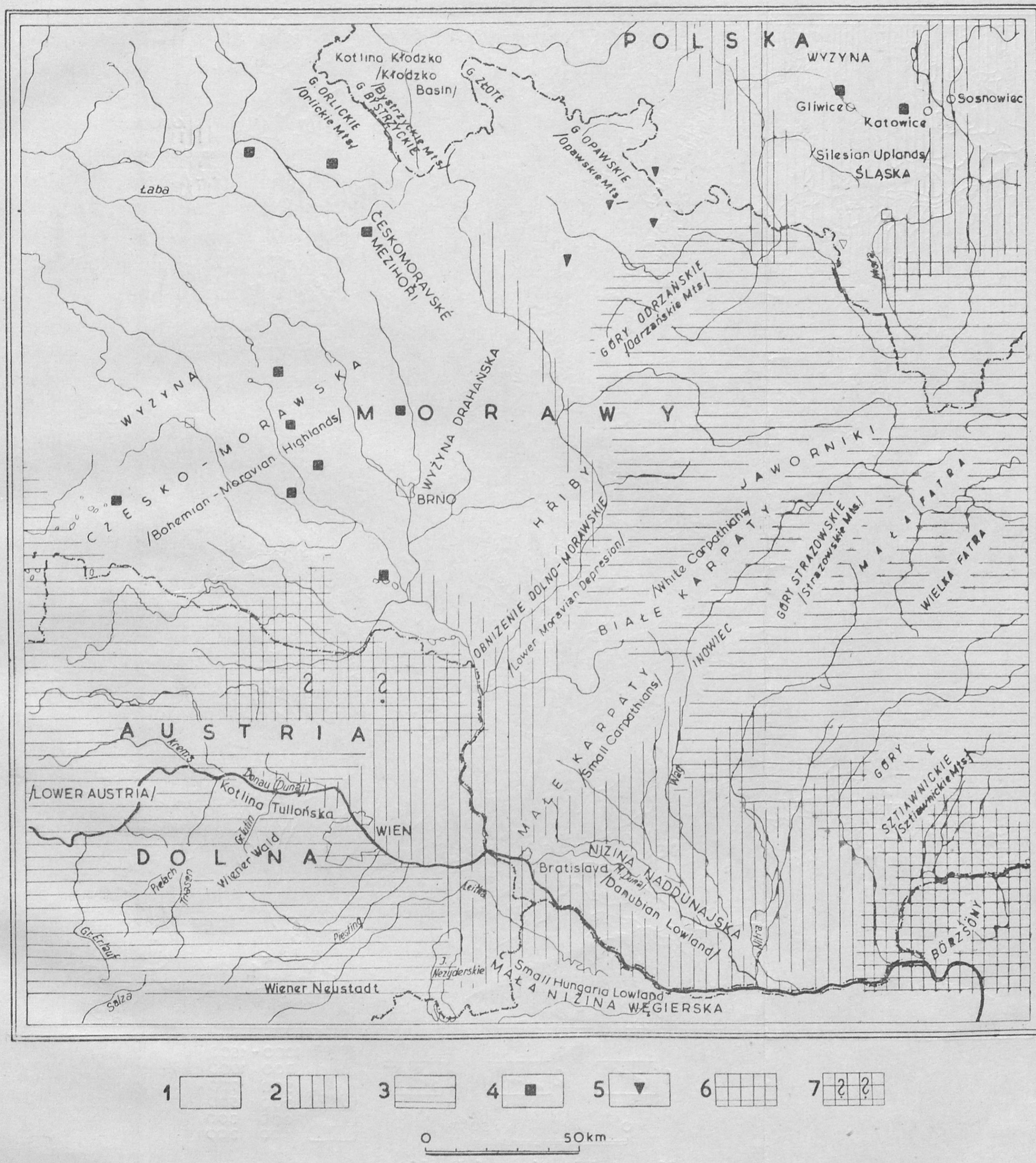
According to R. Mertens (1928), in the postglacial period the yellow-bellied toad spread eastwards from its western refuge, invading the Carpathians among other territories. It may be taken on the basis of its distribution in Upper Silesia, in the region of the Moravian Gate, and in the adjoining areas described above that the route of this species from the Alps to the Carpathians led through the Bohemian-Moravian Highlands, East Sudetes, and Moravian Gate. Then I resolved to carry out additional study so as to check the occurrence of the yellow-bellied toad in the Bohemian-Moravian Highlands and the areas bordering on them. It was expected that, unless this form occurred there in masses, it had at least left some traces of migration such as isolated relic localities or hybrids. In the course of the study it turned out that not only the yellow-bellied toad was lacking there completely, but there were localities of the fire-bellied toad, and then, what is more, of its pure form. The exploration of the wide zone from the Kładzko Basin southwards revealed rich localities at Rychnov (1), Ústi on the Orlici (2), Ořechův (3) near Křyžanov, Bobrova (4), Černy Les (5) north of Brno, and Velká Biteš (6). Besides, at Jadovnice (7) at the foot of Macocha an uncommonly abundant locality of the fire-bellied toad was found, but the conditions of catching were so hard that no specimens were taken. Rich localities of the fire-bellied toad were also in the south-eastern part of the Bohemian-Moravian Highlands. The material collected from them was put at my disposal in the Moravian Museum in Brno. The localities were particulary abundant at Jihlava (8), Popice (9), Studenecké Rybniki (10) at the foot of Mrakotin, and in the region of Tulešice (11). Only in this last locality the presence of some impure forms with an admixture of characters of the yellow-bellied toad was found, which may have been connected with the close vicinity of the Alps. However, on account of its geographic situation this locality has no bearing on the problem discussed. Thus, the hypothesis of the migration of the yellow-bellied toad by way of the Bohemian-Moravian Highlands had to be ruled out.

There is another possibility left, that is to say, the immediate migration from the Alps to the Carpathians through the region of Vienna and that of Bratislava to the Malé and Bîle Karpaty. To solve this problem the exploration was extended over the area stretching from Brno south-eastwards up to Gabčikovo in the Danube Lowlands. The results were as follows: localities of the fire-bellied toad were found at Pohořelice (12) and Břeclav (13), from which some specimens were, however, impure (Class II). Fire-bellied toads with a remarkable admixture of characters of the yellow-bellied toad (Class III) were found at Šamoryn (17) and its pure form at Gabčikovo (18). The Malé Karpaty Mts. were also searched, but no specimens of Bombina or habitats suitable for it were found. Only at the foot of these mountains, at Pernek (19) one specimen of the fire-bellied toad was collected. In addition, I received the material from two localities, Zahor (20) and Šur (21), in the foreland of the Malé Karpaty from Mr. J. Lác of the Slovakian Academy of Sciences. They were also fire-bellied toads of Class I. Localities of the yellow-bellied toad were ascertained at Myjava (22) and Vélka (23) on the border of the Malé Karpaty with the Bîlé Karpaty. They were either pure forms or with a slight admixture of characters of the fire-bellied toad. The same was found on the border of the Bîlé Karpaty and the Upper Moravian Depression at Hradište (24). At Blatnice (25) some intermediate forms were found in addition to the pure forms of the yellow-bellied toad.

Local small migrations of *Bombina* have often been observed (L. Horbulewicz, 1927; R. Mertens, 1928; I. A. Bayger, 1937; J. Michałowski, 1958). I also observed such migrations and, besides, often met yellow-bellied toads in meadows or, sometimes, even in quite dry places. The reasons for these migrations are various: drifting with water at the time of flood, drying of water reservoirs, looking for breeding sites or food sources, and retreats for hibernation. All these migrations are probably of great biological significance, because they keep off the danger of inbreeding and, first of all, contribute to an increase of the number of individuals and to their dispersal.

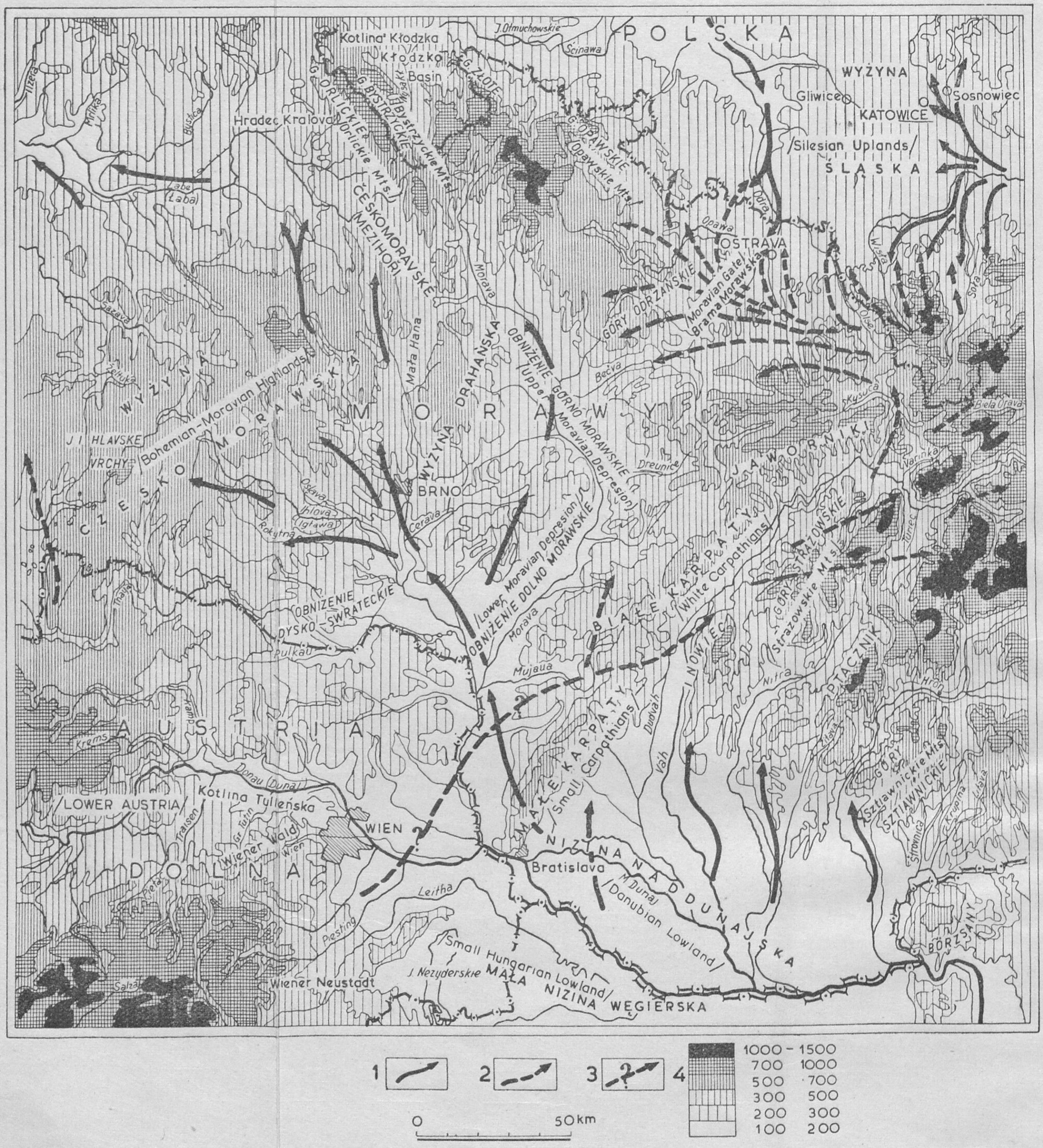
The migrations on a large scale result from small migrations continued for a very long time. To frame a hypothesis as to their direction one must necessarily base oneself on indirect evidences such as the geographic distribution, occurrence of insular localities, or the ascertainment of an admixture of character of the opposite species where the ranges of both species do not overlap. Map 3 shows the geographic distribution of *Bombina* in the study area and the adjoining territories, for which the data were obtained from literature (J. Lác, 1961; E. Frommhold, 1959; I. Szabó, 1959). It presents the ranges of both species and the zones of their overlapping. Basing on the data shown on the map, and on my own field observations I cautiously made an attempt to trace the directions of migrations of both species in the study area. The results are shown on Map 4.

The explanation of migrations of the fire-bellied toad does not present difficulties. It is quite apparent that this form migrates along river valleys.



Map. 3. Range of *Bombina*

1 — No *Bombina*, 2 — Continuous range of *Bombina bombina*, 3 — Continuous range of *Bombina variegata*, 4 — Insular localities of *Bombina bombina*, 5 — Insular localities of *Bombina variegata*, 6 — Zone of overlapping of the ranges of both species, 7 — Zone in which the presence of Bombina was not checked



Map. 4. Migrations of *Bombina*

1 — Direction of migration of *Bombina bombina*, 2 — Direction of migration of *Bombina variegata* 3 — Supposed direction of migration of *Bombina variegata*

The insular localities in the Bohemian-Moravian Highlands can be explained by the presence of large fish ponds and marshes, to which fire-bellied toads came from lowlands along river valleys. Having found convenient conditions, they have multiplied considerably in spite of the great altitude of the region.

The only way by which the yellow-bellied toad could come from the West Beskids to the East Sudetes led through the Moravian Gate. The biotope of this region, as may be inferred from the detailed description, was favourable, its clay soils playing the chief role. The area abounded presumably in pools, muds and the like after the last glaciation. Then, many claypits and ditches were formed as a result of human activity, providing good conditions for migration. The migration was brought to a stop in the Jesenîk Hrubý owing to the lack of suitable conditions.

The essential problem, i. e., the passage of the fire-bellied toad from the Alps to the Carpathians remains to be discussed. If the hypothesis of R. Mertens (1928) is right, this migration led through the regions of Vienna and Bratislava. The localities of the fire-bellied toad with a remarkable admixture of characters of the yellow-bellied toad at Šamoryn and Lewař are the only evidence supporting this hypothesis. These admixtures may be regarded as a relic from the period of migration of the yellow-bellied toad in this region, as it is not the zone where the ranges of both species overlap. Even if the yellow-bellied toad lived here once, it disappeared when the climate changed (rise in temperature, lack of its typical habitats). If we, however, reject this hypothesis as ill grounded, we shall have to seek quite a different solution. It might be the assumption that the yellow-bellied toad got to the Carpathians by a roundabout way, not from the west but from the east, from the north-western Balkans. Hence it moved through Rumania northwards and westwards, finally reaching the Sudetes. This alternative is acceptable to the extent that according to Karaman (1922) the yellow-bellied toad occurs in the regions of Zagreb and Belgrade, and so in the western part of the Balkans. In Rumania, as recorded by B. Stugren and N. Popowic (1961), the yellow-bellied toad appears in the Carpathians and both species, ecologically isolated, in Transylvania. A close examination of this alternative is, however, beyond the scope of the present work.

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STRESZCZENIE

Rodzaj kumak (*Bombina* Oken, 1816) reprezentowany jest w faunie europejskiej przez dwa gatunki. Są to: kumak nizinny (*Bombina bombina* (Linnaeus, 1761) i kumak górski (*Bombina variegata* (Linnaeus, 1758). Gatunki te stanowią interesujący przedmiot badań. Zróżnicowanie się tych gatunków wiąże się z epoką plejstoceńską (R. Mertens, 1928), w czasie której plioceńska populacja kumaka, zamieszkująca wówczas prawdopodobnie równiny całej Europy, została zmuszona do wycofania się przed transgresją lodowca na wschód i na zachód. W nowych i różnych warunkach środowiska miały powstać dwa odmiennie przystosowane gatunki kumaków. Po zniknięciu zapory lodowej rozprzestrzeniły się one ponownie, przy czym kumak górski ze swych zachodnich ostoi przenosi się ku północnemu wschodowi, kumak nizinny ze swych ostoi wschodnich rozprzestrzenia się ku północnemu zachodowi. Na gruncie tej hipotezy powstało sporo problemów wymagających wyjaśnienia jak np. różnice morfologiczne obydwu gatunków, różnice ekologiczne, rozmieszczenie geograficzne oraz kierunki ich migracji. Problemy te zostały opracowane w niniejszej pracy. Przy wyborze obszaru badań chodziło o tereny zróżnicowane pod względem ekologicznym, na których występują oba gatunki, a nadto leżące na szlaku przypuszczalnych wędrówek kumaków w okresie postglacjalnym.

Obszar badań leży na styku różnych jednostek fizjograficznych wchodzących w skład terytorium Polski i Czechosłowacji. Są to: Sudety Wschodnie, część Beskidów Zachodnich, południowa część Wyżyny Śląskiej oraz obniżenia rozdzielające te jednostki fizjograficzne, a więc Brama Morawska z Kotliną Ostrawsko-Karwińską, Kotlina Raciborsko-Oświęcimska z Płaskowyżami Głubczyckim i Rybnickim. Nadto dla wyjaśnienia kierunków migracji kumaków przebadano mniej dokładnie szeroki pas biegnący od Kotliny Kłodzkiej przez

południowo-zachodnią część Wyżyny Czesko-Morawskiej, Czesko-Morawskie Międzygórze, okolice Brna i dalej ku południowemu wschodowi przez Małe i Białe Karpaty, okolice Bratysławy aż do Niziny Naddunajskiej.

Materiał gromadzono w latach 1959—1961 i uzyskano ponad 2000 okazów pochodzących z 251 stanowisk. Materiał zbierano z każdego napotkanego stanowiska, starając się złowić 10 okazów w każdym.

Ze względu na różnorodność zagadnień wyróżniono w niniejszej pracy dwie części: część taksonomiczną i część fizjograficzną. Część taksonomiczna zawiera statystyczną analizę cech zewnętrznych służących przede wszystkim do odróżnienia obu gatunków. Omówiono tu kolejno takie cechy, jak ubarwienie skóry i brodawki skórne, wskaźniki biometryczne i jako nie uwzględnioną dotąd cechę systematyczną — ubarwienie jąder u samców.

Z dokonanej analizy wynika, że cechą o najwyższej wartości taksonomicznej jest u kumaka nizinnego obecność izolowanych plam pomarańczowych leżących na pograniczu brzucha i ud, u kumaka górskiego zaś obecność dwu żółtych plam leżących na piersiach i łączących się łukowato z żółtymi plamami brzusznej strony ramienia. Pozostałe cechy, aczkolwiek są przydatne w taksonomii, nie mogą stanowić jednoznacznego kryterium dla odróżnienia obu gatunków.

Analiza wskaźników biometrycznych T : L, F : L, P : L wykazała, że między obydwoma gatunkami kumaków istnieją różnice w proporcjach ciała. Kumak górski ma goleń i udo dłuższe niż nizinny, a ponadto u kumaka górskiego występują różnice płciowe w długości goleni i uda utrudniające i uniemożliwiające często wyznaczenie wartości granicznej wskaźnika.

W wyniku analizy ubarwienia jąder u samców stwierdzono, że występują tu różnice między obydwoma gatunkami kumaków. U kumaka nizinnego przeważa czarne zabarwienie jąder, u górskiego w większości przypadków jądra są bezbarwne.

W drugiej, fizjograficznej części pracy autor przedstawia występowanie obu omawianych gatunków na badanym obszarze i warunki, w jakich one występują. Na podstawie zdobytych danych wykreślono mapę zasięgu obu gatunków. Mapa ta, jak również obserwacje terenowe posłużyły do rozważań nad kierunkami postglacjalnych migracji kumaków.

Z badań autora wynika, że areał kumaka górskiego obejmuje Beskidy Zachodnie, Pogórze Śląsko-Morawskich Beskidów z częścią Kotliny Ostrawsko-Karwińskiej, Bramę Morawską i przyległą do niej części Sudetów Wschodnich, Góry Odrzańskie i Jesionik Niski. Kumak nizinny występuje na badanym obszarze w dolinach rzek: Wisły i Przemyszy na wschodzie oraz Odry na zachodzie. Między areałami obydwu gatunków występuje tu sfera przejściowa obejmująca Pogórze Śląskie (bez okolic Cieszyna) i okolice Ostrawy. Występują tu obydwa gatunki, najczęściej w formie nieczystej lub formy pośrednie. Ponieważ zasięg kumaka nizinnego na tym obszarze jest rozerwany przez Wyżynę Śląską i Płaskowyż Rybnicki, stąd i strefa przejściowa wykazuje rozerwanie w okolicach Cieszyna i Karwiny, gdzie występuje wyłącznie kumak górski. Ponadto występowanie kumaka nizinnego stwierdzono w całej dolinie rzeki Morawy, w okolicach Brna i — co stanowiło zupełne zaskoczenie — na Wyżynie Czesko-Morawskiej, gdzie sięga wysokości około 600 m npm.

Rozważania nad postglacjalnymi wędrówkami kumaków oparto z konieczności na dowodach pośrednich wobec zupełnego braku materiałów kopalnych. Jako podstawę przyjęto rozmieszczenie geograficzne, występowanie stanowisk wyspowych, bądź stwierdzenie domieszki cech drugiego gatunku tam, gdzie zasięgi obu gatunków nie pokrywają się. Kumak nizinny na badanym obszarze wędruje wyłącznie dolinami rzek. Obecność stanowisk wyspowych na Wyżynie Czesko-Morawskiej tłumaczy się zdaniem autora występowaniem tam dużych stawów rybnych i moczarów, do których zawędrowały kumaki z nizin dolinami rzek. Znajdując tak dogodne warunki, mimo znacznej wysokości, silnie się rozmnożyły.

Kumak górski na obszar Sudetów Wschodnich mógł przywędrować tylko z Beskidów Zachodnich przez Bramę Morawską. Biotop tego regionu sprzyjał temu. Przede wszystkim odegrały tu rolę gleby gliniaste. Jak można przypuszczać, po ostatnim zlodowaceniu były tu kałuże, błota itp. Potem znów skutkiem działalności człowieka powstawało wiele glinianek, rowów, a tym samym powstawały warunki migracji. Na Jesioniku Wysokim zatrzymał się on z braku odpowiednich warunków środowiska.

Zasadniczym problemem jest wyjaśnienie migracji kumaka górskiego ze swych ostoi zachodnich na Karpaty. Początkowo sądzono, że droga jego wędrówki wiodła z Alp przez Wyżynę Czesko-Morawską do Sudetów Wschodnich, a stąd przez Bramę Morawską do Beskidów Zachodnich. Po stwierdzeniu jednak, że na Wyżynie Czesko-Morawskiej występuje wyłącznie kumak nizinny i to w czystej formie, hipotezę taką należało odrzucić. Wobec tego pozostały dwie inne możliwości. Pierwsza z nich przyjmuje, że kumak górski przywędrował bezpośrednio z Alp do Małych i Białych Karpat przez okolice Wiednia i Bratysławy. Za jej przyjęciem przemawiają stanowiska kumaka nizinnego ze znaczną domieszką cech kumaka górskiego w okolicach Bratysławy (Samoryn i Leváre). Domieszki te mogą być uważane za relikt z okresu wędrówki kumaka górskiego w tym rejonie, ponieważ obszar ten nie stanowi strefy nakrywania się zasięgów obu gatunków kumaków. Jeżeli kiedyś był tutaj kumak górski, to zniknął ze zmianą klimatu (ocieplenie, brak typowych dla tego gatunku warunków biotycznych) i nie wytrzymał konkurencji z kumakiem nizinnym. Przeciw tej hipotezie przemawia całkowity brak kumaków w Małych Karpatach.

Drugą, bardziej prawdopodobną hipotezą jest, że kumak górski przedostał się w Karpaty ze swych ostoi zachodnich drogą okrężną nie od zachodu, lecz od wschodu. Mógł on mianowicie przywędrować z Alp wzdłuż Gór Dynarskich na północno-zachodni Bałkan, stąd zaś na Karpaty Wschodnie i dalej wzdłuż Karpat rozprzestrzenił się na zachód docierając do Sudetów Wschodnich. Dokładne prześledzenie tej przypuszczalnej drogi migracji wykracza już jednak poza ramy niniejszej pracy.

РЕЗЮМЕ

Род жерлянок (*Bombina* Oken, 1816) представлен в европейской фавне двумя видами: жерлянкой краснобрюхой [*Bombina bombina* (Linnaeus 1761)] и жерлянкой желтобрюхой [*Bombina variegata* (Linnaeus, 1758)] Виды эти являются интересным предметом исследований. Дифференциация их относится к плейстоцену (Mertens, 1928), в течение которого плиоценское распространение жерлянки, в то время занимавшее вероятно равнины всей Европы, было вынуждено отступить перед трансгрессией ледника на восток и на запад. В новых условиях среды образовались два, по разному приспособленные вида жерлянки. После исчезновения ледникового барьера распространились они вновь, при чем желтобрюхая жерлянка из своих западных поселений переходит на северо-восток, а краснобрюхая жерлянка распространяется из своих восточных поселений к северо-западу. На основе этой гипотезы образовался ряд проблем требующих выяснения, на пр. относительно морфологической и экологических отличий между обома видами, географического распределения их и направления их миграции. Этим проблемам и посвящена настоящая работа. При выборе области для исследований обращено внимание на области дифференцированные в смысле экологии, на которых представлены оба вида, а которые находятся на пути предположительного передвижения жерлянок в послеледниковую эпоху.

Исследованная область расположена на рубежах разных физиографических единиц, составляющих территорию Польши и Чехословакии. Она заключает: Восточные Судеты, часть Западных Бескид, южную часть Силезской возвышенности, а также пониженные области, разделяющие эти физиографические единицы, т. е. Моравские Ворота с Остравско-Карвинской котловиной и Рациборско-Освенцимскую котловину с Глубчицской и Рыбникской возвышенностями. Кроме того, для выяснения направления миграции жерлянок, была исследована менее подробно широкая полоса, простирающаяся от Клодзкской котловины, через западную часть Чешско-Моравской возвышенности, Чешско-Моравское междигорье, окрестности Брна и далее к юго-востоку через Малые и Белые Карпаты, окрестности Братиславы по Наддунайскую низменность.

Материалы были собраны в 1959—1961 гг. Было собрано свыше 2.000 образцов из 251 местонахождения. Материалы собирались из каждого встреченного местонахождения, причем собиратели старались выловить из каждого по 10 образцов.

В связи с разновидностью проблемы, настоящая работа делится на две части: таксономическую и физиографическую. Таксономическая часть содержит статистический анализ внешних признаков, служащих прежде всего для отличения обоих видов. Здесь обсуждаются такие признаки, как окраска кожи и кожаные бородавки, биометрические показатели и до сих пор не рассматривавшийся систематический признак: окраска мошонок у самцев.

Из произведенного здесь анализа следует, что самым ценным таксономическим признаком жерлянки краснобрюхой является наличие изолированных пятен оранжевого цвета на рубеже живота и бедер, а у желтобрюхой жерлянки наличие

двух желтых пятен на груди, дугообразно соединяющихся с желтыми пятнами брюшной стороны плеча. Остальные признаки, хотя и полезные для таксономии, не могут являться однозначными критериями для отличия обоих видов.

Анализ биометрических показателей T:L, F:L, P:L показал, что между этими видами жерлянок имеются разницы в пропорциях тела. У жерлянки желтобрюхой голень и бедро длиннее, чем у жерлянки краснобрюхой, а кроме того у жерлянки желтобрюхой имеются половые разницы в длине голени и бедра, которые часто препятствуют и делают невозможным определение предельной величины показателя.

В результате анализа окраски мошонок у самцев определено, что и здесь имеются разницы между обома видами жерлянок. У жерлянки краснобрюхой преобладает черная окраска мошонок; у желтобрюхой — в большинстве случаев мошонка лишена окраски.

Во второй, физиографической части работы автор представляет наличие обоих видов в исследованной области и условия, в каких они выступают. На основании собранных сведений была составлена карта распространения обоих видов. В свою очередь, эта карта и наблюдения на местах использовались для рассуждений о направлении постглациальной миграции жерлянок.

Из исследований автора следует, что желтобрюхая жерлянка распространена в Западных Бескидах, во взгорьях Силезско-Моравских Бескид и в части Остравско-Карвинской котловины, в Моравских Воротах и примыкающей к ней части Восточных Судетов, в Одерских горах и Есёнике-Ниском.

Краснобрюхая жерлянка распространена в исследованной области в долинах рек Вислы и Пржемши на востоке и реки Одры на западе.

Между районами распространения обоих видов была обнаружена переходная полоса, в состав которой входит Силезское взгорье (без окрестностей Тешина) и окрестности Остравы. Тут живут оба вида, главным образом в нечистой, или промежуточной форме. Места распространения жерлянки краснобрюхой в этой полосе расторжены Силезской возвышенностью и Рыбникским плоскогорьем, в следствие чего и переходная полоса расторжена в окрестностях Тешина и Карвины, где встерчается исключительно желтобрюхая жерлянка. Кроме того краснобрюхая жерлянка была обнаружена во всей долине реки Моравы, в окресностях Брна и на Чешско-Моравской возвышенности, на которой ее наличие совсем неожиданно, т.-к. она доходит там до около 600 м над уровнем моря.

Рассуждения о постглациальных перемещениях жерлянок пришлось построить на косвенных доказательствах, т.-к. ископаемых материалов нет. В качестве основания было принято при том географическое распространение, отдельные местонахождения-острова, или примеси признаков другого вида там, где распространены не оба вида. В исследованной области краснобрюхая жерлянка передвигается исключительно долинами рек. Ее местонахождения — острова на Чешско — Моравской возвышенности объясняются, по мнению автора, наличием больших рыбных прудов и болот, к которым жерлянки пришли из низин долинами рек. В благоприятных условиях они там, не смотря на большую высоту, сильно размножились.

Желтобрюхая жерлянка смогла прийти в Восточные Судеты только из Западных Бескид через Моравские Ворота. Биотоп этого района способствовал ей. Самую главную роль сыграла при том глинистая почва. По всей вероятности, после последнего обледенения остались здесь лужи, болота и пр., а в следствие деятельности человека появились там многочисленные глиняные карьеры и канавы, создавшие благоприятные условия миграции. Из-за отсутствия соответствуюших биологических условий миграция эта задержалась на Есёнике Высоком.

Основной проблемой является выяснение миграции желтобрюхой жерлянки из запада в Карпаты. В начале считалось, что ее путь вел из Альп через Чешско-Моравскую возвышенность к Восточным Судетам, а оттуда через Моравские Ворота к Западным Бескидам. Однако установив, что на Чешско-Моравской возвышенности находится одна только краснобрюхая жерлянка, да и то в чистом виде, гипотезу эту следовало отбросить. Остаются две другие гипотезы. Первая из них принимает, что желтобрюхая жерлянка пришла непосредственно из Альп в Малые и Белые Карпаты через окрестности Вены и Братиславы; ее доказательством являются местонахождения жерлянки краснобрюхой со значительной примесью признаков жерлянки желтобрюхой в окрестностях Братиславы. (Саморын и Леваре). Примеси эти можно считать остатками из эпохи миграции желтобрюхой жерлянки в этом районе, т.-к. он не является районом распространения обоих видов жерлянки. Если когда-нибудь здесь была желтобрюхая жерлянка, то она исчезла в связи с изменением климата (отепление), отсутствие типичных для этого вида биотических условий) и не выдержала соперничества с краснобрюхой жерлянкой. Против этой гипотезы говорит полное отсутствие жерлянки в Малых Карпатах.

Более вероятна другая гипотеза, по которой желтобрюхая жерлянка пришла в Карпаты из своих западных местонахождений кружным путем — не из запада, а из востока. Именно, она могла прийти из Альп вдоль Динарских гор в северо-восточные Балканы, а оттуда в Восточные Карпаты и вдоль Карпат распространиться на запад по Восточные Судеты. Однако точное исследование этого предположительного пути миграции выходит за пределы настоящей работы.

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