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Studies on the Relationship of *Bombina bombina* (LINNAEUS) and *Bombina variegata* (LINNAEUS)

II. Some taxonomic characters of tadpoles of both species and of tadpoles obtained from crosses under laboratory conditions

[9 Tables and 3 text-figures]

Badania nad pokrewieństwem *Bombina bombina* (LINNAEUS) i *Bombina variegata* (LINNAEUS) II. Niektóre cechy taksonomiczne kijanek obydwu gatunków i kijanek otrzymanych z ich skrzyżowania w laboratorium

Исследование родства у *Bombina bombina* (LINNAEUS) и *Bombina variegata* (LINNAEUS) II. Некоторые таксономические признаки головастиков обоих видов и головастиков, полученных путём лабораторного скрещивания этих видов

INTRODUCTION

In 1959 I started a series of experimental and descriptive studies concerning the external morphology as well as the anatomy, histology, and cytology of *Bombina*. Their purpose was to obtain more information on the degree of the evolutionary affinity between the two species of *Bombina* inhabiting Europe.

The first portion of results concerning the problems of biometry of metamorphosed forms has been published under the somewhat different joint title (Studies on species characters in *Bombina variegata* (L.) and *Bombina bombina* (L.) MICHAŁOWSKI, 1961).

The objective of the present work was 1) to analyse the most important taxonomic characters of *Bombina* tadpoles so far recorded in literature on my own material, 2) to try to find new characters, 3) to work out the taxonomic characters quantitatively as far as possible, 4) to accomplish reciprocal crosses of *Bombina*, and 5) to describe the characters of hybrid tadpoles.

* Deceased January 29, 1966.

Thus, in addition to taxonomic problems this paper is devoted to some genetic-evolutionary problems restricted to the obtainment and description of hybrids, because the principal element of studies on the degree of relationship of given animal forms is to get knowledge of the kind and degree of the isolating mechanisms occurring between them and, in consequence, of the possibilities of crosses. The fertility of eventual hybrids, and so the possibility of genic exchange between populations regarded as species, is the next problem that calls for inquiry.

So far as *Bombina* is concerned, the first successful crosses were obtained by HÉRON-ROYER as early as 1891. However, the experiment has not been repeated by other investigators; they limited themselves only to suppositions on the mixed nature of forms occurring in some regions. Intermediate specimens, which could not be definitively included in either species, were treated as hybrids. This does not seem right, for, as will be seen from HÉRON-ROYER'S paper (1891), the true hybrids are somewhat more similar to the Fire-Bellied Toad. This fact agrees with the observations made on hybrids of the vast majority of the crossing pairs of amphibian species, which are as a rule similar to one of the parents.

A repetition of crossing experiments with *Bombina* is also necessary for some other reasons. It should be remembered that at the time when HÉRON-ROYER (1891) published his papers there was no system of classification of *Bombina* characters, and genetics did not exist as a science, either. The systems giving a relatively large number of taxonomically significant and suitably sorted-out characters of *Bombina* appeared as late as about 1960 (MICHAŁOWSKI, 1958; STUGREN, 1959; MADEJ, 1964). The proper interpretation of the phenotype of hybrids and its variability became possible at the same time owing to the achievements of the contemporary genetics.

It was necessary to analyse the classificatory characters of tadpoles of parental species closely in order to describe and classify the distinctive characters of hybrids obtained, because the number of these differential characters given in literature is downright slight and, for this reason, cannot form the basis for a more extensive elaboration.

Basing myself on my own observations as well as on the data from literature on the appearance of *Bombina* tadpoles and the methods of elaboration of *Salentia* tadpoles in general, I occupied myself, above all, with the structure of the mouth and then with the proportions and maculation of the tail fin of *Bombina* tadpoles. It should be emphasized here that the objective of this study was not the exhaustive description of the morphology of *Bombina* tadpoles, e. g. the full description of their body coloration or the analysis of the proportions of the head. I rather attempted to concentrate my attention on a relatively small number of selected characters, but such as might make it possible to distinguish hybrid tadpoles from those belonging to the parental species.

MATERIAL AND METHODS

1. The derivation of parental forms

The initial material used to obtain hybrid tadpoles and control tadpoles was collected in the Kraków and Katowice Provinces.

The principles of collection of the material were as follows:

a) catching *Bombina* before the mating season or at its very beginning (the end of April or the first decade of May);

b) picking out specimens derived from regions characterized by the occurrence of exclusively typical forms for experimentation. The areas chosen for this purpose were those for which the geographical distribution of *Bombina* was worked out in detail either by the author of this paper (MICHAŁOWSKI, 1958) or by other Polish herpetologists (MADEJ, 1964);

c) using only the most typical specimens of the species.

The experiment was repeated three times (in 1961, 1962, and 1963). The tadpoles of 1961 were used only for preliminary observations, those obtained in 1962 costituted the main material for study, whereas the material of 1963 served to complete the investigations.

In the particular years the derivation of the parental forms was as follows:

1961. Yellow-Bellied Toads from the region of Mogilany, Świątniki and Myślenice (Kraków and Myślenice Districts, 300—400 m a. s. l.), Fire-Bellied Toads from the peripheries of the towns of Ruda Śląska and Zabrze.

1962. Yellow-Bellied Toads from the regions of Biertowice (Myślenice District, about 270 m a. s. l.) and Izdebnik (Wadowice District, about 290 m a. s. l.), Fire-Bellied Toads from the periphery of Katowice (Kościuszko Park region).

1963. Yellow-Bellied Toads from the Mogilany region (Kraków District, about 380 m a. s. l.), Fire-Bellied Toads, as in 1962.

2. The obtainment and breeding of tadpoles

The *Bombina* specimens were placed in aquaria, 2—3 pairs in each, with an addition of water plants. The tops of the aquaria were tightly covered with nylon net to prevent the animals from escaping. The following combinations of pairs were used: a) *Bombina bombina* (LINNAEUS) ♀ × *Bombina bombina* (LINNAEUS) ♂, b) *B. bombina* (LINNAEUS) ♀ × *B. variegata* (LINNAEUS) ♂, c) *B. variegata* (LINNAEUS) ♀ × *B. bombina* (LINNAEUS) ♂, and d) *B. variegata* (LINNAEUS) ♀ × *B. variegata* (LINNAEUS) ♂. It came soon to spontaneous amplexus between the pairs of the combinations b and d placed in the aquaria. Single injections of gonadotrophin(50 U. J.) into the dorsal lymph sac were applied in all the specimens to bring about amplexus in the combinations a and c and the early and abundant laying of spawn in the combinations b and d.

It appeared necessary to inject gonadotrophin twice to induce amplexus and spawning in the experiments with the combination c carried out both in 1961 and in 1962.

No exact records of the numbers of laid and fertilized eggs were kept, but it was found in general that the number of eggs laid by females did not differ from normal (some scores of eggs per female) in any combination. A very great proportion of the eggs (about 90%) developed into normal tadpoles in the particular combinations. The only exception was the cross of *B. variegata* (LINNAEUS) ♀ × *B. bombina* (LINNAEUS) ♂ in 1961. The number of eggs obtained in this case was very small (some dozen), and only three of them developed into normal tadpoles.

The tadpoles were kept in aquaria, about 50 specimens in about 15·5 l of water (i. e., about 3 tadpoles in 1 l). They were fed pulverized nettle. In the season of metamorphosis the amount of water in the aquaria was reduced and more water plants and some pieces of wood were added so as to produce favourable conditions for the animals to leave the water. Metamorphosis took place about 2 months after the eggs had been laid in *B. variegata* (LINNAEUS) and about 3 months in *B. bombina* (LINNAEUS). Hybrid tadpoles represented intermediate values in this respect. The maximum length reached by the tadpoles of all the four categories did not exceed 36 mm. It came to metamorphosis in most of the tadpoles, and the young frogs obtained were used for a study, the results of which will be published separately. The part of the material designed for the present study was taken at the stage of larval life in the form of tadpoles not less than 20 mm in total length (only in the case of control *B. bombina* (LINNAEUS) smaller specimens were taken as well) and fixed in 60% alcohol. Prior to this, when the tadpoles were still kept in the aquaria, general supravital observations were made.

All in all, 59 tadpoles of *Bombina bombina* (LINNAEUS), 28 of *Bombina variegata* (LINNAEUS), 60 from the cross *B. bombina* (LINNAEUS) ♀ × *B. variegata* (LINNAEUS) ♂ and 34 from the cross *B. variegata* (LINNAEUS) ♀ × *B. bombina* (LINNAEUS) ♂, which made a total of 181 tadpoles, were fixed and examined. Not all the tadpoles were, however, fit to be worked out in detail with respect to all the characters under study (e. g., owing to damages), which caused some discrepancies between the now given numbers of tadpoles and the numbers offered in particular tables of the section „Results".

3. Chosen characters and methods of their elaboration

a) Structure of the mouth

Tadpole mouths were examined using a low-power binocular microscope (magnification 25 ×). The shape of the upper lip, the relations between the lengths of the tooth-rows in the upper lip, the shape of the upper jaw and, finally, the course of the tooth-rows of the lower lip — paying regard to the presence or the lack of a diastema in the first of them — were determined.

These characters were defined qualitatively. For quantitative studies the mouths observed under the microscope were drawn by means of ABBE'S apparatus (35 ×). The height of the upper lip and the width of the mouth were measured on the drawings, as shown in Fig. 1a, and next the results were converted to real values.

b) Tail fin

Using the binocular microscope (6 ×) and a milimetre gauge, I measured the length of tadpoles to an accuracy of 0·5 mm and then the length of the body part that was not covered by the fin, in a similar manner (Fig. 3a). In addition, the degree of maculation of the tail fin was determined qualitatively.

Further details concerning the methods applied both in item a and in b are given in the section „Results", with the particular characters. In order to work out and describe the material, it was divided into groups according to the origin and size of tadpoles: a group of tadpoles with a total body length of 20—29 mm (medium-sized tadpoles), another including lengths of 30—39 mm (large tadpoles), and, in *B. bombina* (LINNAEUS), a group of tadpoles 10—19 mm long (small tadpoles). No division into size groups was applied for the description of some structural characters of the mouth. For the quantitative treatment of the characters the material was worked out statistically and the following values were calculated: number of specimens (n), arithmetic mean ($\bar{x}$), standard deviation (σ), and standard error of the mean $\left(\frac{\sigma}{\sqrt{n}}\right.$, this is not given in the tables$\left.\right)$. The quantitative differences in question were, in each case, checked statistically, using the „t" test. Working at particular characters, I divided the material into classes according to the values represented by the specimens and I determined which classes were characterized by the largest numbers of members (modal classes). The values used in the tables were generally middle values of these classes (medians). The arithmetic means and then the values of the modal classes were used to evaluate the particular groups of the material.

RESULTS

1. The shape of the upper lip

The observational data which have not been included in the table show that the upper lip of tadpoles resembles a triangle in shape in *B. bombina* (LINNAEUS) and an ellipse in *B. variegata* (LINNAEUS) Fig. 1b, f). In hybrids I (♀ *B. bombina* (LINNAEUS)) the shape of the upper lip is intermediate and in hybrids II (♀ *B. variegata* (LINNAEUS)) elliptical (Fig. 1d, e).

2. The height of the upper lip

The measurements are presented in Table 1.

It will be seen from the table that

a) the tadpoles of *B. bombina* (LINNAEUS) have the definitely highest upper lip (Fig. 1b),

b) the medium-sized tadpoles of hybrids I have the same height of the lip as the tadpoles of *B. bombina* (LINNAEUS), whereas the large tadpoles,

Table 1

Upper-lip height

	B. bombina	Hybrid I. (♀ *B. bombina*)	Hybrid II. (♀ *B. variegata*)	*B. variegata*
A. Tadpoles with a body length of 10—19 mm				
Statistical data *	13 0·76 ± 0·06 0·70			
B. Tadpoles with a body lenght of 20—29 mm				
Statistical data	24 1·11 ± 0·10 1·10	20 1·07 ± 0·10 1·10	19 0·97 ± 0·11 0·90	9 0·86 ± 0·13 0·90
C. Tadpoles with a body lenght of 30—39 mm				
Statistical data	3 1·33 ± 0·13 1·30	15 1·02 ± 0·15 1·00	15 1·06 ± 0·10 1·10	12 0·97 ± 0·08 0·90

* n followed by $\bar{x}$, σ, and median of the modtal class, in mm.

in which the height equals that in the medium-sized specimens (this fact indicates the inhibition of the growth of the upper lip in the course of ontogenesis), do not differ from *B. variegata* (LINNAEUS), and

c) the medium-sized tadpoles of hybrids II have an intermediate upper-lip height; the large tadpoles hold an intermediate position, too, but they become somewhat similar to *B. variegata* (LINNAEUS).

3. Upper-lip height: body length ratio

At the preliminary stage of my work on the results it seemed that the best method to demonstrate specific differences in the shape of the upper lip would be to determine the correlation between the upper-lip height and the mouth width. If the mouth width were the same in both the species, this ratio for

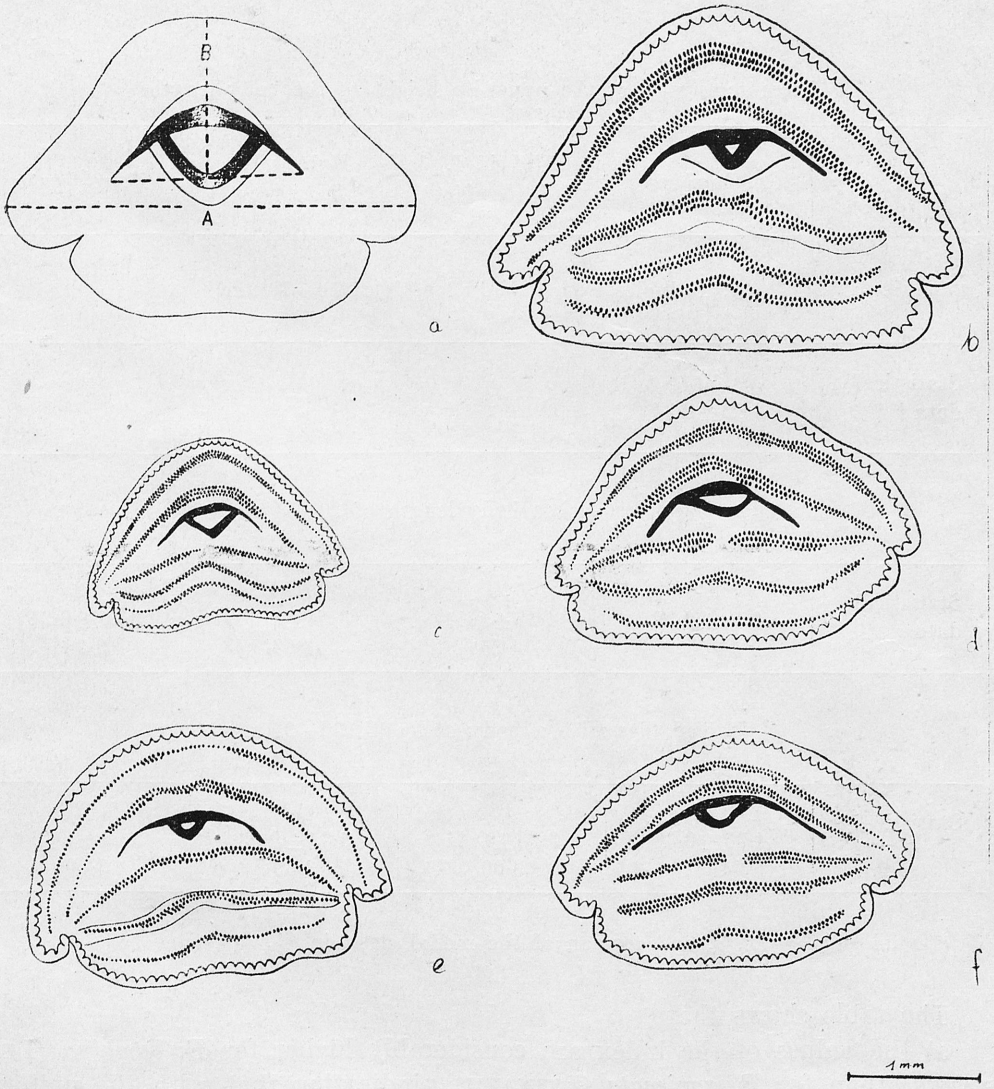

Fig. 1. The mouths of tadpoles of *Bombina bombina* (LINNAEUS), *Bombina variegata* (LINNAEUS) and of hybrid tadpoles. a) measurements of the mouth, A — mouth width, B — height of the upper lip, b) medium-sized tadpole of *Bombina bombina* (LINNAEUS), c) small tadpole of *Bombina bombina* (LINNAEUS), d) medium-sized hybrid tadpole I, e) medium-sized hybrid tadpole II, f) medium-sized tadpole of *Bombina variegata* (LINNAEUS)

the Fire-Bellied Toad, which has its upper lip high and triangular, would differ from that for the Yellow-Bellied Toad, whose lip is elliptical and not high, but, as will be seen from Table 3, the Yellow-Bellied Toad has not only the lower but also narrower mouth, and for this reason this method would not be adequate. Since both these species reach the the same length, I decided to use the percentage relation of the upper-lip height to the total body length. The data obtained in this manner are presented in Table 2.

Table 2

Percentage ratio of the upper-lip height to the body length

	B. bombina	Hybrid I. (♀ *B. bombina*)	Hybrid II. (♀ *B. variegata*)	*B. variegata*
A. Tadpoles with a body length of 10—19 mm				
Statistical data *	13 4·52 ± 0·34			
B. Tadpoles with a body length of 20—29 mm				
Statistical data	24 4·19 ± 0·32 4·00	20 4·25 ± 0·64 4·25	19 3·54 ± 0·38 3·63	9 3·25 ± 0·21 3·38
C. Tadpoles with a body of length 30—39 mm				
Statistical data	3 4·33 ± 0·36 4·00	15 3·23 ± 0·44 3·00	15 3·35 ± 0·33 3·50	12 3·06 ± 0·16 3·00

* n followed by x, σ, and median of the modal class, in %.

The table shows that

a) the values of the index are considerably higher for *B. bombina* (LINNAEUS) than for *B. variegata* (LINNAEUS), indicating that with the uniform body lengths the upper lip is higher in *B. bombina* (LINNAEUS);

b) all the groups of the material are generally characterized by a decrease in the index value in the course of ontogenesis, which means that the growth of the mouth (upper lip) does not keep up with the increase of the body length. In other words, the mouths of large forms are relatively smaller. The group

of large tadpoles of *B. bombina* (LINNAEUS) and hybrid tadpoles II depart from this rule;

c) the index value for medium-sized hybrid tadpoles I approximates to that for *B. bombina* (LINNAEUS), and the value for large specimens to that found in *B. variegata* (LINNAEUS). The index value for hybrid tadpoles II is usually intermediate in both these groups, but it approximates more to the values determined for *B. variegata* (LINNAEUS).

4. Width of the mouth

The measurements are listed in Table 3, from which it will be seen that

a) *B. bombina* (LINNAEUS) has a wider mouth than *B. variegata* (LINNAEUS) (Fig. 1b, f);

Table 3

Mouth width

	B. bombina	Hybrid I. (♀ *B. bombina*)	Hybrid II. (♀ *B. variegata*)	*B. variegata*
A. Tadpoles with a body length of 10—19 mm				
Statistical data *	16 2·34 ± 0·29 2·40			
B. Tedpoles with a body length of 20—29 mm				
Statistical data	31 3·14 ± 0·39 3·20	20 3·14 ± 0·27 3·20	19 3·04 ± 0·26 2·80	9 2·80 ± 0·46 2·80
C. Tadpoles with a body length of 30—39 mm				
Statistical data	3 3·82 ± 0·24 4·00	15 3·17 ± 0·30 3·20	15 3·43 ± 0·23 3·20	12 3·31 ± 0·23 3·20

* n followed by x, σ, and median of the modal class, in mm.

b) the medium-sized hybrid tadpoles I come near to *B. bombina* (LINNAEUS), whereas the large ones resemble *B. variegata* (LINNAEUS) (the lack of increment in the width of the mouth brings about its small measurements in the group of large tadpoles, which makes them similar to *B. variegata* (LIN-

NAEUS), characterized by smaller measurements of the mouth than *B. bombina* (LINNAEUS);

c) hybrids II, as medium-sized tadpoles, have an intermediate mouth width and, as large tadpoles, a width approximating to that in *B. variegata* (LINNAEUS).

5. Interrelations between the tooth-rows of the upper lip

The observations consisted here in establishing which of the tooth-rows of the upper lip in *Bombina* is longer. On account of the quantitative nature of this character and the necessity of introduction of classes, a system of points has been adopted for evaluation of characters to make the comparison of various groups of the material easier. The results obtained are summed up in Table 4, which shows that

Table 4

Tooth-rows of the upper lip

Material	n	Upper row longer at least on one side, in %	Rows of the same length, in %	Lower row longer at least on one side, in %	Total of points *
B. bombina 10—19 mm	21	28·6	52·4	19·0	209·1
B. bombina 20—39 mm	38	13·0	42·0	44·0	167·3
Hybrid I. (♀ *B. bombina*) 20—39 mm	56	71·4	23·2	5·4	266·8
Hybrid II. (♀ *B. variegata*) 20—39 mm	34	50·0	41·2	8·8	241·5
B. variegata 20—39 mm	22	59·0	27·3	13·7	245·3

* 1% of specimens with the upper row longer — 3 points.
1% of specimens with equal rows — 2 points.
1% of specimens with the lower row longer — 1 point.

a) the tadpoles of *B. bombina* (LINNAEUS), divided into size groups, present evident ontogenetic differences. In small tadpoles (10—19 mm), in opposition

to the other specimens of this species, the upper tooth-row is more often longer (Fig. 1b, c) and, consequently, the lower tooth-row is longer far more rarely. Therefore, small tadpoles have an intermediate position between the medium-sized and large tadpoles of *B. bombina* (LINNAEUS) and the tadpoles of *B. variegata* (LINNAEUS);

b) the longer upper tooth-row predominates in *B. variegata* (LINNAEUS) (Fig. 1f);

c) in hybrids I and II the proportions are similar to those in *B. variegata* (LINNAEUS) (Fig. 1d, e).

6. Shape of the upper jaw

In order to give a detailed account of various shapes of the upper jaw, they were classified in 7 groups (Fig. 2); the strongly concave type of the

Table 5

Shape of the upper jaw *

	B. bombina	Hybrid I. (♀ *B. bombina*)	Hybrid II. (♀ *B. variegata*)	*B. variegata*
A. Tadpoles with a body length of 10—19 mm				
Statistical data **	19 3·16 2			
B. Tadpoles with a body length of 30—39 mm				
Statistical data	26 3·93 4	15 2·87 2	16 2·44 2	11 5·37 5
C. Tadpoles with a body length of 30—39 mm				
Statistical data	3 4·00 4	12 2·00 2	18 2·50 2	8 4·50 4

* Upper-jaw arch strongly concave — 7 points
„ „ „ sligthly „ — 6 points
„ „ „ almost even — 5 points
„ „ „ slightly convex — 3 points
„ „ „ strongly „ — 1 point

** n followed by x, σ and modal class, in points.

upper-jaw arch (Fig. 2a) was marked with the largest number of points (7), and next the number of points diminished successively to 1 for the most convex arch of the jaw (Fig. 2g). The table provides the mean for each group of the material, calculated from the number of points of all its members. Table 5 reveals that

Fig. 2. Shape of the upper-jaw arch of *Bombina* tadpoles a) strongly concave — 7 points, b) concave — 6 points, c) slightly concave — 5 points, d) almost even — 4 points, e) even — 3 points, f) slightly convex — 2 points, g) strongly convex — 1 point

a) some changes in the shape of the upper-jaw arch take place in the Fire-Bellied Toad and Yellow-Bellied Toad in the course of ontogenesis. The upper jaw ranges from slightly convex (Fig. 2f) in small tadpoles of *B. bombina* (LINNAEUS) and slightly concave (Fig.2c) in medium-sized tadpoles of *B. variegata* (LINNAEUS) to exactly equal arches in large tadpoles of both species (Fig. 2e);

b) hybrids do not usually differ from each other and in opposition to both the parental forms have the upper jaw slightly convex (Fig. 2f) and remaining unchanged in the course of ontogenesis.

7. Tooth-rows of the lower lip

The tooth-rows of the lower lip of *B. bombina* (LINNAEUS) have, as a rule, a distinctive bend upwards in the middle of their course (Fig. 1b). The tooth-rows of the lower lip of *B. variegata* (LINNAEUS) are generally fairly even (Fig. 1f) and the first of them has often an indentation in the middle. In the hybrids the first tooth-row is even and the second bent upwards in the middle. The third row is even in hybrids I and bent upwards in hybrids II (Fig. 1d, e).

8. Gap in the first lower tooth-row

Table 6 shows that

a) changes in the occurrence of a gap in the first lower tooth-row are observed during the ontogenesis of *B. bombina* (LINNAEUS). The gap is almost always present in small tadpoles (Fig. 1c), similarly to that in tadpoles of *B. variegata* (LINNAEUS), whereas in large and medium-sized tadpoles it occurs rarely (Fig. 1b);

Table 6

The frequency of a gap in the first lower tooth-row

Material	n	Gap present in %	No gap in %
B. bombina 10—19 mm	21	95·2	4·8
B. bombina 20—39 mm	38	18·0	82·0
Hybrid I. (♀ *B. bombina*)	56	66·0	34·0
Hybrid II. (♀ *B. variegata*)	34	14·7	85·3
B. variegata	20	90·0	10·0

b) in *B. variegata* (LINNAEUS) the gap in the first tooth-row of the lower lipis present in the vast majority of the specimens examined (Fig. 1f);

c) in hybrids I the frequency of gaps is rather intermediate in relation to the tadpoles of parental species, and in hybrids II the situation is analogous to that in *B. bombina* (LINNAEUS) (Fig. 1e).

9. Length of tail fin

The A:B index has been calculated from the total length of tadpoles (A) and the length of the body part which is not covered by the fin (B) (Fig. 3a). The results are given in Table 7.

As can be seen from this table

a) the length ratio of the whole body to its finless portion (A:B) generally undergoes an evident reduction in all the groups of the material in the course of ontogenesis; consequently, in older tadpoles the fin does not reach as far towards the head as in the younger ones;

b) the changes mentioned in a) are statistically insignificant in *B. variegata* (LINNAEUS), which is connected with the fact that even in small tadpoles of this species the fin extends only as far as the base of the tail;

c) *B. bombina* (LINNAEUS) and *B. variegata* (LINNAEUS) differ visibly in the degree to which the tail fin goes beyond the base of the tail on to the dorsum (Fig. 3b, e);

d) both of the types of hybrids do not differ in substance from each other; the medium-sized tadpoles do not differ from the tadpoles of *B. bombina* (LINNAEUS), the large ones generally hold an intermediate position between the parental species, with some inclination towards *B. bombina* (LINNAEUS).

Table 7

Ratio between the total body length and the length of the body portion uncovered with the fin

	B. bombina	Hybrid I. (♀ *B. bombina*)	Hybrid II. (♀ *B. variegata*)	*B. variegata*
A. Tadpoles with a body length of 10—19 mm				
Statistical data *	16 6·96 ± 1·29 7·00			
B. Tadpoles with a body length of 20—29 mm				
Statistical data	31 5·34 ± 0·87 5·00	20 5·08 ± 0·76 5·00	19 5·33 ± 1·15 5·00	10 3·53 ± 0·36 4·00
C. Tadpoles with a body length of 30—39 mm				
Statistical data	3 4·87 ± 0·48 5·00	17 4·37 ± 0·12 4·00	15 4·42 ± 0·74 4·00	13 3·38 ± 0·22 3·00

10. Maculation of the tail fin

Table 8

Maculation of the tail fin **

	B. bombina	Hybrid I. (♀ *B. bombina*)	Hybrid II. (♀ *B. variegata*)	*B. variegata*
A. Tadpoles with a body length of 10—19 mm				
Statistical data ***	24 1·09 1			
B. Tadpoles with a body length of 20—29 mm				
Statistical data	32 1·88 2	16 2·75 3	16 3·32 3	13 3·46 4
C. Tadpoles with a body length of 30—39 mm				
Statistical data	3 3·00 3	13 3·77 4	18 4·00 4	8 3·75 4

* n followed by x, σ, and median of the modal class.

** Intensely spotted fin (numerous and large spots) — 4 points.
Moderately spotted fin (less numerous and smaller spots) — 3 points.
Poorly spotted fin (small and thinly distributed spots) — 2 points.
Non—spotted fin (no spots) 1 point.

*** n followed by $\bar{x}$ and modal class, in points.

The maculation of the tail fin was determined qualitatively using a four-degree scale (see Table 8). The results obtained are offered in Table 8 and illustrated in Fig. 3. The table indicates that

a) with the exception of *B. variagata* (LINNAEUS) whose, even medium-sized, tadpoles are already strongly spotted, all the other groups show an increase in maculation during ontogenesis;

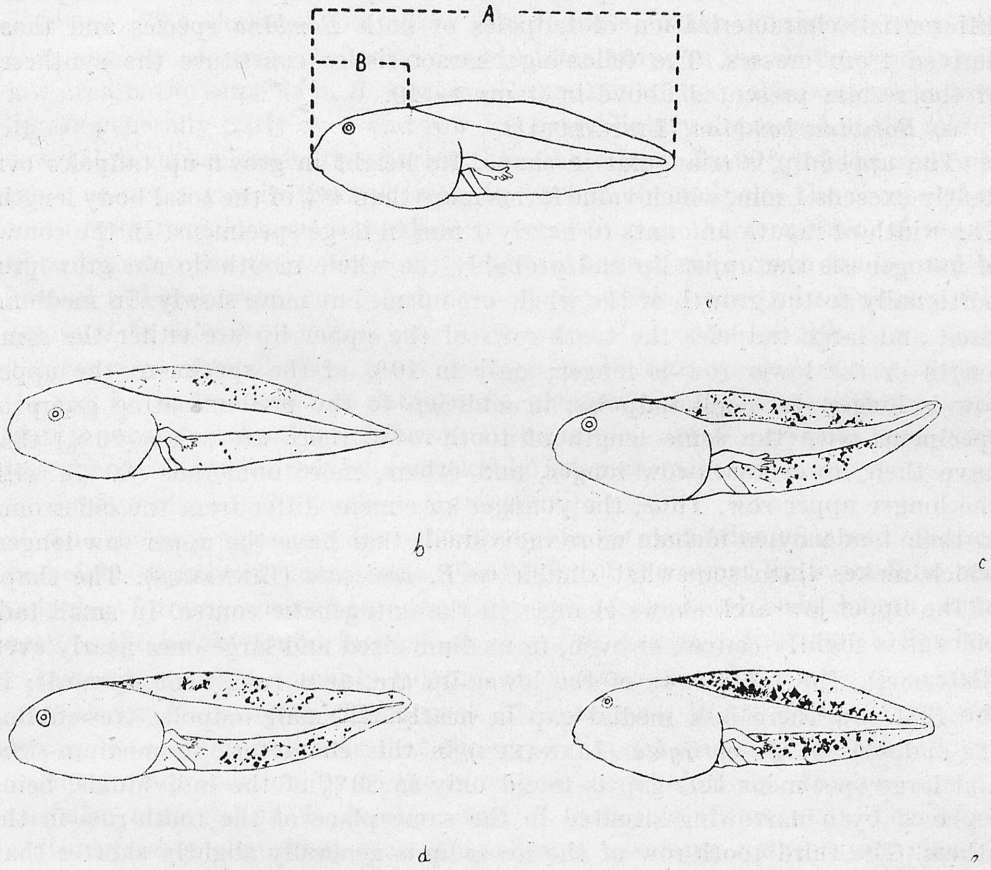

Fig. 3. The length (I) and maculation (II) of the tail fin of *Bombina* tadpoles. I. Fin length, a) measurements of the fin length: A — total body length, B — length of the body portion uncovered with the fin, b) *Bombina bombina* (LINNAEUS), A:B = 4·64, c) hybrid I, A:B = 4·38, d) hybrid II, A:B = 4·0, e) *Bombina variegata* (LINNAEUS), A:B = 3·66. II. Maculation of the fin: b) *Bombina bombina* (LINNAEUS) — poorly spotted fin, c) hybrid I — moderately spotted fin, d) hybrid II — moderately spotted fin, e) *Bombina variegata* (LINNAEUS) — profusely spotted fin

b) the tail fin of *B. bombina* tadpoles is evidently less spotted than that of the tadpoles of *B. variegata* (LINNAEUS) (Fig. 3b, e);

c) there are no major differences between hybrid tadpoles, both of type I and of type II. The medium-sized tadpoles are characterized by intermediate

maculation as compared with the tadpoles of parental species (hybrids II with an inclination towards *B. variegata* (LINNAEUS)), whereas the large tadpoles have the same degree of maculation as *B. variegata* (LINNAEUS) (Fig. 3 c, d).

CHARACTERISTICS OF *BOMBINA* TADPOLES

Now, on the basis of the qualities examined, it is possible to attempt the differential characterization of tadpoles of both *Bombina* species and those derived from crosses. The following characteristics constitute the syntheses of the results presented above in items 1—10.

a) *Bombina bombina* (LINNAEUS)

The upper lip is triangular in shape. Its height in grown-up tadpoles evidently exceeds 1 mm, which value forms more than 4% of the total body length. The width of mouth amounts to nearly 4 mm in large specimens. In the course of ontogenesis the upper lip and probably the whole mouth do not grow proportionally to the growth of the whole organism, but more slowly. In medium-sized and large tadpoles the tooth-rows of the upper lip are either the same length or the lower row is longer; only in 10% of the specimens the upper row is longer. In small tadpoles, in addition to the predominating group of specimens with the same length of tooth-rows, there are some (20%) that have their lower tooth-row longer, and others, more numerous (30%), with the longer upper row. Thus, the younger specimens differ from the older ones in their tendency to include more individuals that have the upper row longer, which makes them somewhat similar to *B. variegata* (LINNAEUS). The shape of the upper-jaw arch shows changes in the ontogenetic course. In small tadpoles it is slightly convex or even, in medium-sized and large ones nearly even (flattened). The tooth-rows of the lower lip are, as a rule, bent upwards; in the first row there is a medial gap in nearly all small tadpoles (resembling the tadpoles of *B. variegata* (LINNAEUS) in this character), in medium-sized and large specimens this gap is found only in 20% of the individuals, being replaced by a narrowing situated in the same place of the tooth-row in the others. The third tooth-row of the lower lip is generally slightly shorter than the second. The tail fin extends on to the dorsum fairly far beyond the base of the tail. The length ratio of the whole body to its portion uncovered by the fin amounts to about 5, and in small tadpoles to about 7. This means that in large tadpoles the fin does not reach as far towards the head as it does in small specimens. There are no dark spots on the tail fin until the tadpole reaches the medium size; then, the spots are small and thinly distributed. They become larger and more numerous, as the animal grows.

b) *Bombina variegata* (LINNAEUS)

The upper lip is elliptical in shape. Its mean height does not reach 1 mm and so the lip is obviously lower than in the Fire-Bellied Toad. The upper-lip height forms a little more than 3% of the total body length. As in *B. bombina* (LINNAEUS), the upper lip and probably the whole mouth do not grow in pro-

portion to the growth of the whole organism but more slowly. The mouth width of grown-up specimens is about 3 mm, and so less than in *B. bombina* (LINNAEUS). This, as well as the data on the upper lip height, indicates that the mouth of *B. variegata* (LINNAEUS) is conspicuously smaller than the mouth of *B. bombina* (LINNAEUS). In most cases (about 60%) the upper tooth-row of the upper lip is longer than the lower one, in about 25% of the specimens both these rows are the same length, and in the rest of tadpoles the lower tooth-row is longer. The shape of the upper jaw changes in the course of ontogenesis from slightly concave to almost even. In large tadpoles the shape of the upper-jaw arch is the same as in *B. bombina* (LINNAEUS). The tooth-rows of the lower lip are generally fairly even and row I is even slightly depressed in the middle; row III is rather evidently shorter than the others. In 90% of the specimens there occurs a gap in the first row. In part of the tadpoles the course of the tooth-rows reveals some irregularities consisting in the formation of connections between the rows. The tail fin does not, as a rule, reach far beyond the base of tail and hence the length ratio of the whole body to its finless portion amounts to 3·5. No changes are observed in the value of this ratio during ontogenesis. Instead, there is an increase in the number and size of spots on the tail fin in the course of ontogenesis, though in comparison with the analogous groups of *B. bombina* (LINNAEUS) the tadpoles of *B. variegata* (LINNAEUS) are always characterized by remarkably intenser maculation.

c) Hybrids I (♀ *B. bombina* (LINNAEUS))

The shape of the upper lip is intermediate between triangular and elliptical, its height slightly exceeds 1 mm. The height of the upper lip in medium-sized tadpoles, forming somewhat more than 4% of the total body length, comes near to the height found in the tadpoles of *B. bombina* (LINNAEUS). For large tadpoles this value amounts to somewhat more than 3% and approximates to that for *B. variegata* (LINNAEUS). This decrease in the value of the ratio during ontogenesis indicates that the upper lip and probably the whole mouth do not grow proportionally to the growth of the whole body. This phenomenon was also observed in *B. bombina* and *B. variegata* (LINNAEUS). The mouth width averages somewhat more than 3 mm, assuming values approximating to those for *B. bombina* (LINNAEUS) in medium-sized tadpoles and to those for *B. variegata* (LINNAEUS) in the large ones. The lengths of tooth-rows of the upper lip resemble the arrangement in *B. variegata* (LINNAEUS), because the upper row is mostly the longer of the two, though in a number of specimens (about 25%) the tooth-rows are the same length, and in very few tadpoles (about 5%) the lower row is longer. The shape of the upper-jaw arch is slightly convex and shows no major changes during ontogenesis. At the same time it differs from the shape observed in the tadpoles of the parental species. Out of the tooth-rows of the lower lip, rows I and III are generally even (as in *B. variegata* (LINNAEUS)) and tooth-row II is bent in the middle (as in *B. bombina* (LINNAEUS)). A gap in the first row is present in nearly 70% of the tadpoles of this group, which value is rather intermediate between the 20% in the

Fire-Bellied Toad and 90% in the Yellow-Bellied Toad. In medium-sized tadpoles the tail fin reaches a fairly long distance towards the head (the index value is 5, as in *B. bombina* (LINNAEUS)), in large tadpoles it does not extend far beyond the base of the tail (the index amounts to 4 and lies between those for the parental species, displaced a little towards *B. bombina* (LINNAEUS)). The maculation of the tail fin increases in the course of ontogenesis, being intermediate in medium-sized specimens and equalling that in *B. variegata* (LINNAEUS) in the large ones.

d) Hybrids II (♀ *B. variegata* (LINNAEUS))

In medium-sized tadpoles the upper lip is elliptical, in large ones it assumes a form which is more intermediate between an ellipse and a triangle. Its height fluctuates about 1 mm, having intermediate values in medium-sized tadpoles, and still intermediate, but approximating more to those found in *B. variegata* (LINNAEUS), in large tadpoles. The upper lip height forms about 3·5% of the total body length. The value of this index is approximately intermediate in relation to the values for the tadpoles of parental species; in medium-sized specimens it is, however, somewhat displaced to the side of the values for *B. variegata* (LINNAEUS). As may be inferred from the fact that no changes of the index value take place during ontogenesis, the upper lip as well as, probably, the whole mouth, grows proportionally to the growth of the whole organism. The mouth width is about 3 mm, in medium-sized tadpoles it takes intermediate values and in large ones approximates to the typical width of *B. variegata* (LINNAEUS). The lengths of tooth-rows of the upper lip are similar to those in *B. variegata* (LINNAEUS). The shape of the upper-jaw arch reveals no distinct changes in the course of ontogenesis and is, in opposition to the shape in the tadpoles of parental species, very slightly convex. The second and third tooth-rows of the lower lip are, as a rule, bent upwards in the middle; this is sometimes true of the first row as well. A gap is very rarely present in the first row. The course of the tooth-rows and, usually, the lack of the gap make hybrids II similar to *B. bombina* (LINNAEUS). An additional, rather reduced, fourth tooth-row was observed in one tadpole. The tail fin of medium-sized tadpoles extends a fairly long way forward (the index amounts to 5, just as in *B. bombina* (LINNAEUS), in large tadpoles it does not go far beyond the base of tail (the value of the index is 4 and lies between the values for the tadpoles of parental species, being somewhat displaced towards *B. bombina* (LINNAEUS)). The maculation of the tail fin increases in the course of ontogenesis; in medium-sized tadpoles it is intermediate and in large ones the same as in *B. variegata* (LINNAEUS).

DISCUSSION

The method of collection of material adopted for this study departs from the method generally used in studies of this type, consisting in artificial insemination. The method of artificial insemination, especially that recommended

by RUGH (1948), has many advantages. Among other things, owing to the possibility of fertilization of a part of eggs of one female with the sperm of its own species and the other part with the sperm of another species, this method makes it possible to carry out a comparison between control specimens and those obtained from crosses as regards their viability and external characters. However, the use of this method for *Bombina*, the females of which produce very few eggs, would not be very fruitful. In addition, the evasion of the mechanisms of natural pre-mating isolation through the application of artificial insemination, to be sure, facilitates the obtainment of the progeny, but gives no information on the nature of these mechanisms, so poorly known just in *Bombina*. The crossing of *Bombina* carried out in this work was not quite natural (e. g., injections of gonadotrophin), none-the-less it was possible to establish that, for instance, a male of *B. variegata* (LINNAEUS) and a female of *B. bombina* (LINNAEUS) are very easily induced to join in amplexus. It is interesting that the cases of interspecific amplexus between members of *Bombina*, observed by the author at Paszkówna, Wadowice District, (MICHAŁOWSKI, 1958) also concerned males of *B. variegata* (LINNAEUS) and females of *B. bombina* (LINNAEUS). The author has never observed spontaneous amplexus in the reversed direction. Consequently, to provoke amplexus and obtain spawn it was necessary to apply very strong hormonal stimulation in two successive seasons (besides, in different specimens). Moreover, in the first year of experimentation very little spawn was obtained from the cross between male Fire-Bellied Toads and female Yellow-Bellied Toads, and only a small proportion of this spawn developed into tadpoles. These observations suggest that the crosses of *Bombina* in this direction take place very rarely under natural conditions.

Two forms of pre-mating isolation may come into play here. One of them is differences in mating voices of males of both species, for, as has been established in a number of species of the *Salientia*, especially the American ones, the females of anurans recognize the voices of their own or a related species and following them choose their mates (BLAIR & LITTLEJOHN, 1960; FOUQUETTE, 1960; LITTLEJOHN et al., 1960; MECHAM, 1961). In the given case these differences would be particularly significant to female *B. variegata* (LINNAEUS). Isolation resulting from differences in the degree of roughness of the dorsal skin, which is smooth in *B. bombina* (LINNAEUS) and rough in *B. variegata* (LINNAEUS), may be also of some importance. In this case the distinguishing party would be the male.

For the sake of accuracy it should be mentioned that sometimes the author encountered also difficulties in bringing about amplexus between a male of *B. bombina* (LINNAEUS) and a female of the same species. For this reason one cannot exclude the possibility that under laboratory conditions males of *B. bombina* (LINNAEUS) show disinclination for amplexus irrespective of the species represented by the female mated to them.

The present investigations throw some light also on the occurrence of such forms of after-mating isolation in *Bombina* as those resulting from the disa-

greement of sex cells and the inviability of hybrids. As it appeared, the percentage of fertilized eggs, the embryonic development and, lastly, the development of tadpoles in the progeny of crossed specimens did not differ from those in the controls. The phenomenon of heterosis, frequent in hybrid larvae of amphibians (BENAZZI, 1957; FOUQUETTE, 1960; SPURWAY & CALLAN, 1960; VOLPE, 1960), has not been found in tadpoles of *Bombina*. In the end, all the available data indicate that, however not unlimited, crossing between members of *Bombina* in the wild and the survival of the offspring that arises from it are greatly probable.

In addition to the methodical problems analysed above and the problems, associated with them, concerning the possibility of obtainment of *Bombina* hybrids, the picture of characters of *Bombina* tadpoles on the background of the data from literature requires a wide discussion.

Out of the most striking characters, the comparatively small size of tadpoles, though not worked out in detail in this study, is worth mentioning. A number of authors give the following measurements of *Bombina* tadpoles: SCHREIBER (1912) 40—50 mm for *B. variegata* (LINNAEUS) and 50 mm for *B. bombina* (LINNAEUS), WERNER (1932) 36 mm for *B. variegata* (LINNAEUS) and 50 mm for *B. bombina* (LINNAEUS), TERENTYEV and CHERNOV (1949) 50 mm for both species. The tadpoles used for this study were, at most, 36 mm long, approximating in size to the tadpoles recorded by BAYGER (1937), with their length of 35—40 mm in both species and those of JUSZCZYK and SZARSKI (1950) measuring up to 40 mm. Perhaps the tadpoles from Poland, really, do not go beyond the limits given by these authors, or we have here to do with the effect of laboratory conditions, in which tadpoles are often smaller than at liberty (MORIYA, 1954).

In this work, special attention was given to the morphology of the mouth in tadpoles. In literature, great stress has so far been laid, above all, on the specific differences in the shape of the closed mouth, or in the shape of the upper lip, which is triangular in the Fire-Bellied Toad and elliptical in the Yellow-Bellied Toad (SCHREIBER, 1912; WERNER, 1932; BAYGER, 1937; JUSZCZYK & SZARSKI, 1950; FROMMHOLD, 1959; MERTENS, 1960b; BERGER & MICHAŁOWSKI, 1963). This trait is considered to be the principal taxonomic character distinguishing the tadpoles of both species, and this opinion has been corroborated by the results of investigations obtained by the author. It appears as well that the value of this character can be expressed quantitatively in the form of an index — upper-lip height: body length — and that the ranges of variation of the index are different in these species. At the same time it will be seen from the data given in Tables 1 and 3 that both the height and width of the mouth are conspicuously larger in *B. bombina* (LINNAEUS), i. e., that the mouth in this species is altogether larger. This can also be seen in Fig. 1b, f. Although this distinctive character has not been described hitherto, it should be emphasized that the drawings of mouths of *Bombina* offered in the keys by WERNER (1932), BAYGER (1937), and MERTENS (1960b) would indicate a similar situation.

The shape of the upper-jaw arch has not been analysed in detail before; however, the data obtained from the drawings published by different authors (in particular SCHREIBER, 1912; WERNER, 1932; TERENTYEV & CHERNOV, 1949; FROMMHOLD, 1959) seem to point to the fact that the upper-jaw arch is convex in the middle in *B. bombina* (LINNAEUS) and concave in *B. variegata* (LINNAEUS) (BERGER & MICHAŁOWSKI, 1963). In the light of the present investigations it turns out that the convex shape of the upper-jaw arch is characteristic only of small tadpoles of *B. bombina* (LINNAEUS), whereas the slightly concave arches are typical only of medium-sized tadpoles of *B. variegata* (LINNAEUS). Therefore, the size of specimens being described is of great importance to the quality of results, and the data obtained hitherto, based perhaps only on specimens of small size, should be treated with reserve.

Few data are also provided in literature as far as the course and length of the labial tooth-rows are concerned. The drawings presented by various authors in their papers show that the upper tooth-row (I) of the upper lip is longer than the lower row (II) in the Fire-Bellied Toad, whereas this relation is reversed in the Yellow-Bellied Toad (MERTENS, 1960b, and other authors). My own investigations reveal that it is just in the Yellow-Bellied Toad that the upper row is generally longer and in the Fire-Bellied Toad the tooth-rows are either the same length or the lower one is longer. Thus, these results disagree with the data established so far, and the fact that in *B. bombina* (LINNAEUS), in accordance with the observations published in literature, the upper row is longer much more frequently in small tadpoles than in large ones deserves notice. Small tadpoles of *B. bombina* (LINNAEUS) approximate to some extent to the tadpoles of *B. variegata* (LINNAEUS) in this respect, which is the more interesting because the similarity can also be observed in the occurrence of a gap in the first tooth-row of the lower lip, which will be discussed below.

According to the available data these two species differ also in the tooth-rows of the lower lip. The course of these tooth-rows in *B. variegata* (LINNAEUS) is fairly even and even slightly indented. The first of the rows is continuous. In *B. bombina* (LINNAEUS) they are bent upwards in the middle, and the first of them (the upper one) is interrupted in the middle (SCHREIBER, 1912; WERNER, 1932; BAYGER, 1937; TERENTYEV & CHERNOV, 1949; MERTENS, 1960b; BERGER & MICHAŁOWSKI, 1963). The results obtained by the author are on the whole in keeping with the data found in literature in so far as the course of tooth-rows itself is concerned, but they differ as to the presence or lack of a gap, for its occurrens appears to be typical just of *B. variegata* (LINNAEUS) (about 90% of the cases) as well as of small tadpoles of *B. bombina* (LINNAEUS). Medium-sized and large tadpoles of the latter species have a narrowing in the middle of the first tooth-row, whereas the gap is present in only about 20% of the specimens.

To conclude these considerations on the labial teeth it should be mentioned that the dental formula was 2/3 in nearly all the specimens of *Bombina* tadpoles in the author's material, which is consistent with the data from literature.

and only in one hybrid II it was 2/4. Thus, no distinct variation of the dental formula was found such as that observed in a number of species of the genera *Bufo*, *Scaphiopus* and *Rana* (VOLPE, 1955; VOLPE & HARVEY, 1958; KAWAMURA & KOBAYASHI, 1960; MERTENS, 1960a; VOLPE et al., 1961; HARVEY et al., 1963).

In addition to the characters of the mouth, some characters of the tail fin were also examined. A fairly great convexity of the dorsal portion of the tail fin in the Fire-Bellied Toad, in which, besides, this fin is said to extend markedly farther towards the head than in the Yellow-Bellied Toad, is evident in the drawings of *Bombina* tadpoles offered by different authors (SCHREIBER, 1912; TERENTYEV & CHERNOV, 1949; JUSZCZYK, 1954; MERTENS, 1960b). The present investigations show that in *B. bombina* (LINNAEUS) the tail fin really extends farther towards the front of the body than it does in *B. variegata* (LINNAEUS), but they do not confirm the existence of differences in the shape of the upper part of the fin. Either these differences appear only in very young tadpoles, which have not been included in these studies, or they arose under the influence of laboratory conditions, for the shape of the tail fin is changeable and often depends on living conditions (MERTENS, 1960a).

The observations on the maculation of the tail fin provide some instructive data. So far attention has generally been given only to the network formed by thread-like processes of melanophores in the tail and characteristic of the genus *Bombina*. This distinctive trait, worked out in detail by HOYER (1911), is used as an important generic character at identification. Besides this network, on the tail fin there occur more or less numerous dark spots, which are accumulations of dendritic (stellate) melanophores. The maculation increases in the course of ontogenesis and it is far intenser in the yellow-bellied toad. Some fragmentary data, in line with those given above, can be found also in such authors as HOYER (1911), SCHREIBER (1912), and MERTENS (1960b). The increase of maculation on the tail and tail fin during ontogenesis seems to be a fairly general property of tadpoles of the Salientia, as it has been found, for instance, in *Rana pipiens* SCHREBER (VOLPE, 1955), *Bufo valliceps* WIEHMANN and *B. fowleri* HINCKLEY (VOLPE, 1956), *Rana palmipes* SPIX (VOLPE & HARVEY, 1958), and *Hyla avivoca* VIOSCA (VOLPE et al., 1961).

The data obtained by the author make it possible to augment the number of distinctive characters for both the *Bombina* species. The table of the most significant and reliable taxonomic characters presented below, however, refers to tadpoles which are somewhat grown up (body length 20 mm or more, stage 53 after NIEUWKOOP & FABER, 1956). Besides, it should be kept in mind that almost each character analysed in this paper shows ontogenetic variation, and for this reason tadpoles used for comparisons ought to be picked out so as to resemble each other in size and developmental stage. Finally, it may be added that at the work with considerably larger tadpoles than those described here there is a great probability of finding somewhat different proportions and then the data given below would require a preliminary verification.

Table 9

The most important taxonomic characters of *Bombina* tadpoles

No	Character	*Bombina bombina* (LINNAEUS)	*Bombina variegata* (LINNAEUS)
1.	Shape of the upper lip in the relatively closed mouth	triangular	elliptical
2.	Relative size of the mouth in more or less uniform specimens	mouth evidently larger	mouth evidently smaller
3.	Course of tooth-rows of the lower lip	bent upwards in the middle	even or even indented
4.	Gap in the first tooth- row of the lower lip	rarely present	nearly always present
5.	Numerical value of the relation of the total length to the length of the body portion uncovered with the fin	about 5·0	about 3·5
6.	Maculation of the tail fin in more or less equal specimens	evidently poorer	evidently more intense

Next to the determination of the taxonomic value of characters for tadpoles of parental species, the phenotype of hybrids and its variability deserve careful consideration. In the first place, it is evident that the appearance of hybrids generally varies with direction of crosses. Only in 4 out of the 10 characters taken into account the hybrids are more or less analogous; these are the size of the mouth, the shape of the upper jaw, and the length and maculation of the tail fin. The shape of the upper jaw is different from that in either of the parents.

A number of alleles, showing no distinct domination and cooperating with one another, seem to be responsible for the quantitative nature of the characters discussed in this paper and for the great variation and heterogeneity of F_1 hybrids (SRB & OWEN, 1959 — polygenic determination of characters). Moreover, the non-homozygosis of the parents in respect of some of these alleles should also been taken into consideration, since in view of the lack of uniformity it is greatly possible even in control tadpoles.

Qualitatively, the phenotype of hybrids shows indubitable and simultaneous maternal and paternal influences. The characters of the upper lip, such as its shape and height, reveal, especially at the earliest of the ontogenic stages examined by the author, the influence of the mother. On the other hand, various

characters of the tooth-rows of the upper and lower lips derive evidently from the father (see Tables 1, 4, and 6, the characteristics of particular groups of *Bombina* tadpoles, Fig. 1).

The heterogeneity of hybrids cannot be explained by the sex-linkage of some characters, though this conception might seem suggestive. If such a linkage came into play, not only both types of hybrids would differ from each other, but also within a population of either of them males would be unlike females, which would produce a two-peak course of the frequency curve. However, it has been established on the basis of the material used for study that particular characters are represented by one-peak curves.

It should be emphasized that, whereas medium-sized hybrid tadpoles I are similar to *B. bombina* (LINNAEUS) in most of their characters and medium-sized hybrid tadpoles II are generally intermediate in comparison with the tadpoles of parental species, the large tadpoles of both types of hybrids rather resemble *B. variegata* (LINNAEUS) in respect of most of their characters. This would thus indicate that the majority of the dominant alleles responsible for particular characters under discussion are included in the genotype of *B. variegata* (LINNAEUS).

VOLPE (1956, 1959b, 1960) obtained similar results for hybrids of various species of American toads, and KAWAMURA and KOBAYASHI (1960) for hybrids between *Rana japonica* GUENTHER ♀ and *R. arvalis* NILSSON ♂. Their materials, too, showed a mosaic of parental characters in hybrids, which however at the same time approximated to the tadpoles of one of their parents. KAWAMURA and KOBAYASHI (1960) obtained different dental formulas for hybrid tadpoles according to the direction of crossing. VOLPE (1959) was concerned in the quantitative aspect of some of the characters examined and in the role played by polygenes in the induction of great variation in the characters of hybrid tadpoles of American toads. Some particularly interesting data were published by MONTALENI (1933), who failed to find any paternal characters in very young hybrid tadpoles derived from *Bufo bufo* (LINNAEUS) ♀ and *B. viridis* LAURENTI ♂. These characters appeared at a later stage of ontogenesis. A similar change in the penetrating power of genes of the parental species during ontogenesis is quite evident in the present study as well and, as has already been mentioned, the penetrating power of the genes of *B. variegata* (LINNAEUS) increases with the age of tadpoles.

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STRESZCZENIE

Celem badań niniejszych było: 1) przeanalizowanie na materiale własnym podawanych w dotychczasowej literaturze najważniejszych cech taksonomicznych kijanek kumaków, 2) ewentualne wyszukanie nowych cech, 3) ilościowe w miarę możliwości ujęcie opracowywanych cech taksonomicznych, 4) dokonanie wymiennej krzyżówki kumaków, 5) opisanie fenotypu kijanek-mieszańców. Materiał wyjściowy (dorosłe żaby) pochodził z terenów dobrze opracowanych pod względem rozmieszczenia geograficznego kumaków i zasiedlonych wyłącznie przez formy typowe. Otrzymano kijanki z następujących kombinacji par rodzicielskich: a) *Bombina bombina* (LINNAEUS) ♀ × *B. bombina* (LINNAEUS) ♂, b) *B. bombina* (LINNAEUS) ♀ × *B. variegata* (LINNAEUS) ♂, c) *B. variegata* (LINNAEUS) ♀ × *B. bombina* (LINNAEUS) ♂, d) *B. variegata* (LINNAEUS) ♀ × *B. variegata* (LINNAEUS) ♂. Przed połączeniem par stosowano injekcję gonadotropiny. Ponieważ rozwój kijanek przebiegał na ogół we wszystkich kombinacjach prawidłowo a w kombinacji b) stwierdzano wielokrotnie spontaniczny amplexus jeszcze przed podaniem zwierzętom gonadotropiny, dlatego też istnieją podstawy do twierdzenia, że krzyżowanie się kumaków, choć nie nieograniczone, może mieć miejsce w wolnej przyrodzie.

Na utrwalonych kijankach rozpatrzono następujące cechy: kształt górnej wargi, wysokość górnej wargi, stosunek wysokości górnej wargi do długości ciała, szerokość pyszczka, wzajemną długość pasm ząbków wargi górnej, kształt górnej szczęki, przebieg pasm ząbków wargi dolnej, występowanie przerwy środkowej w I (górnym) pasmie ząbków wargi dolnej, długość płetwy ogonowej, plamistość płetwy ogonowej. Opisywane cechy ujęto w miarę możliwości ilościowo i opracowano statystycznie. Najistotniejszymi dla celów taksonomicznych okazały się następujące cechy: kształt górnej wargi (trójkątny u kumaka nizinnego i eliptyczny u kumaka górskiego), względna wielkość pyszczka (kumak nizinny posiada pyszczek znacznie większy), przebieg pasm ząbków wargi dolnej (wygięte ku górze u kumaka nizinnego a proste u kumaka górskiego), występowanie przerwy w I pasmie ząbków wargi dolnej (rzadko obecna u kumaka nizinnego, prawie zawsze obecna u kumaka górskiego), długość płetwy

ogonowej (u kumaka nizinnego sięga ona znacznie dalej dogłowowo niż u kumaka górskiego), plamistość płetwy ogonowej (u kumaka górskiego jest znacznie bardziej plamista). Kijanki-mieszańce obydwu typów wykazują dość dużą zmienność i są do siebie pod względem większości cech niepodobne. Za ten stan rzeczy jest prawdopodobnie odpowiedzialna poligeniczna determinacja rozpatrywanych cech i niehomozygotyczność form rodzicielskich. Dają się również zauważyć wyraźne wpływy matczyne lub ojcowskie na determinację niektórych cech. Można za to raczej wykluczyć ewentualne sprzężenie niektórych cech z płcią. Ogólnie mieszańce są bardziej podobne do kijanek kumaka górskiego, a podobieństwo to uwidacznia się szczególnie w późniejszych okresach ich ontogenezy.

РЕЗЮМЕ

Целью настоящих исследований было: 1) анализ на собственном материале основных таксономических признаков головастиков жерлянок, описанных до сих пор в литературе, 2) обнаружить, по возможности, новые признаки, 3) охватить в исследованиях как можно большее количество обнаруженных таксономических признаков, 4) проведение переменного скрещивания жерлянок, 5) описание фенотипа головастиков гибридов. Исходный материал (взрослые жерлянки) добывался в местностях, хорошо исследованных в смысле географического размещения жерлянок и заселённых исключительно типичными формами. Получено головастики следующих комбинаций родительских пар: a) *Bombina bombina* (Linnaeus) ♀ × *B. bombina* (Linnaeus) ♂, b) *B. Bombina* (Linnaeus) ♀ × *B. variegata* (Linnaeus) ♂ c) *B. variegata* (Linnaeus) ♀ × *B. bombina* (Linnaeus) ♂, d) *B. variegata* (Linnaeus) ♀ × *B. variegata* (Linnaeus) ♂.

Перед случением пар применялась иньекция гонотропина. Так как развитие головастиков проходило в общем во всех случаях правильно, а в комбинации в) неоднократно обнаруживался спонтанический амплексус ещё перед применением гонадотропина, поэтому имеется основание к утверждению, что скрещивание жерлянок, хотя и неограниченное, может однако иметь место в природе. У фиксированных головастиков наблюдениям подвергались следующие признаки: форма верхней губы, высота верхней губы, соотношение высоты верхней губы к длине тела, ширина лицевой части головы, взаимоотношение длины рядов зубков верхней губы, форма верхней челюсти, размещение рядов зубков нижней губы, выступание срединного промежутка в I (верхнем) ряде зубков нижней губы, длина хвостового плавника, пятнистость хвостового плавника. Исследованиям подвергалось как можно большее количество вышеуказанных признаков и проведена их статистика. Самыми существенными для таксономических целей оказались следующие признаки: форма верхней губы (треугольная у крснобрюхой жерлянки и элипсообразная у желтобрюхой жерлянки), относительная вели-

чина лицевой части головы (у краснобрюхой жерлянки лицевая часть головы значительно больше), расположение зубков нижней губы (выгнуты вверх у краснобрюхой жерлянки и ровные у желтобрюхой), выступание промежутка в I полосе зубков нижней губы (очень редко выступает у краснобрюхой жерлянки и почти всегда присутствует у желтобрюхой жерлянки), длина хвостового плавника (у краснобрюхой жерлянки тянетса гораздо дальше к голове, чем у желтобрюхой жерлянки), пятнистость хвостового плавника (у краснобрюхой жерлянки гораздо более пятнистый). Головастики-гибриды обоих типов обнаруживают большую изменчивость и большенством признаков отличаются друг от друга. Причиной такого явления является вероятно полигеническая детерминация рассматриванных признаков и не гомозиготичность родительских форм. Наблюдается также ярко выраженное материнское либо отцовское влияние на детерминацию некоторых признаков. Можно зато исключить возможное соединение некоторых признаков с полом. В общем головастики имеют большее сходство с желтобрюхой жерлянкой и это сходство становится особенно выразительным в позднейших стадиях онтогенеза.

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