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TAXONOMIC STUDIES ON THE MOUTH PARTS OF LARVAL ANURA

WITH THREE FIGURES AND EIGHT CHARTS

BY

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CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE UNIVERSITY OF ILLINOIS
No. 510

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CONTENTS

INTRODUCTION

After some years of using Wright's "Synopsis and Description of North American Tadpoles" (1929), and after discussing various aspects of the paper upon several occasions with Dr. H. J. Van Cleave, it was decided that certain aspects merited further investigation. These were, namely, (1) the uncertain specificity of some described tadpoles, (2) the acknowledged application of the characters used in classifying tadpoles to only "mature" tadpoles, (3) the use of certain relative measurements as taxonomic characters, particularly those of the rows of horny teeth and the beaks of the larval mouth apparatus, without any statement as to the reliability of such relative measurements or as to how and why the particular relative measurements used were chosen. It was at once obviously desirable (1) to determine the applicability to younger tadpoles of characters used in distinguishing "mature" tadpoles, and (2) to determine whether or not there exists any sound and reliable basis for using relative measurements.

It was decided to use the temporary larval mouth apparatus as the object of this study. There were several reasons for choosing the mouth apparatus as an object for such a study. Should it afford satisfactorily constant taxonomic characters, they would be preferable to other characters, because the mouth apparatus will withstand the "hardships of preservation" with less alteration of character than will perhaps any other structure or feature of the tadpole. The body or tail may become torn or shriveled, and colors may fade; but the mouth apparatus remains relatively intact. Also, although taking measurements of small rows of teeth may become tedious, such measurements can be obtained with a great deal more accuracy than is forthcoming from an attempt to determine whether certain spots are "pinkish cinnamon" or "apricot buff"!

The larval mouth apparatus (Fig. 1) is composed of two lips, an upper and a lower. These so-called lips are not entirely separate or distinct; and the apparatus thus has the general shape and appearance of a somewhat flattened or slightly concave disc when the lips are not rolled or curled at the edges. For this reason the apparatus is frequently spoken of as a funnel or disc, and will hereinafter be designated as the "oral disc." The laterally-extending diameter of this disc may be somewhat greater than the antero-posterior diameter. The disc is bordered to a varying extent with papillae, the exact extent and number of rows of which vary in different families and genera. In the center of the disc is the mouth opening, which is immediately bounded by upper and lower "horny" mandibles or beaks. The term "beak," or "horny beak," is more nearly appropriate and avoids confusion. Accordingly, these "horny" beaks will hereinafter be referred to as "upper beak" and "lower beak" respectively. Situated more or less concentrically on the disc are ridges, each of which bears one or two rows of teeth, which teeth are keratinized cells. The number and disposition of these rows of teeth vary in different groups.

However, the number and approximate disposition of the rows of teeth are similar in the species included in this study. A description of the features in common follows.

There is only one row of teeth on a ridge. The rows have the following distribution (Fig. 1): There is an extreme anterior or upper row extending almost completely across the disc. This row is designated variously by different authors (cf. below under "Historical Review"). The more pertinent term, especially when comparing it with other rows of teeth, seems to be "first upper labial row." A second row of teeth is located posterior and/or ventral to the first upper labial row. The lateral ends of this second row are approximately even with those of the first

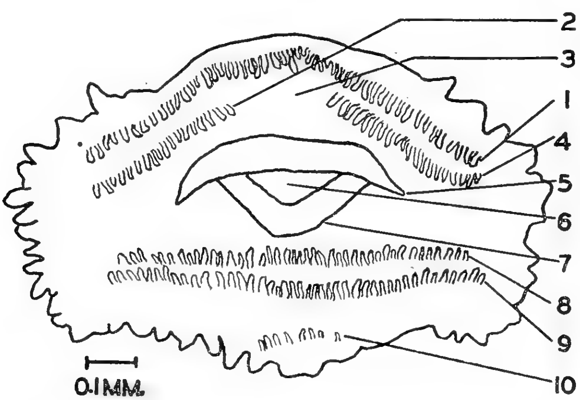

FIG. 1.—Camera lucida drawing of mouth parts of a tadpole of *Pseudacris nigrita triseriata* to show arrangement of teeth. (Body length of specimen, 3.57 mm.)

Key

1. First upper row of teeth
2. Right part of second upper row of teeth
3. Median space in second upper row of teeth
4. Left part of second upper row of teeth
5. Upper beak
6. Mouth opening
7. Lower beak
8. First lower row of teeth
9. Second lower row of teeth
10. Third lower row of teeth

upper row. However, there is a median space devoid of teeth that interrupts the second row, dividing it into right and left parts. This second row is the "second upper labial row."

Below and/or posterior to the mouth opening are three rows of teeth, each of which is more or less complete. There are exceptions which will be discussed later under the heading of the species concerned. These rows are respectively from nearest the mouth opening toward the periphery of the disc "first lower labial row," "second lower labial row," and "third lower labial row." The first and second of these lower rows are approximately of equal lengths and are slightly shorter than the upper rows. The third of the lower rows is shorter than any other row.

Since all the rows are "labial" rows, the terminology adopted for use throughout this study has been shortened and may be introduced at this point as follows (cf. labels of Fig. 1): The first upper labial row is designated as the "first upper row." The second upper labial row is designated as the "second upper row" when the row is referred to as a unit or a *single* row. When reference is to the right or left parts of this row, the terms, "right part of the second upper row," or "left part of the second upper row," are used respectively. The toothless space between the right and left parts is designated as the "median space in the second upper row." The lower rows of teeth are designated respectively as "first lower row," "second lower row," and "third lower row." The first and second upper and first and second lower rows are frequently referred to as the "four longer rows."

The taxonomic characters involving the rows of teeth and the horny beaks that have been used are (1) numbers of rows of teeth, (2) the location of these rows, and (3) the ratios between the lengths of certain rows of teeth and between the length of a given row of teeth and the lateral length of the upper beak. It was decided ultimately to restrict this study to these ratios, or relative measurements, with particular respect to their constancy or variation in tadpoles of different sizes or ages.

In order to study the mouth apparatus in tadpoles of different ages, it was first necessary to secure series of tadpoles of as nearly uniform hereditary constitution as possible and reared under identical conditions so that identity could not be questionable, and so that variation that might occur in individuals of a series could only be attributed to the normal tendency of a given hereditary complex to vary. Collections were made in Mississippi in 1932 and in Illinois and Indiana in 1933.

A review of the literature revealed only the use of relative measurements of the rows of teeth—that is, the relation of the length of one row of teeth to the length of another row of teeth—in identifying mature tadpoles without revealing any systematic study of the constancy of these relative measurements at different ages, or of the basis, real or imaginary, of using such relative measurements at all.

The next step in the study was the taking of various measurements of the body and mouthparts, i.e., rows of teeth and the horny beaks, of each tadpole of each of the series collected. Then a study was made of relative measurements, which were obtained graphically from the actual measurements by plotting various combinations of the latter. From these analyses and studies certain conclusions have been drawn, namely, as to a method and an explainable basis for the use of relative measurements of the mouthparts, as to the combinations of actual measurements affording the most constant relative measurements at all ages, and as to the specific distinctiveness of these relative measurements, and finally as to the reliability of the use of such relative measurements as taxonomic characters.

HISTORICAL REVIEW

A careful survey of the literature has failed to disclose any previous attempts at an analysis such as is made in the present study of the growth phenomena of the parts of the mouth apparatus of tadpoles. Neither has anyone attempted to determine the constancy or lack of constancy at different ages of such ratios of measurements of mouthparts as are used as taxonomic characters. The general attitude seems to have been to limit such characterizations to fully grown tadpoles, with either no indication of the degree of applicability to younger tadpoles of such characterizations, or with an acknowledgment of the limited use to which the characters may be put taxonomically. However, studies on the mouthparts of larval Anura have been abundant, and various characters afforded by the mouthparts have been recognized and recorded by many authors. Therefore, to afford a historical background for the present study, the course of the development of the particularly taxonomic studies on the mouthparts of larval Anura will be reviewed. Reference will also be made to outstanding studies of other than taxonomic aspects.

The earliest reference to studies of any kind on the mouthparts of larval Anura seems to be that made to the *Biblia Naturae* of Swammerdam published in 1738. Swammerdam described and figured the mouth apparatus of a tadpole, distinguishing and describing the individual parts. However, it was approximately a century later before any other observations on mouthparts were made. The first published descriptions after this lapse of a century were those by Martin Saint-Ange in 1831 and Duges in 1834. The first recorded investigation into the formation and development of the horny teeth and mandibles was that of Carl Vogt, published in 1842. He made histological studies of the formation and structure of the teeth and of the mandibles.

Stricker in 1857 described the structure of the papillae of the oral disc and attributed to them the function of tactile organs. Meanwhile various observers had published less pioneer articles involving only mere mention or general descriptions, or treating the histogenesis of the teeth.

The publication marking the beginning of the use of features of the mouth apparatus as taxonomic characters was a paper by Van Bambeke appearing in 1863. He studied the formation and structure of the teeth, mandibles, and papillae of four European species and called especial attention to the fact that there were distinct differences between the respective parts of the mouth apparatus in the different species studied by him. This is the first recorded instance in which attention is called to the fact that differences in the mouth apparatus of different species do exist.

Leydig, in 1874, also called attention to the differences in form and disposition of the mouthparts in different species. Lataste, in 1879, accorded taxonomic value to the forms of individual teeth in different species.

The first detailed studies on differences in the parts of the mouth apparatus in several different species appeared almost simultaneously in America and in Europe. The European publication was a "preliminary communication" by Heron-Royer and Van Bambeke, in which the mouth apparatus of tadpoles of six European species of Anura were described. This "preliminary communication" was followed by a series of papers by Heron-Royer, in which papers the mouth apparatus of more species was described. A final paper by both authors, i.e., Heron-Royer and Van Bambeke appeared in 1889. In this paper are treated the formations of the teeth and mandibles and papillae; but more important from the point of view of the present study are the descriptions of the mouth apparatus in tadpoles of twenty-two species of European toads and frogs. In addition, the distinguishing characters of different species, the characters in common possessed by species of a given genus, and characters possessed by all genera of a family are pointed out. The characters used as taxonomic by these authors are the shape of the oral disc, the number of rows of teeth on a ridge, the number and disposition of the rows of teeth, any peculiarities of the mandibles, and the characters of the individual teeth. However, relative measurements of rows of teeth were not used.

Meanwhile, in January 1882, Mary Hinckley communicated to the Boston Society of Natural History a paper "On some differences in mouth structure of tadpoles of Anourous Batrachians found in Milton, Mass." Miss Hinckley's paper was published only a few months (nine) after the preliminary communication of Heron-Royer and Van Bambeke. That Miss Hinckley was unaware of this European publication when writing her paper is indicated by the fact that she acknowledges the same in a "note" at the end of her paper. Therefore, the two papers may be considered as concurrent. And it is of interest and of note that two such similar studies were under way coincidentally in old and new worlds. Miss Hinckley's paper marked the advent of Americans into the development of the study at hand.

She described the mouth apparatus of tadpoles of nine species, pointing out the family, generic, and specific differences. The characters she used are form of oral disc ("lips"), number, color, and distribution of papillae, and number and disposition of rows of teeth ("fringed folds"). She states, "After the parts of the mouth are developed I have observed no change of form in the folds or papillae." The meaning of this statement depends altogether on how "change of form . . . ." is to be interpreted. Presumably, the intended meaning is that the general pattern of the oral disc (or "lips") and its parts remains about the same. If Miss Hinckley meant that the outlines, proportionate lengths, and interruptions of the rows of teeth ("fringed folds") remain unchanged, her statement must be challenged on the basis of the results of the present study.

She also pointed out that in the Ranidae the papillae are quite frequently replaced by or bear short groups of teeth.

Other papers appearing before the final work of Heron-Royer and Van Bambeke are those by Schultze and by Keiffer in 1888. Both authors treated the formation and distribution of the horny teeth in their respective studies. In 1890 Gutzeit published an account of his studies, both gross and histological, on the formation of the horny teeth and mandibles.

In 1891 G. A. Boulenger published "A Synopsis of the Tadpoles of the European Batrachians." The synopsis is of all larval characters, with considerable attention paid to those of the mouth apparatus. In addition to the characters of the mouth apparatus used by previous authors, Boulenger introduced the use as taxonomic characters of the relationships between the lengths of different rows of teeth. The only rows he used for such purposes were the second and third lower rows, expressing the third lower row as being a certain fraction of the second lower row. It might be stated at this point that Boulenger numbered the lower rows of teeth from the periphery toward the mandible, this method of numbering the lower rows of teeth being the reverse of that used in the present study. The reference above to second and third lower rows is according to the method of numbering used in the present study. Boulenger also described the second upper row ("series") as being "widely" or "narrowly" interrupted. This could, however, hardly be termed a very exact description of the relative width of the median space in the second upper row. As mentioned above, the relation of the length of the third lower row of teeth to the length of the second lower row was expressed as a definite fraction. Therefore, this publication by Boulenger must be considered as marking the beginning of the use of such exact relative measurements of rows of teeth as taxonomic characters. Attention may also be called to the fact that the character descriptions in Boulenger's paper refer only to fully grown tadpoles. To quote his statement, "The development of the larvae is left out of consideration; my descriptions apply merely to the fully-developed tadpole, in the condition generally known as the "third period" in the larval development, the period between the budding of the hind limbs and the bursting out of the fore limbs."

Practically the same synopsis is included in the section on tadpoles of Boulenger's *The Tailless Batrachia of Europe* (1897).

Since these early works no attempts at comprehensive synopses of larval Anura have been made until within recent years. However, many descriptions of tadpoles examined have included a description of the mouth apparatus as a part of the routine description. The characters of the mouth apparatus described are invariably the shape of the oral disc, and the number and distribution of the rows of teeth. Yet, no use seems to have been made generally of the relationships existing between the lengths of rows of teeth as taxonomic characters.

From the time of Miss Hinckley's rather brief paper in 1882 no one attempted a comprehensive survey of the American tadpoles until 1929, when Wright's "Synopsis and description of North American tadpoles" appeared. This was preceded by Wright's "Life Histories of the Anura of Ithaca, New York," which appeared in 1914. These rather widely separated publications represent, according to their author's introductions, studies which began in 1906-1907. Relative measurements of the rows of teeth and the upper mandible were used in characterizing the tadpoles of the eight different species treated in the earlier publication (Wright, 1914). However, since the same species are treated and the same relative measurements are used in the later publication (Wright, 1929), detailed review will be restricted to the latter.

Although this synopsis (Wright, 1929: p. 2.) is specified as applying only to "mature" larvae, since "Half-grown larvae . . . . are often quite abnormal in the usual characters used in larval descriptions" yet rather abundant utilization is made of relative measurements of and ratios between different rows of teeth and/or certain rows of teeth and the upper beak as taxonomic characters. Therefore, this latter being true, and, since the synopsis forms the "point of departure" for the present study, those parts of the synopsis dealing with characters of the horny teeth and beaks may be noted more fully.

If the synopsis or key (Wright, 1929) be examined for the different relative measurements of rows of teeth and/or of rows of teeth and upper beak; and, if the interpretations of many questionable statements be the same as made here, not less than fifty different expressions will be encountered, each being used from one to twenty times. Of these fifty or more ways of expressing the relative measurements used, not less than fifteen are either mathematical impossibilities or of very uncertain meaning.

Further, the number of different terms applied to what is presumably the chord length of a given row or of the upper beak is apparently infinite, and the order of description of various characters is not at all uniform. In a continuous discussion, variations of a given term might be justified as avoiding monotonous repetition without being confusing. But such variations in terms in isolated phrases of a synopsis are both unnecessary and confusing.

It is, of course, obvious that many expressions of relative lengths are synonymous; but more are synonymous than are at first apparent. It might be surprising to discover that relationships of only nine different combinations of lengths of rows and of rows and upper beak are expressed. These nine relationships of lengths or relative lengths could be expressed as simple ratios (of chord lengths), the ratios being expressed as ratios to one. The nine combinations actually involved in the synopsis are as follows: (1) first upper row/second upper row; (2) first lower row/third lower row; (3) second lower row/third lower row; (4) median space in second upper row/right or left parts of the second upper row; (5) first upper row/upper beak; (6) second upper row/upper beak; (7) first lower row/upper beak; (8) second lower row/upper beak; (9) third lower row/upper beak.

Aside from rather questionable or ambiguous statements and lack of uniformity in terminology, attention may be directed to the irregular sequence in the listing of characters in the synopsis. It could be that the order in which characters are listed is an order of importance in being distinctive, although no statement to this effect has been found.

The foregoing has been no attempt to belittle the synopsis (Wright 1929). Rather, it is to be regretted, after such an expenditure of time and effort in collecting the tremendous amount of data which form the basis of the synopsis, that such lack of uniformity in arrangement, presentation, and expression of the material at hand should detract from the usefulness and value of the synopsis.

Since the present study was begun, *Frogs of the Okefinokee* (Wright 1932) and *Handbook of Frogs and Toads* (Wright and Wright 1933) have been published. In the latter publication relative measurements of the rows of teeth are not used in characterizing tadpoles of the different species of frogs and toads. In the former publication (Wright 1932) the synopsis from the 1929 publication is used verbatim except for the omission of the descriptions of twelve species not occurring in the Okefinokee swamp. Eight species not occurring in the Okefinokee swamp are retained in the synopsis, of which eight species three "should" occur in the swamp. However, two other species that do occur and three others that "should" occur in the Okefinokee swamp are not included in the 1932 version of the synopsis. The *"Bufo (Raleigh)"* of the 1929 synopsis is changed to *"Bufo fowleri"* in the 1932 version. Otherwise the two synopses are identical and the later one need be discussed no further.

Noble (1931) does not think that characters of the mouth apparatus have any value as indicating relationships, but does infer that they may afford taxonomic characters. In discussing the value of larval characters in classification, Noble (1926) makes no reference to such characters as form the basis of this study.

The only publication to date that has dealt specifically with variations in the mouth apparatus of tadpoles is a study by Scott-Biraben and Fernandez-Marcinowski that appeared in 1921. Their studies were on groups of tadpoles and treated only variations in number and disposition of the rows of teeth, rows irregularly placed, the substitution of groups of teeth for papillae, the extension of rows of teeth by the appearance of teeth through the papillary border of the oral disc, etc. It may be recalled that Hinckley (1882) also called attention to certain of these variations. However, in no instance have such studies been carried out on a series of tadpoles graded consecutively with respect to age or size.

Considerable reference has been made during the course of this study to Huxley's *Problems of Relative Growth* (1932).

The historical background for this study on the mouth apparatus of tadpoles may be summarized as follows: The mouth apparatus was first described and figured by Swammerdam in 1738, first studied histologically (as to formation of parts) by Vogt in 1842, first recognized as affording taxonomic characters by Van Bambeke in 1863, first studied extensively for specific characters by Heron-Royer and Van Bambeke in Europe in 1881-1889 and by Hinckley in America in 1882, first used as affording specific relative measurements by G. A. Boulenger in a synopsis of European tadpoles in 1891, first studied extensively in American tadpoles for specific relative measurements by Wright in 1914-1929, and first studied particularly as to variations in parts by Scott-Biraben and Fernandez-Marcinowski in 1921, but has never been studied as to constancy (or variation) of specific relative measurements at different (particularly young and intermediate) ages until the present.

MATERIALS AND METHODS

Collections

Pseudacris nigrita triseriata.—The series of tadpoles of *Pseudacris nigrita triseriata* used in this study were reared from the eggs obtained from field-mated pairs taken between 8:00 and 10:00 P.M., March 31, 1932, from a temporary swamp west of Clinton, Mississippi. Each pair taken in amplexus was placed immediately in a separate container. At about 10:30 P.M. these pairs were transferred to separate battery jars. The battery jars contained about two and one-half or three inches of water, in which had been placed a few twigs and dead grass stems. Each battery jar was covered with gauze held in place by rubber bands. All pairs had produced eggs by seven o'clock the next morning. These clutches of eggs were removed to separate containers and allowed to develop. Elodea and algae were kept in the battery jars in which the tadpoles developed.

Samples of from two to six specimens were taken twice daily from April 3rd to April 20th, and once daily thereafter until the supply of tadpoles was exhausted (May 1st). The tadpoles were fixed in Bouin's fluid, and, after the routine washing in alcohols, were finally preserved in 75-80% alcohol. Samples from different clutches of eggs were of course kept separate. However, the studies here reported have shown complete intermingling of characters, so that absolutely no distinction on any basis could be made between the individuals from different parents. All the mated pairs were preserved in formalin on April 4th. Identification of these pairs has recently been made by Dr. G. K. Noble, of the American Museum of Natural History, New York City.

Bufo fowleri.—Eggs were taken in the late afternoon of April 20, 1933, from a small puddle of water in the lily pond on the south campus of the University of Illinois. These eggs are known to have been deposited during the same afternoon in which they were collected. Only *B. fowleri* were observed at this time or at any time during the several days of excessive spawning activity.

The tadpoles were reared in battery jars in which were kept algae and Elodea. The diet of the tadpoles was supplemented with "Justrite" fish food and with fresh beef and liver. The water in the battery jars was kept fresh; and approximately the same number of tadpoles was kept in each jar.

Samples were taken every four hours, beginning the day collected. After the rows of teeth appeared to be well formed, the number of samples per day was reduced, ultimately to two. Samples of this series were taken through May 15th. This series was designated as "B. f.-33-A." The series was supplemented by later collections.

On June 12th Dr. H. J. Van Cleave collected from the same pond from which the eggs were taken earlier a series of tadpoles and young toads. In body size of individuals this series overlapped considerably the series B. f.-33-A; and this series was designated as "B. f.-33-B."

On June 9th, 1934, the author collected a series of tadpoles from the same pond, the body sizes of individuals of which overlap the series B. f.-33-B, and attain the maximum size of tadpoles of the species. This series has been designated as "B. f.-34-A."

The tadpoles of all series of *B. fowleri* were preserved by the same method as that employed in the preservation of the tadpoles of *P. nigrita triseriata.*

It might be stated at this point that the only toads collected or observed over a period of several years anywhere in the vicinity of the pond from which the tadpoles of these series were taken have been *B. fowleri.*

In the actual study of the tadpoles the only selection of any kind exercised was one to secure as even a distribution of body size as possible. Obviously only tadpoles having some traces of rows of teeth and/or horny beaks were studied in detail.

Rana pipiens.—The eggs from which the tadpoles of this species were reared were collected on April 9, 1933 from a pool near Veedersburg, Indiana, by Dr. H. J. Van Cleave. There were two clutches of eggs; and the eggs of each were in all stages of gastrulation the morning of April 10th, when brought to the laboratory.

Samples were taken at intervals of not more than four hours from April 11th to April 23rd, and once or twice daily from the latter date through May 15th.

The tadpoles were reared in finger bowls in which were kept Elodea and algae. The diet of the tadpoles was supplemented with "Justrite" fish food. Beef and liver were not very readily eaten by tadpoles of *R. pipiens,* although offered to them frequently. Water in the finger bowls was kept fresh, and samples were taken from different bowls so as to maintain approximately the same number of tadpoles in each bowl.

The tadpoles of the two series of *R. pipiens* were preserved by the same method as that employed in the preservation of the tadpoles of the other species previously discussed.

Specimens from the preserved series were selected for detailed study, the selection being only to secure as even a distribution of body size as possible over the range of sizes included in the series. Too, only tadpoles with some traces of rows of teeth and/or horny beaks were studied in detail.

Apparatus and Methods of Study

After some "trial and error" the routine technique as described below was followed for all animals examined.

Apparatus.—All studies of animals were through the use of a dissecting binocular microscope. Illumination was from an adjustable spotlight ("Point-a-light"). All body measurements were taken with an ocular micrometer in a 10x ocular, with 55 mm. objective.

Drawings were made through the use of a camera lucida fitted on the dissecting binocular. Some difficulty was experienced in the preliminary attempts in securing uniform magnification in all drawings and in each drawing over the entire field of the microscope. An apparatus was, however, assembled to overcome this difficulty. An adjustable dissecting lens holder was secured. This lens holder had a heavy base, a long arm that could be bent to table level, and a screw adjustment similar to and with about the ratio of that on any ordinary microscope.

In place of the loop holding the lens and forming part of a universal joint there was inserted a ring support, of which the ring was about 10 cm. in diameter. On this ring a "stage" was securely fastened by means of comparatively fine wire. This stage was simply a heavy, layered piece of cardboard about 12 cm. square. Circles were cut from the center of the upper two of the three layers so as to form a "pit" in the center of the stage. These circles were of such a diameter as to exactly accommodate a Syracuse watch glass. Thus a watch glass could be turned in the circular pit thus formed on the stage but could not slip at all from side to side as the stage was placed at precarious angles. Further, this stage could be tilted at any angle and in any plane, and could be raised and lowered by means of the screw adjustment of the lens holder supporting it.

With this adjustable stage entirely apart from the dissecting binocular microscope, the microscope could be set at a fixed elevation, and the arm length and angle of the mirror of the camera lucida set at a fixed length and angle respectively. These "fixed" adjustments were such as to insure uniform magnification of the entire field and at all times, provided the object examined were at all points in sharp focus, to insure which latter involved tilting the adjustable stage so that the object examined would have its plane perpendicular to a line drawn through the axis of the objective used in making the camera lucida drawings.

10x oculars and 25 mm. objectives were used; and through use of a slide micrometer the above mentioned adjustments were so made as to make possible a drawing of a magnification of exactly 100 diameters. These adjustments, namely, the "elevation" of the microscope, the length of the arm and the angle of the mirror of the camera lucida, were not disturbed throughout the making of the drawings, although the magnification was checked at frequent intervals. An exception was made in the case of the tadpoles of series B. f.-34-A. The large size of the mouthparts of these tadpoles forced substitution of the 40 mm. objective for the 25 mm. objective. The adjustments were reset to make possible drawings of the same magnification, i.e., 100 diameters, as were made throughout all series.

A Syracuse watch glass was thickly lined with paraffin. In the bottom of this paraffin-lined watch glass a somewhat funnel-shaped depression was made at such an angle so that when the tail of a tadpole, ventral side uppermost, was inserted in this depression, the mouthparts of the tadpole would be in the plane most facilitating study (cf. above). Very fine elbow insect pins were used to hold the tadpoles in place while drawings were being made. The "elbows" were inverted on the pins; and the pins could be inserted in the paraffin so that the "elbow" points rested sufficiently firmly on the tadpole to hold it in the most desirable position for study and drawing.

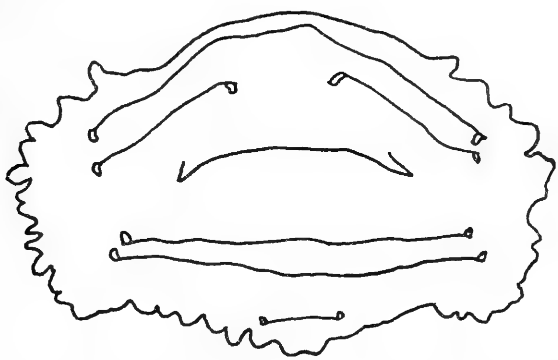

FIG. 2.—Camera lucida outline drawing of mouth parts shown in Fig. 1. This outline illustrates the type from which all measurements have been taken.

Drawings and Observations.—Outline drawings were made of the mouth apparatus of each tadpole selected as above described for each series. Each of these drawings was made as follows (cf. Fig. 2): An outline of the disc itself was made. Then a line was drawn along each row of teeth so as to follow the bases of the teeth. The end teeth in each row or part of a row were outlined so as to give more definite and exact terminations to the lines representing the rows. Teeth in unusual positions and teeth in irregular rows were also individually outlined. At the same time the outlines of the rows of teeth were drawn the number of teeth in each row was determined. Counting the teeth in each row was in some instances rather tedious and difficult. However, no count was permanently recorded until the same number could be obtained in three successive counts. The upper and lower beaks were also outlined; and it was often necessary to change the focus (by adjustment of the stage) in order to have the ends of the upper beak clearly defined. This was usually done after the rows had been outlined and teeth had been counted.

Making such drawings had the advantage over taking direct measurements of being far less difficult with no loss, if not a gain, of accuracy, and forming a permanent and readily accessible record.

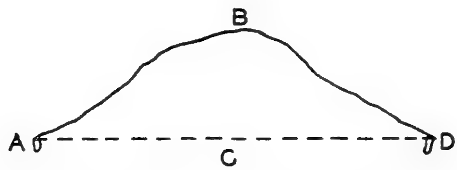

FIG. 3.—Outline of a single row of teeth to show difference between chord and arc lengths. Broken line, ACD, is chord length of row of teeth, ABD. Solid line, ABD, is arc length of row of teeth, ABD.

Measurements.—Since all drawings were made at a magnification of 100 diameters, the taking of measurements from the drawings was much simplified. A vernier caliper equipped with rather sharp divider points was used in taking the measurements from the drawings. The caliper read to tenths of millimeters; and, since magnification was 100 diameters, the measurements could be taken without interpolation or correction actually to thousandths of millimeters.

The measurements taken are all referable to the bases of the rows of teeth. The difference between the length of a row of teeth as measured from the bases of the terminal teeth and the length as measured from the tips of the terminal teeth might perhaps not be proportionately a significant difference in large tadpoles, but it is significantly large in smaller tadpoles.

Two different measurements of each row of teeth were taken (cf. Fig. 3). One of these measurements was the shortest distance between the ends of a given row. If a row of teeth were considered an arc, this measurement, i.e., the shortest distance between the ends of the row, would represent a chord subtending the arc. Accordingly, this measurement will hereafter be referred to as the "chord measurement" or "chord length" of a row. It was thought that the actual lengths of the rows might show some correlations with body measurements that chord lengths would not show. Hence, the actual length of each row was measured. This measurement was taken with a cartometer, an instrument which could be rolled along the lines on the drawings, which lines were outlines of the rows of teeth. The cartometer used could be read to 1/32 inch. The vernier caliper used was graduated both to sixty-fourths of inches as well as to tenths of millimeters, and could therefore be used in very readily translating the cartometer readings into millimeters. The actual length of a row of teeth thus obtained will hereafter be referred to as the "arc measurement" or "arc length" of a given row.

The median space in the second upper row of teeth was also measured. The distance between the bases of the right and left parts of this row is the measurement used in the comparisons made in this study. However, since Wright (1929) makes no mention of exactly what criteria are used in determining the width of this space, the minimum distance between right and left parts was also taken, although in the course of the study this measurement proved more irregular. Differences between the two measurements might not be of any proportionate significance in large tadpoles; but in smaller ones the differences are proportionately large.

Both chord and arc lengths of the upper beak were also taken. Due, however, to the position of the beaks relative to the rows of teeth, the arc length of the upper beak as taken is perhaps without significance. The lower beak is hidden from view to a greater or lesser extent by the upper beak, and could thus not be measured.

The greatest width (laterally) of the oral disc was also taken, although the degree to which the papillary borders were curled inward was too irregular to permit this measurement as taken to be of reliable consequence.

A summary of the various measurements and counts made of the mouthparts may be given here. They are chord length, arc length, and number of teeth of each of the rows as follows; first upper, right part of the second upper, left part of the second upper, first lower, second lower, and third lower; chord length of the second upper row as a "unit" or single row; minimum width of the median space in the second upper row, and the width of the space as taken between the bases of the terminal (median) teeth of right and left parts; arc and chord lengths of the upper beak; width of the oral disc; and in some instances of irregularities the actual length of that part of a row actually bearing teeth.

In view of the possible correlations that might be found to exist the following body measurements were taken: (1) body length (tip of snout to posterior border of anus), (2) tail length (anus to tail tip), (3) greatest body width, and (4) greatest body depth.

As the observations, body measurements, and drawings of each tadpole were completed, each tadpole was given a number and marked to maintain its identity in a given sample in event of possible need for re-investigation of individuals. The marking of the tadpoles consisted in clipping with very fine scissors V-shaped pieces from the upper and lower parts of the tail fin, the number given any tadpole being a fraction, the numerator and denominator of which indicated the number of pieces cut from the dorsal and ventral parts respectively of the tail fin.

Method of Analysis of Data.—Instead of calculating the ratio between two given measurements, e.g. the ratio of the chord length of one row to the chord length of another row, or the ratio of the arc length of a row to the chord length of the same row, such "pairs" of measurements from each animal of a series were plotted against each other graphically, or as coördinates. Lines of "equal proportion" were drawn on each such resulting graph. Any individual ratio could be determined by passing such a line of equal proportions (i.e., a line through zero) through the plotted point in question. The ordinate value of the point at which such a line passes through a point having a value of 1.00 on the axis of abscissas is the ratio to one that exists between the two coördinates (plotted measurements), determining the point through which the line of "equal proportions" has been drawn. The value, however, of this method of studying ratios between two sets of measurements is not particularly in the simplification of determining the ratios. The successive changes of ratio with increase in values of the measurements concerned, the minimum and maximum ratios, the variation of ratios, the trend of the majority of ratios, etc., are all at once obvious when measurements of two parts or two measurements of the same part are thus plotted as coördinates. Examples of the type of graph obtained and used in determining the ranges of ratios discussed later in this study are shown in Charts 1 to 8.

This graphic method of analysis was also used in studying the numbers of teeth in given rows as compared with the arc lengths of the rows (Chart 3).

The proportionate numbers of teeth in the different lengths of the corresponding row on different animals were readily compared on such graphs, and the actual number of teeth per unit length of row could be determined just as ratios between two measurements were determined (cf. above). This method applied to the study of tooth numbers has the same advantages that the method has in a study of ratios.

ANALYSIS AND DISCUSSION OF RESULTS

Bufo fowleri

Description and Analysis of the Mouth Parts

General Features.—The disposition of the rows of teeth are the same in *B. fowleri* as in the common type described in the introduction (pages 2-4).

The upper beak appears (becomes heavily pigmented) before the presence of any teeth can be detected. Teeth first become apparent in the first upper row, but only very shortly before teeth appear in the other rows. In some instances teeth of the second upper row appear shortly after teeth appear in the first upper row and before teeth appear in any other row. In all except some of the largest animals examined teeth are present in each lower row if present in any. In no instance in younger tadpoles is any row of teeth complete before at least some teeth of the other rows have appeared. However, those rows in which teeth first appear are usually the rows to first become complete. The row first complete, if any, in a given case is the first upper row.

The only rows developing any general irregularities or variations are the first and second lower rows. These variations or irregularities, if such these changes may be called, are divisions of a row into two or more parts, with spaces of varying widths separating the parts.

The first lower row is divided in almost half of the tadpoles examined. In half of the instances in which there are divisions, the division of this row is into two equal parts without an appreciable space, if any, developing between the right and left parts. Such an appreciable space is not greater than the width of one or two teeth. The two parts in the case of such a division tend to take the shapes of arcs of smaller, separate circles, rather than remaining as separate parts of the same arc. This will be further discussed later. If the row is divided into two unequal parts or into more than two parts, the parts are usually somewhat separated, and remain more as arcs of the same circle. In the smallest animals in which the row has been fully formed, it is undivided. In slightly larger animals it is irregularly divided. And in still larger animals the row tends to be divided into two regular parts (as described above). In the largest animals the row is rarely divided in any other way than into two equal, unseparated parts. Such a division occurs in about one-fourth of the largest animals.

The second lower row is divided in about one-sixth of the animals studied. In about one-third of these cases, division is into two approximately equal parts. In the other of the cases the divisions may be into as many as four parts. The same general sequence of divisions with increase in size occurs in this row as in the first upper row. However, divisions of any kind of the second upper row are rare.

There are no other rows in which changes are quite so frequent. In about 6% of the animals examined the first upper row is divided into two unequal parts which may be more or less separated. However, the parts do not assume the proportions of arcs of separate circles. In other rows irregularities are rare (1-2%).

When the rows of teeth disappear with the onset of the metamorphic climax, the third lower row disappears first, or at least begins to disappear first. The others disappear almost simultaneously, the first upper row being perhaps the last to disappear completely. The lower mandible disappears before the upper mandible. The mandibles apparently either disappear before the rows of teeth disappear or before the teeth disappear completely.

As was stated in the introduction, one of the objects of this study has been to determine whether or not there might be some basis for the possible existence of constant relationships between different parts of the mouth apparatus. Since the series of *Bufo fowleri* tadpoles includes individuals representing the entire size range of tadpoles of this species, it was decided to use the data from this series of tadpoles as the basis of an analysis of growth phenomena in the mouth apparatus; which analysis should discover or disprove some explainable basis justifying the use of relative measurements as taxonomic characters.

It was decided first to determine whether or not the various rows of teeth have regular or characteristic growth rates in relation to body size. There are several measurements of the body that might be used as a basis of comparison. Of these, body length was chosen as being the least affected by various conditions of preservation, amount of feeding prior to preservation, changes during early metamorphosis, and handling during study.

First Upper Row.—From examination of Chart 1 it will be seen that the curve representing the averages of this row of teeth is S-shaped. There are two possible explanations, namely, either there is a second acceleration of the rate of growth of the row as metamorphosis approaches, or the second upturn of the curve is due only to the larger tadpoles being of a different series. It is possible that these animals, due to different seasonal and other conditions, had not passed the period of greatest rate of growth of the row, although their size is greater. However, the data for the different groups overlap sufficiently to make this doubtful.

For the entire group the length of the row per 10 mm. of body length varies from 1.22 mm. to 2.60 mm. (cf. Table I). Exclusive of what appear to be extremely irregular or unusual cases, the variation is from 1.45 to 2.38 mm. per 10 mm. of body length. The average length varies between 1.45 and 2.13 mm. per 10 mm. of body length. Omitting the smaller animals in which the row is not fully formed, the first and last averages are about equal per unit length of body. Although the actual length of the row varies between wider limits in larger animals, the length per unit body length varies less.

Since the arc length of the row may more nearly approximate its actual "value" as a growing part, this length was plotted against body length to determine whether some more definite relation might obtain. The curve is of the same general contour as that of chord length/body length. The actual variation in arc length of the row per a given body

TABLE I.—*Bufo fowleri:* CHORD LENGTHS (IN MM.) OF MOUTH PARTS PER 10 MM. OF BODY LENGTH

Row	Minimum	Maximum
First upper	1.22	2.60
Average of right and left parts of second upper	0.35	1.09
First lower	1.24	2.20
Second lower	0.68	2.00
Third lower	0.80	2.00
Upper beak	0.90	1.53

length may be noted to be greater in larger animals. However, the variation per unit of body length is no greater, if as great, until shedding of the teeth begins (the teeth appear to be shed irregularly in short groups). The actual variation of row length per 10 mm. body length is also greater as compared with chord lengths for the group as a whole.

Now, if the chord length be plotted against the length of body plus tail a much smoother curve of averages is obtained. However, the variation of length of row per unit of total length of body plus tail varies just as much as it does per unit of body (only) length.

When arc length of the row is plotted against length of body plus tail, this arc row length per unit of body plus tail length is seen to vary slightly less as compared to its length per unit body (only) length. A very smooth curve of averages is obtained and the data are grouped about this curve with apparently less general variation than in the other combinations tried. This is taken to indicate that in this comparison exists a condition more nearly approximating one of relative growth.

As metamorphosis progresses the relation becomes more irregular. This is due most likely to irregularities both in row and in total body length which do not vary similarly, as in earlier instances. In the case of the latter the irregularity is apparently primarily a result of irregularity in tail length, since row length varies in these cases more per unit of total length than per unit of body (only) length. This is to be expected, particularly when autolysis of the tail begins.

It also indicates that whatever conditions may affect tail length must also affect the length of the row of teeth. Thus, since total length includes a variable governed by conditions similar to or the same as those affecting row length, row length has a more nearly regular relation to total length than to body length alone, until the climax of metamorphosis approaches.

Number of teeth in the row is more irregular per unit of body length or of total length than are either chord or arc lengths, although it was thought probable that number of teeth might be more constant or regular per unit of body length. Number of teeth per 10 mm. of body length varies from 64 to 176, and per 20 mm. of total length from 53 to 158. For a given total length, e.g., between 284 and 290 mm., number of teeth may vary from 53 to 84 per 20 mm. of total length, or, actually, from 76 to 117. (Also, e.g., from 75 to 156 per 20 mm. total length at 8.5-9.5 mm. total length, or, actually, from 32 to 75.) Thus, it is obvious that number of teeth per row is not at all constant nor does it increase regularly per unit body or total length, although there is a general actual increase as growth proceeds.

Although it is desirable to determine just what unit or character of measurement of a row bears the more nearly "characteristic" growth relation to the body, it is not primary for the purpose at hand. Regardless of the measurement used or relation obtained, if two or more rows are found to be similar in such relations, it follows that such rows would in turn be comparable. Also, if certain irregularities in the rows are referable to differences in the different samples constituting the series, this, too, would be of no unfavorable consequence. It would rather determine whether all rows were relatively equally affected by the diverse conditions. Thus, the object of this portion of the study is ultimately to qualify rows for comparison.

Second Upper Row.—This row, being divided, might be considered either as a single row or as two separate rows. Is each portion to be considered a single growing part, or are the right and left parts fractions of one unit? If considered as one row or one unit, there are four instead of two ends from which lengthening may occur. Thus, if growth should occur equally at all points and the row grow actually as much as the others, the proportionate increase of its chord length as compared with those of other rows would be less. If each part be considered a separate row, and if each increases in proportion to its original size, increase in length of the row as a unit should still be less than that of other rows. (This, of course, presupposes that increase in length of a row is a constant fraction of the sum of growth complexes of the row.) Moreover, it can be determined whether or not the median space between right and left portions is encroached upon by the growth of either of these portions. If not, then growth might be assumed to occur only at the outer ends of each of the parts. Should this be the case, it is to be expected that the outer ends extend twice as rapidly in proportion to row length as do the other rows. If the median space is encroached upon by growth of right and left parts, it might be expected that the outer ends of the rows would increase only in proportion to original row length. This would mean that the ends of the first upper labial row would extend progressively further beyond the outer ends of the right and left parts of the second row. The same would be expected if the second row were considered as a unit. If increase in length, as already presupposed, be a constant fraction of the entire complex of growth of a row, and if rate of growth is proportional to original size, then the first upper row should increase in length more rapidly than the second upper row. Thus, if these two rows are compared graphically by plotting the length of the first against that of the second, the curve obtained should show an increasing ratio. Such, however, is not the case. The chord lengths, whose relation to arc lengths will be discussed later, remain within limited ratios, namely, between a ratio of 0.90/1.00 and one of 1.25/1.00 with a nearly constant average of slightly more than 1/1. Unraveling the premises of the above assumptions, it will be seen that increase in length of a row is not a constant fraction of total proportionate growth of the row.

The median space in the second row is not obliterated and does not become actually smaller, but it does become a progressively smaller fraction of the row as a whole. This must mean that, as the space itself grows, the right and left parts of the row grow into the space at a rate slightly less than that at which the space increases. Thus, the right and left parts do grow at each end and yet the outer ends continue to grow as rapidly as those of the first upper row, which has only two points of lengthening. This, then, lends support to the idea that increase in length of a row is not a constant fraction of total proportionate growth of the row. It seems likely that each end of any row advances at a rate that is independent of what may be occurring in other parts of the row, although all the processes may be affected and similarly, by the same factors.

It must also be borne in mind that the entire disc is enlarging, and relative points on the disc are being diverged along radii, perhaps unequal and disproportionate. A row may be considered an arc from a circle whose radius is increasing with the center as a fixed point. The arc, then, is forced peripherally and must "stretch" to meet the "demands" of an increased circumference. This "stretching" is apparently brought about by cell division in the plane of the radius and at right angles to the surface of the disc. Teeth may be observed to "split" from the base outward, indicating that a cell division in such a plane has occurred. Thus, the increase in length of a row appears reduced to the result of two processes; namely, the ends of the row are carried apart by the growth of the disc, being "ideally" pushed outward in straight lines by the lengthening radii, and the ends of the arc at the same time are themselves moving further around the circumference. These two processes are perhaps fundamentally similar, yet in the first the already formed ridge is lengthening, while, in the second new material is being added to it. At any rate, it seems that the advance of the ends around the circumference would occur independently of the other process. This may be determined experimentally.

Furthermore, if the percentage increase in length of the first upper row and that of the second upper row be plotted against actual increase in length of the body, it may be seen that, although the two curves have similar contours, they are widely divergent. This is true both in the percentage increase over original size and in percentage increase over each preceding increase.

Aside from showing two periods of growth, this adduces proof that the different rows of teeth are similarly affected by the various conditions of growth, but that the responses of the various rows is not to be measured in constant fractions of their original lengths.

By comparing the percentage increases in the average lengths of right and left portions of the second upper row with the percentage increase in width of the median space, it will be seen that the increases in the two dimensions concerned are reciprocally correlated. This indicates that when the rows are lengthening at their greatest rates, the median space is broadening more slowly, due to the rapid encroaching of the inner ends of the rows. It is possible that the entire disc, of which the "median space" is only a portion, may enlarge at a fairly constant rate, while the rows of teeth increase in length in "spurts." Thus, what appear to be periods of "negative growth" of the median space are only periods during which the rows of teeth are growing faster than the space. When the rate of growth of rows of teeth drops, the space appears to broaden more rapidly. All this lends further proof to the apparent fact that the ends of the rows of teeth encroach upon the circumferences, of which they are arcs, rather independently of other growth processes concerning the disc.

First Lower Row.—When the chord length of the first lower labial row is plotted against body length, the same type of curve results as in the case of the upper rows. The variation in length of row per 10 mm. of body length is from 0.77 to 2.18 (omitting cases where part of row is missing). Excluding very young and exceptional cases (less than 5%

of total) the variation is from 1.24 to 2.03 mm. per 10 mm. of body length, with the rows of teeth of the smallest and of the largest animals nearer the lower limit of this range.

A curve showing average percentage increase in length of the row has similar contours to those of the rows previously studied; but it varies somewhat from them in actual percentages.

Second Lower Row.—Because this row appeared to be subjected to less irregularities than the first or third lower rows of teeth, it was chosen as the lower row for more complete comparison with body size. Chord length, arc length, and number of teeth were each plotted against body length. In each instance the same type of curve is obtained, namely, the same S-shaped curve as in the cases of other rows. Per 10 mm. of body length, chord length of the row varies between 0.68 and 2.00 mm.; arc length varies between 0.80 and 2.15 mm.; and number of teeth in a row varies between 49 and 122. One point of possible note about this row is that when number of teeth in the row is plotted against body length, the points on the graph representing the 1934 collection of tadpoles form such a distinct group that it indicates the probability that the characteristic second upturn of the curves of relative growth in this series is due to different conditions of growth of the sample rather than being a second growth period (as was discussed earlier).

Third Lower Row.—The chord length of this row, when plotted against body length, gives a curve similar to that of the other rows. The curve of percentage increase is also similar to those of other rows, although its modes are higher than those of the other complete rows.

Upper Beak.—Although the upper and lower parts of the horny beak are quite different from the rows of teeth, at least the upper part, when plotted against body length, shows a similar course of growth to that of the rows of teeth. Percentage increase is also similar, and the curve of this percentage follows very closely those of the first upper and first and second lower rows, both in contours and in actual percentage values. Per 10 mm. body length the upper beak varies in chord length between 0.90 and 1.53 mm. (exclusive of a few instances of tadpoles whose beaks could not be satisfactorily measured because of mechanical damage caused while making other measurements and counts.

Curvature of the Rows of Teeth.—From a study of the curvature of the rows of teeth, that is, the relation of arc to chord lengths (cf. Chart 2), several facts can be determined. It has been seen that arc length is a more true measure of the row as a growing part. If the same ratio between arc and chord measurements obtains throughout the series, or, if the ratio undergoes the same modifications in all rows, the use of chord lengths in comparisons between rows may be justified.

If, in any given circle, arcs of different lengths are plotted against the respective chords subtending them, it will be seen that the ratio between arc and chord increases as their lengths increase, first slowly and then rapidly until the greatest chord (the diameter) is reached. If a single straight line (other than diameter) is drawn through several concentric circles, and the lengths of the arcs and chords thus formed be compared, it will be found that the ratio between arc and chord length increases from smaller to larger circles. If non-concentric circles of different radii be so drawn that a single chord subtends an arc on each circle, it will be obvious that the ratio of arc length to chord length will be greatest in the smallest circles and least in the largest circles. If in concentric circles two radii be so drawn as to form any given angle, and chords be drawn from one radius to the other at the respective points at which they intersect the circles, the arc/chord ratios will in each case be the same. It follows, then, if for the moment a row of teeth be considered an arc of a "perfect" circle, that, if the increase in length of a row of teeth were due only to the expansion of the disc along its radii, the ratio of arc to chord length would remain the same. If, however, the ends of a row should grow around the circumference so as to extend the arc to points representing projections of the original chord, or to any distance beyond the original radii, then the ratio of arc to chord length will increase. Thus, an increase in arc/chord ratio of a given row would verify the idea that the row grows circumferentially at the same time the disc is expanding and 'over and above' this disc growth.

It must be remembered, however, that in most instances the rows of teeth are probably not arcs of "perfect circles" and that the different radii of the disc do not increase uniformly; and that irregularities in outline as well as differences in curvature, and differences in proportion of circumference concerned will affect the arc/chord ratio. Thus, an exceptionally high ratio would more than likely indicate a row with a wavy outline.

From examination of Table II and Chart 2 it will be seen that there is, in the case of each row, a slight increase in curvature from smaller to longer rows, both as to averages and as to actual least and greatest rows. The greatest arc/chord ratios are to be found in the case of the first upper row. This might be expected since this row is an arc of a greater circle, and also since it follows closely the margin of the disc and thus is more nearly a true arc than the other more centrally located rows, which are somewhat "flattened" in outline. This flattening is perhaps due either to unequal increase of the different radii of the disc or to failure of the rows to maintain a circumferential growth, or, more likely, to both. The third lower row, as expected, is quite similar to the first upper row in arc/chord ratio, although the maximum ratio of not unusual cases does not reach as high a value, due to the fact that the third lower row does not ever attain the length of the first upper row.

If the three lower rows be compared, it will be seen that the arc/chord ratios increase from central to peripheral rows, indicating an increase in curvature of peripheral over more central rows. This is in accord with the above discussion, and shows the apparent existence of a sort of radial gradient that perhaps might be expressed mathematically in a manner similar to the "logarithmic spiral" expressing growth in such structures as the horns of the rhinoceros (Huxley 1932: pp. 151-154).

TABLE II.—*Bufo fowleri:* RATIOS TO ONE OF ARC LENGTH/CHORD LENGTH OF ROWS OF TEETH

Row	Maximum (all included)	Maximum (less extremes)	Row of least chord length	Row of greatest chord length	Approximate average in younger animals	Approximate average in older animals
First upper	1.32	1.21	1.00	1.21	1.06	1.16
Right part of second upper	1.22	1.11	1.00	1.11	1.03–	1.035
Left part of second upper	1.27	1.10	1.00	1.08	1.03	1.04–
First lower	1.14	1.10	1.00	1.05–	1.03	1.035
Second lower	1.17	1.12	1.00	1.08	1.035	1.055
Third lower	1.55	1.13	1.00	1.13	1.03	1.085

The portions of the second upper row might be expected never to develop as high arc/chord ratios as other rows, due to their being proportionately much smaller arcs, i.e., arcs representing a lesser percentage of circumference. However, the ratios are comparable with those of the first and second lower rows. This suggests that each row represents an arc of a circle with a center different from that of the other. Moreover, the outline of the first lower row tends to become emarginate with increase in length. In such instances the arc/chord ratio tends to become a ratio between the sums of two small arcs and two small chords and would thus be of a lesser value. This occasionally happens in the second lower row, but is much less frequent and much less marked. All this indicates the probable existence of at least two centers of expansion of the disc, which centers themselves move apart with growth. The expansion from these two centers must become less individual and merge to give a smoother contour as the periphery is approached.

Aside from the above, the first upper row is more similar to the third lower row than to any of the others in curvature and progressive changes of curvature. The other rows are quite similar to each other. It follows that comparisons of chord lengths within these combinations might be expected to be more valid, provided chord lengths of the rows increase similarly. But chord lengths of the first upper and first and second lower rows increase at more nearly the same rates, while those of the parts of the second upper and of the third lower rows are more nearly alike. From this it must be concluded that the differences in rate of increase of arc length and in changes of curvature so interdigitate or counter-balance each other in the case of the first upper and first and second lower rows that the resulting chord lengths are quite comparable. The same appears to be true to less extent of the parts of the second upper and of the third lower rows. If the percentage increase of arc length per unit increase of body length in the cases of the different rows be compared, it will be seen that, as in the case of chord lengths, the curves have corresponding contours, but are actually of different values. The values probably are not of significant differences, however, between the first upper and first and second lower rows.

Numbers of Teeth in the Different Rows of Teeth.—It was thought that possibly the numbers of teeth in different rows might serve as a more reliable basis than measurements for computing ratios between rows. Hence, the first step in deciding the reliability of ratios between teeth counts was to compare the number of teeth to the arc length in each of the rows.

This was done by plotting the arc lengths against the numbers of teeth in the case of each row (cf. Chart 3). From the graphs thus obtained the numbers of teeth for every tenth mm. of arc length were averaged, and from these averages the number of teeth per 1 mm. of arc length for each average was determined, and plotted against arc length.

Examination of Chart 3 and Table III will show the results. Table III shows the maximum and minimum numbers of teeth per 1 mm. of arc length for each row. The difference between maximum and minimum is in almost each case very nearly 100% of the minimum number. The maximum and minimum numbers in the different rows do not appear to be significantly different in view of such variation. Obviously, the actual number of teeth in a row tends to increase as the row increases in length. But these increases do not seem to occur at coincident rates for the group of animals as a whole. The number of teeth per unit arc length will give a 'fairer' basis of comparison.

From examination of Chart 3 and Table III it will be seen that the number of teeth per unit arc length in any given row is at first small, then increases rapidly, remains at a given value (irregularly) for a while, then diminishes gradually, and then perhaps remains constant until loss of teeth begins. By comparing the different rows in this respect, it will be seen that these variations occur simultaneously in all rows and irrespectively of the actual length of the row concerned. It may also be noted that numbers of teeth per unit arc length are approximately the same in smallest and largest animals. The initial low number may readily be explained as due to the fact that all the teeth in a given row in such a case have not become sufficiently deeply pigmented to be seen. Even, however, after all teeth are completely pigmented, there

TABLE III.—*Bufo fowleri:* NUMBER OF TEETH PER 1 MM. OF ARC LENGTH OF ROW OF TEETH

Row	Maximum	Minimum	Range
First upper	82	37	45
Right part of second upper	74	35	39
Left part of second upper	78	30	40
First lower*	76	36	40
Second lower	72	40	32
Third lower	80	40	40

*This row is so much divided, often with spaces between divisions, that actual length of tooth-bearing portion is used here.

appears to be a further increase in number of teeth per unit arc length. The maximum is, however, reached comparatively early. Since each tooth is derived from a single cell or single column of cells (cf. earlier discussion), unless the teeth become somewhat separated from each other, which they appear not to do, it appears that the size of the teeth and tooth-producing cells must gradually increase with size.

The primary concern in this study, however, is the similarity in variation of tooth numbers in the different rows. From the variation of actual numbers per 1 mm. of arc length it does not appear that ratios between tooth numbers of different rows would be constant. Yet, from the similarity in different rows of variation of average number of teeth per unit arc length, it appears that tooth numbers might be of value as a basis of calculating ratios between rows. The determination of the actual value of these ratios must await comparison of rows through all methods of measuring (cf. later discussion).

INDICATIONS FROM THE ANALYSES

Presuming all rows to develop regularly (which they do not) and knowing (1) that the shorter rows have a greater percentage growth (due to the fact that the ends of any row extend themselves independently of the "size" of the row), and (2) that the rows nearer the periphery develop the greatest curvature, it may be predicted that (1) the greatest range of ratios will exist between the longer and the shorter rows, (2) the ratios in older animals decreasing in general (if calculated as longer row to shorter row); (3) this range will be less and (4) there will be less difference between ratios in old and young animals, if the longer and shorter rows are both peripheral; (5) if the shorter row only is peripheral, the range will still be greater and there will be a greater decrease in ratio with age; (6) ratios between two longer rows (including use of the chord length of a divided row) are apt to be least variable, and (7) if one of these longer rows is a peripheral row, the ratio of peripheral row to a more central row will decrease slightly in older animals (since percentage arc increase is about the same in each, and since arc/chord ratio increases more in peripheral rows); arc ratios in such cases would increase correspondingly; (8) most constant ratios will exist between rows of more nearly equal length and of more nearly corresponding distances from the center or periphery of the disc; (9) ratios between the right or left parts to the separating space of a broken row will vary a great deal, increasing markedly with age. It might be further observed that the use of chord lengths instead of arc lengths is preferable in calculating ratios. Aside from their impracticability, arc lengths are of less value because (1) such ratios between arc lengths are more apt to vary with age, and (2) this greater variation tends to be counteracted by correspondingly increased curvatures if chord lengths are used.

Tooth numbers are (as has been previously observed) of uncertain predictable value. Their valuation must await actual comparison with other means of determining ratios, i.e., through use of arc and chord lengths.

To put these predictions into more concrete terms: (1) Fairly constant ratios may be expected between the first upper row and the first and second lower rows, particularly the second lower row. These may, however, decrease slightly with age. (2) Even more nearly constant ratios may exist between the second upper row (as *one* row) and the first and second lower rows, particularly the first lower row, (since the second upper and first lower rows are correspondingly disposed with respect to the center of the disc, and since the first lower also has a tendency to become two smaller rows (cf. also earlier discussion). There should also be some tendency for these ratios to decrease with age. (3) There should also be constant ratios between the two upper rows (second upper as *one*), the ratio approaching more regularly a 1/1 ratio with age. (4) The ratio of the first lower to second lower row will be rather constant. (5) The ratio of any other row to the average of right and left parts of the second upper row may vary more than any of the ratios suggested above. The least variable ratio in this group would perhaps be that between the third lower row and the average of the parts of the second upper. (6) The ratio of the first upper to the third lower row may also be quite variable, but should change little with age. (7) The ratios between the parts, space, etc., of the second upper row will be of different constancies. (a) The ratio of the average of right and left parts to the median space should be extremely variable. (b) The ratio between the length of the row as a unit and the median space will also be extremely variable, though possibly less so than the former (a). (c) The ratio of the length of the row as a unit to the average length of right and left parts should be much more constant and a better means of expressing the extent of the median space.

It must be remembered, however, that these are only predictions made on the premises of the foregoing analyses, and the actual comparative values of the different combinations must be verified or disproved by the actual comparison of the rows in the various possible combinations. The value of these analyses, then, lies in the fact that, without being prejudiced by a knowledge of the variation or constancy of the different ratios, the ratios, should they fulfill predictions, shall have been shown to have a basis referable to certain rules and reasoning rather than such ratios being mere coincidents or artifacts.

Comparison of Ratios of Different Rows of Teeth to Upper Beak

From a study of the percentage increases of the rows of teeth and the upper beak it was seen that the upper beak increases in chord length at a rate quite comparable to that of some of the rows of teeth, namely, the first upper and first and second lower rows, the former of these in particular. This suggests that a fairly constant ratio of chord lengths between any of these rows and the upper beak might obtain.

Of the nine different combinations of rows, etc., used by Wright in his key (Wright 1929), five of them concern the relation of rows of teeth to the upper beak (cf. also earlier discussion). All rows are used at various times except the right and left parts of the second upper row. For this divided row he uses the chord length as though the row were complete and single, i.e., the straight distance between the outer ends of right and left parts of the row. This measurement will hereafter be designated as the chord length of the second upper row. When right or left parts of the row are used, they will be designated as right and left parts.

Table IV is a summary of the results of plotting the chord lengths of the various rows against the chord length of the upper beak (cf. also Chart 4). All values (except percentages) expressed in the table rep-

TABLE IV.—*Bufo fowleri*: RATIOS TO ONE OF ROWS OF TEETH TO UPPER BEAK

Row	Extreme range			Restricted range			% Variation	Range of averages			% Variation	Approximate general average
	Minimum	Maximum	Amount	Minimum	Maximum	Amount		Minimum	Maximum	Amount		
First upper..........	1.18	2.06	0.88	1.48	1.94	0.44	30.0	1.60	1.72	0.12	3.6	1.60
Second upper..........	1.18	1.92	0.74	1.35	1.80	0.45	33.3	1.35	1.65	0.30	19.4	1.55
First lower..........	0.80	1.62	0.82	1.17	1.62	0.45	38.4	1.20	1.56	0.36	26.1	1.40
Second lower..........	0.70	1.64	0.94	1.10	1.56	0.46	42.0	1.23	1.44	0.21	7.9	1.35
Third lower..........	0.54	1.40	0.86	0.80	1.33	0.53	66.3	0.56	1.27	0.71	39.1	1.05
Average of right and left parts of second upper..........	0.33	0.82	0.49	0.50	0.79	0.29	58.0	0.94	1.44	0.50	21.0	None

rent ratios to one. "Extreme range" includes ratios of all cases in which measurements of both parts concerned could be taken. "Restricted range" does not include ratios of (1) cases of smaller animals where row or beak was too faint to be satisfactorily measured, or (2) obviously exceptional or irregular cases. The omitted cases in no instance constitute more than 3-5% of the total number of animals in the series under consideration. "Amount of range" refers to range of ratio, and is the difference between the maximum and minimum ratios of a given combination. The values under "percentage variation of restricted range" are expressed in the percentages of the minimum ratios of the "restricted ranges" that the ratios may vary in a given combination. The value of the use of these percentages lies in the fact that they give a basis of comparison of the different combinations which takes into account the differences in lengths of the rows in the different combinations. Thus, for example, a difference of .50 between .50 and 1.00 is an entirely different value than a difference of .50 between 1.50 and 2.00 "Range of averages" represents the range of averaged ratios. "Amount of range of averages" is the difference between maximum and minimum averaged ratios. "Approximate general average" is the ratio represented by a line on the graph concerned, so drawn as to pass through the greatest number of "average" points or to divide these points into two approximately equal groups. The values under "percentage variation of average" are given in percentages. They represent in percentage of the "approximate average" the amount that any average may vary either above or below the "approximate average," which is actually an "average of averages." Although the percentages refer to averages rather than to actual range, this is of value because it takes into account the distribution of the majority of cases.

By examination of Table IV and Chart 4 the constancy, value, and validity of these various combinations may be compared.

In order of *amount of extreme range* of ratios to upper beak from least to greatest the rows are respectively, (1) second upper, (2) first lower, (3) third lower, (4) first upper, and (5) second lower. If exceptional or extremely irregular instances are disregarded (not to exceed 3-5% of total number) in each case, the order of the rows from least to greatest range of ratios to upper beak will be (1) first upper, (2) second upper and first lower, (3) second lower, (4) third lower. The differences between the amounts of range do not appear significant in the latter comparison, except for the third lower row, which has a considerably greater range. The other rows have approximately the same ranges. Thus, excluding the unusual ratios in the case of each row, it appears that, with the exception of the third lower row, comparisons between the respective different rows and the upper beak appear to be of equal validity and constancy. However, if this amount of restricted range be considered as a percentage of the minimum ratio in this range in each combination, the different combinations will be represented in a more true perspective. The rows in order from least percentage variation to greatest percentage variation of restricted range of ratios to the upper beak are (1) first upper, (2) second upper, (3) first lower, (4) second lower, and (5) third lower.

However, if the amount of range of *averages* be considered, it will be seen that the ranges of ratios discussed above are much more regularly distributed in some combinations than in others. The order of the rows from least to greatest amount of range of average ratios is (1) first upper, (2) second lower, (3) second upper, (4) first lower, (5) average of right and left parts of second upper, and (6) third lower. If percentage variation of the averages be considered, this same order will be seen to exist, but the differences between the rows appear exaggerated although they are shown in a more true perspective.

From the standpoint of the criteria combined, and to summarize the foregoing it may be said that, as was more or less anticipated from preliminary analyses, the following sequence is the order of value of the rows that have any value as concerns the constancy of ratio of their chord lengths to those of the upper beak: (1) first upper, (2) second upper, (3) second lower, (4) first lower—the first upper being of most distinctive merit as affording a constant ratio to the upper beak.

Actual Test of Relative Values of Different Combinations of Rows of Teeth

Each possible combination of the rows of teeth was determined and a graph of each possible combination was made by plotting the chord lengths of the longer row as ordinates and the chord lengths of the shorter row as abscissae in each instance in which a constant difference in length was obvious (cf. charts 5 and 6). Similar graphs were made of the combinations of measurements of the parts and spaces of the second upper row. On each of these graphs lines representing ratios (lines through "zero") were drawn in pairs (1) so as to include all points, (2) so as to include all but rather irregular or extreme cases (not excluding over 3-5% of total number of animals in the series), and (3) so as necessarily to include only those points representing older animals. The spaces bounded by these pairs of lines represent respectively (1) the "extreme range"—or variation—of ratios, (2) what has been designated for the sake of convenience as "restricted range" of ratios, and (3) range of ratios in "older" animals.

In several instances averages were calculated, but lines drawn as nearly as possible through averages failed to pass through zero, indicating a change of average ratio. Since the combinations are so diverse and since the average ratios change considerably, it was decided not to use averages in comparing the values of the different combinations.

The three sets of "ranges" may be interpreted so as to determine, in addition to the facts their titles indicate, (1) whether the ratio of a given combination is greatest or least in younger or older animals, (2) whether the range of ratio is greater in younger or older animals, and (3) whether there is a tendency for the ratio to shift upward or downward with increase in age.

The "restricted ranges" were taken as a basis of more critical comparisons, since extreme cases are frequently quite isolated, and since this study was not primarily concerned with exceptional cases. Too, these exceptional cases are more often those of younger animals with rows of teeth not completely formed. And even when an older animal has an exceptional ratio, it would be "unfair" to take this exceptional instance as a "characteristic" upper or lower limit of the range of the ratio in question. As a basis of comparison that would take into account the proportion of the range of ratio a percentage value was calculated for the restricted range. This percentage value is the percentage of the median ratio of the restricted range that the range extends above or below this median. (1) This percentage value, (2) the limits of the "extreme range," (3) the actual amount of the extreme range, (4) the limits of the "restricted range," (5) the actual amount of the restricted range, (6) the limits of the range of older animals, (7) the actual amount of this range, and (8) the approximate relative size of the animals with the extreme ratios for each combination of rows are shown in Table V.

In Table VI are listed the combinations of rows used and in respective columns opposite these combinations are listed the relative numerical orders from least to greatest under and according to each of the criteria used.

As criteria for determining the relative value of each combination, the following were used: (1) the percentage variation of restricted range, (2) amount of restricted range, (3) amount of extreme range, (4) amount of range in older animals, and (5) various combinations of (1), (2), (3), and (4). The "final assigned rank" was assigned only after careful analysis of each combination according to these criteria.

Foregoing any discussion of the relative merits of individual combinations, the study of the ratios of the various combinations of rows in *B. fowleri* may be summarized by stating that evaluation, as carried out on the basis of the criteria set forth, of combinations for constancy

TABLE V.—*Bufo fowleri*: RANGES OF RATIOS OF DIFFERENT COMBINATIONS OF ROWS OF TEETH

Combinations	Extreme range			Restricted range				Range in older animals			Relative "ages" of	
	Maximum	Minimum	Amount	Maximum	Minimum	Amount	Percentage variation	Maximum	Minimum	Amount	Maximum	Minimum
1 U/r & 1	5.55	2.20	3.35	4.20	2.18	2.02	31.7	2.92	2.20	0.72	Y	vO
1 U/2 U	1.25	0.90	0.35	1.22	0.98	0.24	11.8	1.12	0.95	0.17	vY	M
1 U/1 L	1.60	0.96	0.64	1.50	1.00	0.50	20.0	1.24	1.00	0.24	vY	M
1 U/2 L	1.74	0.97	0.77	1.48	1.06	0.42	16.5	1.33	1.09	0.24	vY	M
1 U/2 L*	1.60	1.00	0.60	1.52	1.06	0.46	18.5	1.57	1.05	0.52	M	M
1 U/2 L†	2.48	0.94	1.64	1.85	1.06	0.79	27.4	1.47	0.94	0.53	O-M	vY
1 U/3 L	4.04	1.10	2.94	2.22	1.30	0.92	26.1	2.22	1.18	1.04	Y	M
r & 1/m s	4.60	0.36	4.24	2.64	0.60	2.04	63.0	4.60	1.25	3.35	O	vY
2 U/r & 1	5.00	2.00	3.00	3.46	2.13	1.33	24.0	2.96	2.00	0.96	Y	O
1 L/r & 1	4.36	1.52	2.84	3.24	1.79	1.45	29.0	2.52	1.79	0.73	Y	vY
2 L/r & 1	5.00	1.34	3.66	3.56	1.70	1.86	35.5	2.34	1.70	0.64	Y	vY
3 L/r & 1	3.12	0.92	2.20	2.18	1.21	0.97	28.8	1.94	1.09	0.85	vY	vY
2 U/m s	8.50	1.68	6.82	5.75	1.98	3.77	46.3	8.50	2.31	6.19	O	Y
2 U/1 L	1.65	0.86	0.79	1.35	1.00	0.35	15.3	1.25	0.86	0.39	vY	O
2 U/2 L	1.72	0.93	0.79	1.43	1.03	0.40	16.3	1.39	1.03	0.36	vY	Y
2 U/3 L	3.72	1.15	2.57	2.18	1.25	0.93	27.3	1.80	1.25	0.55	Y	M-O
1 L/2 L	1.25	0.81	0.44	1.22	0.88	0.34	16.2	1.22	0.96	0.26	M	Y
1 L/3 L	3.26	1.00	2.26	1.85	1.05	0.80	27.6	1.85	1.03	0.82	Y	M
2 L/3 L	3.46	0.96	2.50	1.80	1.06	0.74	27.8	1.64	1.00	0.64	Y	M

*Arc lengths.
†Numbers of teeth.

KEY

1 U is first upper row.
2 U is second upper row (as a "unit").
m s is median space in second upper row.
r&l is average of right and left parts of second upper row.

1 L is first lower row.
2 L is second lower row.
3 L is third lower row.

Ages: These relative ages, or perhaps more preferably, relative sizes, were determined by relative distance from "zero."
Y is young. M is medium. vO is very old.
vY is very young. O is older.

and reliability of ratio seems to justify the following order of combinations of rows from greatest to least value: (1) first upper/second upper; (2) first lower/second lower; (3) second upper/first lower; (4) second upper/second lower; (5) first upper/second lower; (6) first upper/first lower; (7) first lower/third lower; (8) first upper/third lower; (9) second lower/third lower; (10) third lower/avg. parts second upper; (11) second upper/avg. parts second upper; (12) second upper/third lower; (13) first lower/avg. parts second upper; (14) first upper/avg. parts second upper; (15) second lower/avg. parts second upper; (16) avg. parts second upper/median space second upper; (17) second upper/median space second upper.

TABLE VI.—*Bufo fowleri*: NUMERICAL RANK FROM LEAST TO GREATEST OF THE RANGES OF RATIOS LISTED IN TABLE V.

Combinations of rows of teeth	Criteria				Final assigned rank
	Percentage variation of restricted range	Amount of restricted range	Amount of extreme range	Amount of range in older animals	
1 U/2 U......	1	1	1	1	1
2 U/1 L.......	2	3	5	6	3
1 L/2 L.......	3	2	2	4	2
2 U/2 L.......	4	4	6	5	4
1 U/2 L.......	5	5	4	3	5
1 U/1 L.......	6	6	3	2	6
2 U/r&1.......	7	12	13	14	11
1 U/3 L.......	8	9	12	15	8
2 U/3 L.......	9	10	10	7	12
1 L/3 L.......	10	8	8	12	7
2 L/3 L.......	11	7	9	8	9
3 L/r&1.......	12	11	7	13	10
1 L/r&1.......	13	13	11	11	13
1 U/r&1.......	14	15	14	10	14
2 L/r&1.......	15	14	15	9	15
2 U/m s......	16	17	17	17	17 (-16)
r & 1/m s......	17	16	16	16	16 (-17)

Symbols used for rows are the same as in Table V.

If the values indicated by the preliminary analyses be compared with these assigned values, it may be noted that there is exact coincidence in the valuation of the first six combinations. The predicted and assigned values also coincide as to relative value within groups (as arranged in assigning values). It appears then, that if the series of *Bufo fowleri* tadpoles studied may be considered as representative of the species, the ratios existing between the different rows of teeth and between rows of teeth and upper beak are not chance ratios but are determined by the phenomena of growth and variation in this species. It further appears that, though the length of rows per body or total length may vary under different conditions, the more valued ratios between rows are little, if at all, affected.

The ratios between rows as given in Table V may be said in part to characterize tadpoles of *B. fowleri,* though they may not prove to be individually distinctive. If the phenomena of growth may be presumed to be fundamentally similar in other species, such other species would be forced, indeed, to possess rows of teeth of different proportionate lengths if the ratios between rows are to be distinctive at all.

It may be further observed at this point that the combinations of rows having the more constant ratios are apt to be the ones less distinctive of the species. Hence, it does not follow that the relative values assigned to the different combinations of rows on the basis of constancy of ratio will coincide with the values of the combinations based on the degree to which they are distinctive of the species. These latter values await further study of and comparison with other species.

For the purpose of simplifying comparisons with other species the combinations of row with row and of row with upper beak may be evaluated as a single group and on the basis of the same criteria. When this is done it is found that the combinations involving the upper beak will rank in order immediately following the group of the first six ranking combinations of rows (p. 43) as follows: First upper row/upper beak, second upper row/upper beak, second lower row/upper beak, first lower row/upper beak, third lower row/upper beak. The rank of value then changes to the combination of rows and continues as listed (p. 43) with the only exception being that the rank of the combination, average of right and left parts of second upper row/upper beak, is probably intermediate between the combinations, second lower row/average of right and left parts of the second upper row, and average of right and left parts of second upper row/median space in second upper row, respectively. This evaluation of all combinations as a group will be summarized in comparative tables further on.

Pseudacris nigrita triseriata

Descriptions of the Parts of the Mouth Apparatus

When all rows of teeth have completed their appearance, the rows of teeth in *P. nigrita triseriata* have the same arrangement as the general type described in the introduction (cf. pp. 9-11 and Fig. 1).

The upper mandible becomes sufficiently darkened to be readily measured before any teeth appear. Teeth of the first upper row are generally the first to appear, followed shortly by those of the first and second lower rows, and then those of the second upper row. No one of these rows is completely toothed before teeth of the other three have begun to appear. However, all of these rows are complete some time before the third lower row appears. All rows of teeth except the third lower row may be complete in tadpoles of as small a body length as 2.32 mm., while the third lower row may not appear until the tadpoles have attained a body length of 3.36 mm., and may not be completely toothed when body length is as great as 3.57 mm. However, traces of the third lower row may be seen in tadpoles whose body length is 2.91 mm. The possible significance of the late appearance of this third lower row will be discussed later.

Changes in rows and such division of rows as have been termed irregularities are not frequent in this species. Irregular divisions in any given row do not occur in more than 2-4% of all cases examined after such a given row has become completely toothed.

There is, however, a tendency for the first lower row to become divided so as to form two short rows which are not separated but which are arcs of different circles. Such a division occurs in about 12% of all cases examined, being about equally distributed between the medium-sized and larger tadpoles of the series. A similar division may occur in the second lower row in a few instances (2-3%).

Curvature of the Rows of Teeth

Table VII gives the ratios of arc length/chord length for the rows of teeth. Since the tadpoles of this series studied did not attain the maximum size of the species, it follows that, if arc length increases in relation to chord length throughout larval life, the ratios expressed in Table VII are not as great as might obtain in tadpoles larger than those involved in this study. However, the ratios in the series of *Pseudacris nigrita triseriata* studied are slightly greater than in *Bufo fowleri.* The

Table VII.—*Pseudacris nigrita triseriata*: Ratios to One of Arc Length/Chord Length of Rows of Teeth

Row	Maximum (all included)	Maximum (less extremes)	Minimum
First upper	1.25	1.25	1.05
Right part of second upper	1.29	1.15	1.00
Left part of second upper	1.45	1.21	1.00
First lower	1.32	1.18	1.00
Second lower	1.62	1.28	1.00
Third lower	1.59	1.22	1.00

ratios differ less in tadpoles of different sizes than is the case with *B. fowleri.* That is, the general distribution of ratios does not show any notable change with increase in body size. This indicates then, that arc length/chord length ratios are in general greater in tadpoles of *Pseudacris nigrita triseriata* than in those of *Bufo fowleri.*

It may also be noted that there is a general increase in arc length/chord length ratio from the more central to the more peripheral rows of teeth. This was noted to be true also for *B. fowleri.*

Numbers of Teeth in Different Rows of Teeth

Number of teeth per unit arc length of a given row of teeth does not appear to change with increase in body size as numbers of teeth per unit arc length of rows were seen to vary in *B. fowleri.* This, however, is true because of the fact that the series of *P. nigrita triseriata* does not include a complete range of body sizes.

However, number of teeth per unit arc length of a given row (cf. Table VIII) is almost as variable in *P. nigrita triseriata* as in *B. fowleri* (compare Tables III and VIII).

In general in *P. nigrita triseriata* the minimum numbers of teeth per unit arc length of the different rows are greater, indicating that the teeth may be smaller than in *B. fowleri.* However, maximum numbers of teeth per unit arc length of the rows are not so different in the two species, the numbers being somewhat greater in *P. nigrita triseriata,* indicating further that teeth may be smaller in this species.

The small minimum number of teeth in the case of the third lower is due to the fact that teeth in this row may be widely separated for some time, which fact is in turn because of the fact that some of the teeth are slow to appear. The high maximum number of teeth in this row indicates that the teeth of this row may be of a smaller extreme size than in the cases of the other rows.

Table VIII.—*Pseudacris nigrita triseriata*: Number of Teeth per 1 mm. of Arc Length of Row of Teeth

Row	Maximum	Minimum	Range
First upper	83	45	38
Right part of second upper	82	42	40
Left part of second upper	88	43	45
First lower	83	51	32
Second lower	79	42	37
Third lower	133	29	104

It may be stated finally, then, that numbers of teeth per unit arc lengths of rows of teeth are in general as variable in *Pseudacris nigrita triseriata* as in *Bufo fowleri,* even though the body sizes of the tadpoles of the former species are not of sufficient variation to show the changes in numbers of teeth per unit arc length of row with increase in size as are shown in the tadpoles of *Bufo fowleri* studied.

Combinations of Rows of Teeth and of Rows of Teeth and Upper Beak

The same criteria are used to determine the relative values of the ratios of the different combinations of rows and combinations of rows with upper horny beak in Pseudacris as were used in the similar studies on *Bufo fowleri.* These criteria are (1) amount of extreme range of ratio, (2) amount of "restricted" range of ratio, (3) percentage variation of restricted range, (4) amount of range of ratio in older animals, and (5) the "relation" of the range in older animals with restricted range.

Combinations Involving the Third Lower Row.—Before summarizing the relative values of the different combinations, special attention may be directed to the combinations involving the third lower row. Since in plotting the four combinations involving the third lower row the latter was plotted along the axis of abscissas in each instance (as also cited above), it follows that the maximum extreme ratio is in each instance infinity, because the third lower row does not appear until somewhat later than the others. Thus the amount of extreme ratio is also infinite in each instance, and for this reason the ratio of any combination involving the third lower row would be of no value as a character constant throughout the larval period of this species, i.e., *Pseudacris nigrita triseriata.* Of course the absence of a given row for a given body size might be a valuable character. However, the discussion at this point does not deal with this aspect. Also, the maximum ratio in the restricted range in each instance in this group is taken as the case in which the third lower row is shortest, though present. This omits a much greater percentage of cases than in other combinations. For this reason, then, the combinations considered in this group cannot be "fairly" compared with other combinations. However, the combinations of this group may be evaluated with respect to each other.

Summary of the Combinations of Rows.—From a study of the results expressed in Table IX and subcolumns "A" of Table X it may be stated that the following is the order of the different possible combinations of rows of teeth from least to greatest variability of ratio and from greatest to least value as constant characters through the period of

TABLE IX.—*Pseudacris nigrita triseriata*: RATIOS TO ONE OF DIFFERENT COMBINATIONS OF MOUTHPARTS

Combinations	Extreme range			Restricted range			Variation %	Range in older animals			Relative Age of	
	Minimum	Maximum	Amount	Minimum	Maximum	Amount		Minimum	Maximum	Amount	Minimum	Maximum
1 U/2 U	1.00	1.25	0.25	1.02	1.18	0.16	7.3	1.00	1.18	0.18	O	vY
1 U/1 L	0.98	1.72	0.74	1.08	1.44	0.36	14.3	1.08	1.32	0.24	M	vY
1 U/2 L	1.00	1.96	0.96	1.03	1.37	0.34	14.2	1.03	1.28	0.25	M	vY-(*Y*)
1 U/3 L	2.94	inf.	inf.	3.20	22.33	19.13	74.1	2.94	5.60	2.66	vO	vY-Y
2 U/1 L	0.84	1.37	0.53	0.98	1.28	0.30	13.3	1.01	1.22	0.21	M	M
2 U/2 L	0.83	1.36	0.51	0.92	1.31	0.39	17.9	0.92	1.18	0.26	M	M
2 U/3 L	2.22	inf.	inf.	2.65	20.00	17.35	76.6	2.65	5.50	2.85	M	vY
1 L/2 L	0.82	1.20	0.38	0.87	1.08	0.21	10.8	0.87	1.01	0.14	vY	Y
1 L/3 L	2.31	inf.	inf.	2.68	17.00	14.32	72.8	2.31	7.00	4.69	vO	vY
2 L/3 L	2.54	inf.	inf.	2.76	18.00	15.24	73.4	2.54	4.72	2.18	vO	vY-Y
1 U/r & 1	2.20	5.01	2.81	2.32	3.60	1.28	21.6	2.32	3.05	0.73	M	Y
2 U/r & 1	1.89	3.51	1.62	2.04	3.21	1.17	22.4	1.89	3.51	1.62	M-O	M-O
1 L/r & 1	1.81	3.04	1.23	1.88	2.88	1.00	21.0	1.81	2.46	0.65	M-O	vY
2 L/r & 1	1.65	3.28	1.63	1.91	3.02	1.11	22.7	1.83	2.73	0.90	Y	Y-M
3 L/r & 1	inf.	0.92	inf.	0.14	0.80	0.66	70.0	0.42	0.84	0.42	VYY	M
2 U/m s	1.70	9.60	7.90	2.32	6.50	4.18	45.0	2.32	9.60	7.28	vY	vO
r & 1/m s	0.48	4.28	2.80	0.82	2.86	2.04	55.4	1.00	4.28	3.28	vY	vO
1 U/M	1.45	2.50	1.05	1.55	2.16	0.61	16.7	1.70	2.16	0.46	vY	Y
2 U/M	1.36	2.68	1.32	1.43	1.93	0.50	14.9	1.54	2.00	0.40	vY	M
1 L/M	1.00	2.20	1.20	1.22	1.91	0.69	22.3	1.22	1.91	0.69	vY	vY
2 L/M	1.10	2.31	1.21	1.20	1.89	0.69	22.6	1.34	1.94	0.60	vY	M
3 L/M	inf.	0.64	inf.	0.07	0.59	0.52	44.1	0.34	0.64	0.30	vY	vO
r & 1/M	0.40	1.17	0.77	0.46	0.82	0.36	28.1	0.49	0.93	0.44	vY	M

Symbols used for rows, etc., are the same as in Table V. "M" is upper beak.

TABLE X.—*Pseudacris nigrita triseriata*: NUMERICAL RANK FROM LEAST TO GREATEST OF THE RANGES OF RATIOS LISTED IN TABLE IX

Combinations of rows, etc.	Criteria: Amount of extreme range of ratios		Criteria: Amount of restricted range of ratios		Criteria: Percentage variation of restricted range of ratios		Criteria: Amount of range of ratios in older animals		Criteria: Amount of difference between range in older animals and restricted range		Final assigned values	
	A*	B†	A	B	A	B	A	B	A	B	A	B
1 U/2 U	1	1	1	1	1	1	2	2	1	2	1	1
1 L/2 L	2	2	2	2	2	2	1	1	2	4	2	2
2 U/1 L	4	4	3	3	3	3	3	3	3-4	6-8	3	3
1 U/2 L	6	7	4	4	4	4	5	5	3-4	6-8	4	4
1 U/1 L	5	5	5	5-6	5	5	4	4	5	9	5	5
2 U/M	5	12	2	8	1	6	3-4	10-11	2	3	1	7
1 U/M	2	8	4	10	2	7	3-4	10-11	5	11	3	9
2 U/2 L	3	3	6	7	6	8	6	6	6	10	6	6
1 L/r & 1	7	11	8	14	7	9	8	13	9	15	7	12
1 U/r & 1	11	16	11	17	8	10	9	15	11	17	10	15
1 L/M	3	9	5-6	12-13	3	11	6	4	1	1	4	10
2 U/r & 1	8	13	10	16	9	12	11	17	10	16	9	14
2 L/M	4	10	5-6	12-13	4	13	5	12	4	6-8	...	11
2 L/r & 1	9	14	9	15	10	14	10	16	7	12	8	13
r & 1/M	1	6	1	5-6	5	15	2	9	3	5	2	8
3 L/M	6	?	3	9	6	16	1	7	6	13	5	18
2 U/m s	12	17	13	19	11	17	17	23	13	19	12	17
r & 1/m s	10	15	12	18	12	18	15	21	12	18	11	16
3 L/r & 1	?	?	7	11	13	19	7	8	8	14	13	19
1 L/3 L	?	?	14	20	14	20	16	22	14	20	15	21
2 L/3 L	?	?	15	21	15	21	12	18	15	21	14	20
1 U/3 L	?	?	17	23	16	22	13	19	17	23	17-16	23-22
2 U/3 L	?	?	16	22	17	23	14	20	16	22	16-17	22-23

*Sub-columns headed "A" give ranks of combinations within groups, which groups are (1) combinations involving only the rows of teeth, or (2) combinations involving the rows of teeth on the one hand and the upper beak on the other.

†Sub-columns headed "B" give ranks of combinations as compared with all other combinations.

Symbols used to represent rows are the same as in Table V. "M" is upper beak.

larval existence of *Pseudacris nigrita triseriata* covered by the present study: (1) first upper/second upper; (2) first lower/second lower; (3) second upper/first lower; (4) first upper/second lower; (5) first upper/first lower; (6) second upper/second lower; (7) first lower/average of right and left parts of second upper; (8) second lower/average of right and left parts of second upper; (9) Second upper/average of right and left parts of second upper; (10) first upper/average of right and left parts of second upper; (11) average of right and left parts of second upper/median space in second upper; (12) second upper/median space in second upper; (13) third lower/average of right and left parts of second upper; (14) second lower/third lower; (15) first lower/third lower; (16)-(17) second upper/third lower; (16)-(17) first upper/third lower.

Combinations Involving the Upper Beak.—Subcolumns "A" in Table X show the rank of each combination involving the upper beak according to the same criteria used in evaluating combinations involving only the rows of teeth (cf. also Chart 7).

All ranges of ratios of all combinations of rows of teeth with upper beak are quite similar except in those combinations involving (1) the average of the right and left parts of the second upper row, and (2) the third lower row. Of these two combinations the latter must be counted as least in value because of the late appearance of the third lower row. The former of these two combinations may be considered as ranking first least when all criteria are considered.

The other four combinations, i.e., those involving the first upper, second upper, first lower, and second lower rows respectively do not differ considerably from each other according to any criterion. However, when all criteria are considered, the ratios of the combinations involving the four rows in question rank from least to greatest as follows: second upper, first upper, first lower, and second lower respectively.

Thus, the rank of the different respective combinations involving the upper beak from least to greatest range and variability of ratio and from greatest to least value as a constant character is as follows: (1) average of right and left parts of the second upper row/upper beak; (2) second upper row/upper beak; (3) first upper row/upper beak; (4) first lower row/upper beak; (5) second lower row/upper beak; and (6) third lower row/upper beak.

As a group these combinations are of a rank of value somewhat higher as affording ratios as constant characters than the group of combinations involving the averages of right and left parts of the second upper row, and perhaps slightly less than the group of combinations involving only the four longer rows. Individual combinations, of course, will vary somewhat from such an exact rank. For instance, the combination, third lower row/upper beak, will rank along with the other combinations involving the third lower row.

Comparative Evaluation of All Combinations.—If all combinations, both those involving only the rows of teeth or their parts, and those involving rows of teeth or their parts and the upper beak, be considered collectively according to all criteria, they will be found to rank as follows from greatest to least value as constant characters of the tadpoles of *Pseudacris nigrita triseriata* (cf. subcolumns "B" in Table X): (1) first upper row/second upper row; (2) first lower row/second lower row; (3) second upper row/first lower row; (4) first upper row/second lower row; (5) first upper row/first lower row; (6) second upper row/second lower row; (7) second upper row/upper beak; (8) average of right and left parts of second upper row/upper beak; (9) first upper row/upper beak; (10) first lower row/upper beak; (11) second lower row/upper beak; (12) first lower row/average of right and left parts of second upper row; (13) second lower row/average of right and left parts of second upper row; (14) second upper row/average of right and left parts of second upper row; (15) first upper row/average of right and left parts of second upper row; (16) average of right and left parts of second upper row/median space in second upper row; (17) second upper row/median space in second upper row; (18) third lower row/upper beak; (19) third lower row/average right and left parts of second upper row; (20) second lower row/third lower row; (21) first lower row/third lower row; (22) second upper row/third lower row; (23) first upper row/third lower row.

Rana pipiens

Descriptions of the Parts of the Mouth Apparatus

The number and disposition of the rows of teeth, when all are present, in *Rana pipiens* are the same as the common type described in the introduction (cf. pp. 9-11).

After the upper beak is heavily pigmented or has begun to be apparent, teeth of the first upper row and first lower row appear, followed shortly by the appearance of teeth in the second and third lower rows. The second upper row is quite irregular as to appearance and occurrence.

There is a great degree of irregularity in the animals studied in this series (one hundred individuals, of body lengths from 4.15 mm. to 8.47 mm.).

In the first upper row there occur obvious irregularities in 15% of the animals studied.

The second upper row is entirely absent in 66% of the cases studied. In an additional 5% the row is either very faint or only one of its parts is present. At any rate in only 29% of the cases could satisfactory measurements and counts be taken. (For further discussion cf. below.)

The first lower row is relatively complete and regular in only 28% of the cases studied.

The second lower row is entirely absent when other rows are present in 6% of the cases. It is irregularly divided in other than the median line in 7% of the cases studied.

Although the third lower row shows no tendency to divide into two equal parts, in 8% of the cases it is divided irregularly into from two to an indefinite number of parts. This 8% does not include the many cases in which the teeth in a row are themselves scattered and irregularly distributed. The row is absent in 8% of the cases, and consists of one (visible) tooth in an additional 2%.

The irregularities through the series of *Rana pipiens* studied show practically no correlation with body size or age. The second upper row in a very general way appears with increase in body size (length). The body lengths in the series range from 4.15 mm. to 8.47 mm.; and the smallest animal having the second upper row is 4.65 mm. in body length, while the largest animal not having a second upper row is 7.30 mm. in body length. No other irregularities show even this degree of correlation.

Curvature of the Rows of Teeth

Table XI gives the ratios of arc length/chord length for the rows of teeth of this species, i.e., *Rana pipiens*. The series of tadpoles of this species studied did not attain as great a proportionate size of the species as was the case in the series of the other two species studied. Therefore, from the viewpoint of proportion of possible size attained, the tadpoles

Table XI.—*Rana pipiens*: Ratios to One of Arc Length/Chord Length of Rows of Teeth

Row	Maximum (all included)	Maximum (less extremes)	Minimum
First upper	1.35	1.18	1.04
Right part of second upper	1.12	1.12	1.00
Left part of second upper	1.25	1.10	1.00
First lower	1.26	1.16	1.03
Second lower	1.32	1.27-1.18	1.01
Third lower	1.30	1.12	1.00

of *Rana pipiens* studied should be compared only with the smaller tadpoles of *Bufo fowleri* and of *Pseudacris nigrita triseriata.*

However, in general practically as great arc length/chord length ratios develop in *R. pipiens* as in the other species (cf. Tables XI, VII, and II.) Now in actual range of body size the tadpoles of the series of the different species studied do not differ greatly. Therefore, it may be concluded that arc length/chord length ratios of the rows of teeth correspond more to actual body size than to proportion of possible body size.

There is in *Rana pipiens* a general tendency for an increased arc length/chord length ratio in more peripheral rows of teeth.

Numbers of Teeth in the Different Rows of Teeth

There is no apparent change with age of numbers of teeth per unit arc length of the rows of teeth in the tadpoles of the series of *Rana pipiens* studied. The size attained by the tadpoles of the series is, however, small as compared with possible size; and perhaps no such change could be expected without much larger animals being studied.

Minimum numbers of teeth per unit arc length of row are slightly less than in *Bufo fowleri* and much less than in *Pseudacris nigrita triseriata.* Maximum numbers of teeth per unit arc length of row are much less than in *B. fowleri* and very much less than in *P. nigrita triseriata* (cf. Tables XII, VIII, and III). The differences between maximum and minimum numbers of teeth per unit arc length of row ("range" in the Tables) are also somewhat less in *R. pipiens* than in the other species. This fact may, however, be due to the elimination from consideration of so many rows of teeth, i.e., rows irregularly or only partly toothed. It may be noted, however, that, since numbers of teeth per unit arc length of row are in general less in *R. pipiens* than in the other species studied, it follows that the teeth are generally larger in the tadpoles of *R. pipiens* than in tadpoles of the other two species.

Table XII.—*Rana pipiens*: Number of Teeth per 1 mm. of Arc Length of Row of Teeth

Row	Maximum	Minimum	Range
First upper	53	31	22
Right part of second upper	58	27	31
Left part of second upper	67	28	39
First lower	60	38	22
Second lower	62	32	30
Third lower	59	28	31

TABLE XIII.—*Rana pipiens*: RATIOS TO ONE OF THE DIFFERENT COMBINATIONS OF MOUTH PARTS

Combinations of rows, etc.	Extreme range			Restricted range			% variation	Range in older animals			Relative age of	
	Minimum	Maximum	Amount	Minimum	Maximum	Amount		Minimum	Maximum	Amount	Minimum	Maximum
1 U/2 U	1.05	inf.	inf.	1.05	1.56	0.51	29.0	....	....	....	O	O
1 U/1 L	zero	inf.	inf.	1.05	2.19	1.14	35.2	1.12	2.32	1.20	Y	M
1 U/2 L	zero	inf.	inf.	0.90	2.47	1.49	43.4	1.12	1.87	0.75	Y	Y
1 U/3 L	zero	inf.	inf.	1.53	14.20	12.67	80.6	1.52	12.65	11.13	Y	Y
2 U/1 L	zero	inf.	inf.	0.81	3.16	2.35	59.3	....	....	....	O	O
2 U/2 L	zero	inf.	inf.	0.74	2.32	1.58	51.6	....	....	....	M	O
2 U/3 L	zero	inf.	inf.	0.89	14.33	13.44	88.3	....	....	....	Y	M
1 L/2 L	0.08	inf.	inf.	0.78	10.00	9.22	85.5	0.78	1.09	0.31	M	Y&M
1 L/3 L	0.07	inf.	inf.	0.88	8.60	7.72	81.2	1.13	1.86	0.73	M	Y&M
2 L/3 L	0.62	inf.	inf.	1.03	8.20	7.17	77.7	1.08	1.62	0.54	M	Y-M
1 U/r & 1	3.02	inf.	inf.	3.77	21.50	17.73	70.2	....	....	....	O	O
2 U/r & 1	3.25	20.00	16.75	3.52	15.75	12.23	63.6	....	....	....	all	all
1 L/r & 1	zero*	inf.*	inf.	1.38	24.33	22.95	89.3	....	....	....	..	..
2 L/r & 1	zero†	inf.†	inf.	1.53	27.00	25.47	89.3	....	....	....	..	..
3 L/r & 1	0.69	inf.‡	inf.	0.81	18.00	17.19	91.4	....	....	....	..	..
2 U/m s.	1.03	2.26	1.23	1.10	2.22	1.12	34.0	....	....	....	all	all
r & 1/m s.	1.42	17.67	16.25	0.07	6.33	6.26	97.8	....	....	....	all	all
1 U/M	0.96	1.60	0.64	1.05	1.52	0.47	19.0	1.22	1.60	0.38	M	O
2 U/M	zero	inf.	inf.	0.84	1.32	0.48	22.2	....	....	....	M	O
1 L/M	inf.	1.33	inf.	0.34	1.19	0.85	55.8	inf.	1.26	inf.	all	M
2 L/M	inf.	1.30	inf.	0.50	1.24	0.74	42.5	inf.	1.27	inf.	all	M&O
3 L/M	inf.	1.10	inf.	0.10	0.90	0.80	80.0	inf.	0.90	inf.	all	O
r & 1/M	inf.	0.48	inf.	0.06	0.38	0.32	72.7	....	....	....	all	Y

Note: Symbols for rows used in this table are the same as in Table V. Inf. = Infinity.
*When r&l = zero, 1 L may be 0.21 to 0.96 mm.; when 1 L = zero, r&l may be 0.15 to 0.30 mm.
†When r&l = zero, 2 L may be 0.20 to 0.90 mm.; when 2 L = zero, r&l may be 0.15 mm.
‡When r&l = zero, 3 L may be 0.05 to 0.63 mm.
"M" is upper beak.

Ratios of Combinations of Rows of Teeth and of Rows of Teeth and Upper Beak

Because of such irregularity and of the frequent absence of entire rows, ratios are quite likely to be very irregular and have rather wide ranges in *R. pipiens.* The extreme range of ratio of any combination (except combinations involving only the parts of a single row) is, due to the frequent absence of individual rows, in every instance infinite. The restricted range, as given in Table XIII, includes all cases in which both rows of the combination in question are present if in as many as or more than 5-6% of the cases one of the rows is absent. If in less than 5-6% of the cases one of the rows is absent, the restricted range omits a sufficient number of exceptional cases where both rows are present to make up the 5-6%. Too, the range of sizes of the tadpoles of this series is so small as compared with the size attained before metamorphosis that the range of ratio in "older" animals is without much significance other than indicating the "trend" of the ratios. Too few animals possess the second upper row to segregate the animals as to age in the cases of combinations involving this row or its parts.

Combinations Not Involving the Second Upper Row.—The rank according to value of constancy of ratio of the combinations in this group is as follows: (1) first upper row/first lower row, (2) first upper row/second lower row, (3) second lower row/third lower row, (4) first lower row/third lower row, (5) first lower row/second lower row, and (6) first upper row/third lower row.

Combinations Involving the Second Upper Row and Its Parts.—Since the combinations in this group involve less than one-third of the animals studied, the group is too small to divide with respect to age. Thus, the only criteria to be used in evaluating the combinations are amount of restricted range of ratio and percentage variation of this range.

The following combinations of this group rank in the order listed from least to greatest according to either or both of the above mentioned criteria: (1) first upper row/second upper row, (2) second upper row/median space of second upper row, (3) second upper row/second lower row, and (4) second upper row/first lower row.

In the remaining combinations of this group relative amounts and percentages differ. Considering both criteria, however, the combinations rank from least as follows: (5) second upper row/average of right and left parts of second upper row, (6) second upper row/third lower row, (7) first upper row/average of right and left parts of second upper row, (8) average of right and left parts of second upper row/median space in second upper row, (9) third lower row/average of right and left parts

TABLE XIV.—*Rana pipiens*: NUMERICAL RANK FROM LEAST TO GREATEST OF THE RANGES OF RATIOS LISTED IN TABLE XIII

Set	Group	Combinations of rows, etc.	Criteria: Amount of restricted range of ratio A*	B*	C*	Percentage variation of restricted range of ratio A	B	C	Per both the preceding criteria A	B	C	Final assigned relative values A	B	C
Set	Group	1 U/1 L	9	3	1	5	3	1	6-7	3	1	2	1	1
		1 U/2 L	10	4	2	7	4	2	9	4	2	5	2	2
		2 L/3 L	14	8	3	14	9	3	13-15	7-9	3	7	3	3
		1 L/3 L	15	9	4	17	11	5	16	10	4	8	4	4
		1 L/2 L	17	11	5	18	12	6	13-15	7-9	5	10	6	6
		1 U/3 L	10	12	6	16	10	4	18	12	6	9	5	5
	Group	1 U/2 U	4	1	1	2	1	1	2-3	1	1	12	7	1
		2 U/m s	8	2	2	4	2	2	5	2	2	13	8	2
		2 U/2 L	11	5	3	8	5	3	10	5	3	15	9	3
		2 U/1 L	12	6	4	10	6	4	13-15	7-9	4	16	10	4
		r & 1/m s	13	7	5	23	17	11	19	13	8	20	14	8
		2 U/r & 1	16	10	6	11	7	5	12	6	5	17	11	5
		2 U/3 L	19	13	7	19	13	7	20	14	6	18	12	6
		3 L/r & 1	20	14	8	22	16	10	21	15	9	21	15	9
		1 U/r & 1	21	15	9	12	8	6	17	11	7	19	13	7
		1 L/r & 1	22	16	10	20-21	14-15	8-9	22	16	10	22	16	10
		2 L/r & 1	23	17	11	20-21	14-15	8-9	23	17	11	23	17	11
Set	Group	1 U/M	2	2	1	1	1	1	1	1	1	1	1	1
		1 L/M	7	6	4	9	4	3	8	5	3-4	4	3	3
		2 L/M	5	4	2	6	3	2	4	3	2	3	2	2
		3 L/M	6	5	3	15	7	4	11	6	3-4	6	4	4
	Group	2 U/M	3	3	2	3	2	1	2-3	2	1	11	5	1
		r & 1/M	1	1	1	13	5	2	6-7	4	2	14	6	2

*Sub-columns headed "A" give relative values of the combinations when all are considered; sub-column "B" the relative values within a "set," and sub-column "C" the relative values within a "group."

Symbols used for rows are the same as in Table V. "M" is upper beak.

of second upper row, (10) first lower row/average of right and left parts of second upper row, and (11) second lower row/average of right and left parts of second upper row.

Combinations Involving the Upper Beak.—The combinations in this group rank from greatest to least value of constancy as follows (cf. subcolumns "B" and "C" in Table XIV, and Chart 8): (1) first upper row/upper beak, (2) second lower row/upper beak, (3) first lower row/upper beak, (4) third lower row/upper beak, (5) second upper row/upper beak, (6) average of right and left parts of second upper row/upper beak.

Summary.—The relative values within the groups of the various combinations as affording ratios of reliable constancy in the series studied of this species, *Rana pipiens,* have been given and will not be repeated here. However, the relative values of all combinations, (not grouped) according to all criteria and taking into account the high percentage of absence of the second upper row, may be listed as follows from greatest to least value (cf. subcolumns "A" in Table XIV): (1) first upper row/upper beak; (2) first upper row/first lower row; (3) second lower row/upper beak; (4) first lower row/upper beak; (5) first upper row/second lower row; (6) third lower row/upper beak; (7) second lower row/third lower row; (8) first lower row/third lower row; (9) first upper row/third lower row; (10) first lower row/second lower row; (11) second upper row/upper beak; (12) first upper row/second upper row; (13) second upper row/median space in second upper row; (14) average of right and left parts of second upper row/upper beak; (15) second upper row/second lower row; (16) second upper row/first lower row; (17) second upper row/average of right and left parts of second upper row; (18) second upper row/third lower row; (19) first upper row/average of right and left parts of second upper row; (20) average of right and left parts of second upper row/median space in second upper row; (21) third lower row/average of right and left parts of second upper row; (22) first lower row/average of right and left parts of second upper row; and (23) second lower row/average of right and left parts of second upper row.

It will be noted that the relative values of the combinations in *Rana pipiens* do not correspond to a very great extent to the relative values of similar combinations in *P. nigrita triseriata or in Bufo fowleri.* If the relative values of the combinations (in *R. pipiens*) be estimated without taking into consideration the high percentage of absence of the second upper row (cf. Table XV) the values correspond to a greater extent, but even by this method of comparison the extent to which the different species correspond is not great. This will be further discussed below.

General Considerations Involving All Species Studied

Comparison of Evaluations of Ratios in the Different Species

Through examination of Table XV it will be seen that the corresponding combinations of rows of teeth and of rows of teeth and upper beak do not have the same relative rank (according to value as affording constant characters) in the different species studied, i.e., *B. fowleri, P. nigrita triseriata,* and *R. pipiens.* The greater similarity in relative values of corresponding combinations is between *B. fowleri* and *P. nigrita triseriata. R. pipiens* is quite different from either *B. fowleri* or *P. nigrita triseriata* in relative values of constancy of ratios of corresponding combinations.

It has been seen that the third lower row appears rather late in *P. nigrita triseriata,* thus making the combinations involving this third lower row of less value than any other combinations. Now, if combinations involving this third lower row be eliminated in both *B. fowleri* and *P. nigrita triseriata* and the remaining combinations have their relative values redetermined on the basis of the reduced number, then the relative values of corresponding combinations in the two species, *B. fowleri* and *P. nigrita triseriata* will coincide to a much greater degree. Of the seventeen combinations thus compared there is exact coincidence of rank in six cases, a difference in rank of one in six cases, a difference of two in

Table XV.—Numerical Rank from Greatest to Least Value for Constancy of Ratio of Different Combinations of Mouth Parts Compared in Species Studied

Combination of rows, etc.	Order of relative value			Combination or rows, etc.	Order of relative value		
	B. fowleri	*P. nigrita triseriata*	*R. pipiens*		*B. fowleri*	*P. nigrita triseriata*	*R. pipiens*
1 U/2 U.....	1	1	12	1 U/3 L...	13	23	9
1 L/2 L.....	2	2	10	2 L/3 L....	14	20	7
2 U/1 L.....	3	3	16	3 L/r & 1...	15	19	21
2 U/2 L.....	4	6	15	2 U/r & 1..	16	14	17
1 U/2 L.....	5	4	5	2 U/3 L...	17	22	18
1 U/1 L.....	6	5	2	1 L/r & 1...	18	12	22
1 U/M......	7	9	1	1 U/r & 1..	19	15	19
2 U/M......	8	7	11	2 L/r & 1...	20	13	23
1 L/M.......	9	10	4	r & 1/M....	21	8	14
2 L/M.......	10	11	3	r & 1/m s...	22	16	20
3 L/M.......	11	18	6	2 U/m s...	23	17	13
1 L/3 L.....	12	21	8				

Symbols for rows of teeth are the same as in Table V.

three cases, a difference of three in one case, and in one case a difference of seven. It appears that this is a rather high degree of correlation.

In *R. pipiens* the second upper row has been noted to be absent in almost two-thirds of the animals studied. Thirteen of the twenty-three possible combinations involve this second upper row or its parts or median space. If *R. pipiens* and *B. fowleri* be compared as to respective relative values of the ten combinations not involving the second upper row in any way, the extent of correlation is indeed not great. There is exact coincidence of rank in only two cases; a difference of one in three cases, a difference of three in four cases, and a difference of nine in one case.

If *P. nigrita triseriata* and *R. pipiens* be compared as to relative values of the only six combinations not involving either the third lower row or the second upper row in any way, practically no correlation exists. There is no coincidence of rank, a difference of one in rank in two cases, a difference of three in three cases, and a difference of five in one case. It is true, however, that the six combinations used in this comparison are of not so different actual values in any species studied, and of uncertain relative rank in some instances.

Thus, according to relative rank of corresponding combinations (involving only regular rows), *B. fowleri* and *P. nigrita triseriata* correspond more nearly than any other two species; and *B. fowleri* and *R. pipiens* correspond more nearly than *P. nigrita triseriata* and *R. pipiens*. The "fairness" of such comparisons may be debated. It might appear that comparison on the basis of such a small number of combinations is not sufficiently likely to show much correlation of rank. However, it must be kept in mind that it is granting a point to eliminate from the comparisons the constant "irregularities." Hence, the comparisons as made above show greater degrees of correlation than actually exist. For the constantly high percentage of absence of a given row cannot be overlooked.

It appears, then, that if "irregularities" be overlooked, growth phenomena in the different species may be quite similar. This may actually be true of growth phenomena of the oral disc in general; and the general conclusions as to growth phenomena as drawn from the analyses of the series of *B. fowleri* tadpoles may be concluded to apply to the other species studied. However, the general conclusions do not apply to specific rows, and hence to combinations of rows. Each species constitutes an individual case; and, though the same general phenomena may underlie all cases, each species must have its own combinations of rows and of rows and upper beak relatively evaluated strictly on their own merits of constancy.

Results of Present Study Compared with Characters Used by Wright

Since one of the first objectives in beginning the present study was to determine to what extent, if any, the characters used by Wright as applying to "mature" tadpoles apply to young tadpoles, a comparison may now be made between the characters used by Wright and the results of the present study.

Bufo fowleri.—Wright (1929) describes and places in the "key" the tadpole of a toad to which he refers as "Bufo (Raleigh)." In the "key" included in the *Frogs of the Okefinokee* (1932), the section giving a synopsis of the "Bufo (Raleigh)" tadpoles is used without change to describe the tadpoles of *Bufo fowleri.* It is to be concluded from this that the characters of *B. fowleri* tadpoles are rather constant throughout the geographical range of the species, for Wright has undoubtedly examined tadpoles of this species from a variety of localities. Now, if what Wright means by "normally" corresponds in a general way to "restricted range of ratios" of the author, characters used by Wright should practically coincide with those determined by the author if the characters used by Wright are of any value when applied to all sizes of tadpoles. This should be especially true for *B. fowleri,* since the present study involves tadpoles of maximum size. Examination of Table XVI will reveal that the ranges of ratios of the combinations used as given by Wright are considerably less than those obtained in the present study (no exceptions). In only two instances does the range as given by Wright fail to fall completely within the range determined by the present study. Also, the ranges for *B. americanus* and *B. terrestris* fall within the respective ranges of *B. fowleri* as determined by the present study.

Table XVI.—Ratios of *Bufo fowleri* Compared with Ratios Given by Wright for Species of *Bufo*

Combinations of rows, etc.	Ratios given by Wright (1929)			Ratios obtained in present study
	B. terrestris	*B. fowleri*	*B. americanus*	*B. fowleri*
1 U/M	1.75	1.4-1.5	1.2-1.4	1.48-1.94
1 L/M	1.5	1.2-1.3	1.1-1.2	1.17-1.62
2 L/M	1.5	1.2-1.3	1.1-1.2	1.10-1.56
1 L/3 L	1.2-1.4	1.3-1.6	1.3-1.5	1.05-1.85
r & l/m s	1.4-2.1	1.3-3.0	1.15-2.0	0.60-2.64
3 L/M	1.0 or slightly more	1.0-	......	0.80-1.33
1 U/2 U	......	......	1.0 or greater	0.98-1.22

Symbols used for rows of teeth, etc., are the same as in Table V.

Furthermore, if the ratios of the older animals of the series studied be examined, it will be seen that such ratios fall without exception in the upper values of the respective ranges as given in the present study, and, hence, for the most part, are above the maximum ranges given by Wright. Thus, two conclusions are obvious. (1) The range of ratios of any given combination as given by Wright for mature tadpoles of *B. fowleri* is not of sufficient extent to apply to younger tadpoles. (2) The range of ratios of any given combination as given by Wright is too narrow to include a "normal" percentage of mature tadpoles of *B. fowleri* over the geographical range of the species.

Now if the "normal" range of ratio of a given combination in a given species be of sufficient extent to apply to the cases of younger, as well as mature tadpoles, will the ratio in question be of any value as a distinctive character? This question will be further discussed later.

Pseudacris nigrita triseriata.—Wright (1929) described "Pseudacris (Buffalo)," "Pseudacris (Raleigh)," and *P. ocularis,* and in *Frogs of the Okefinokee* (1932) discussed to some extent also *P. nigrita.* The Pseudacris from Buffalo lacks the third lower row of teeth, although tadpoles described have "embryonic hind legs" and a maximum body length of 8.8 mm. Further, the tadpoles are spoken of as being "quite small." Even though the largest tadpoles of the series examined in the present study are not so large as the "quite small" Pseudacris from Buffalo, the fact that the third lower row of teeth appears later than the other rows in the tadpoles of this series of *Pseudacris nigrita triseriata* raises several questions. If the "Pseudacris (Buffalo)" is a different species, perhaps there may be some systematic significance attached to the order or time of appearance of the rows of teeth. This is, however, unlikely. Or the late appearance of the row in question or its failure to appear may also be a geographical variation. Would the third lower row have appeared later in the "Pseudacris (Buffalo)"? Or had it been lost? Wright apparently presumes its absence to be a specific character. In fact a rather confusing state of affairs prevails, since in the Wrights' *Handbook of Frogs and Toads* (1933) the tadpoles of *Pseudacris nigrita triseriata* are described as having two upper and two lower rows of teeth: ". . . . and the tooth ridges 2/2" (line 13, page 95). This is obviously erroneous, unless a geographical variation in the numbers of rows of teeth occurs in the species.

In the series examined in the present study, tadpoles as small as 2.91 mm. (body length) may have a distinct third lower row; and the row is never absent in tadpoles of more than 3.36 mm. body length, though the teeth may be barely pigmented sufficiently to be readily detected when the tadpoles are as large as 3.57 mm. body length. It appears, then, that the tadpoles upon which Wright and Wright (1933) base the description of *P. nigrita triseriata* tadpoles may not be *P. nigrita triseriata* tadpoles at all.

Table XVII gives the ranges of ratios used by Wright (1929) in describing tadpoles of "Pseudacris (Raleigh)" and *P. ocularis* as compared with the ranges of the corresponding ratios in the tadpoles of *P. nigrita triseriata* examined in the present study. Wright does not describe *P. nigrita* tadpoles in *Frogs of the Okefinokee* (1932), although he discusses at length the life history of the species. Neither are ratios of combinations of rows given by Wright and Wright (1933).

TABLE XVII.—RATIOS OF *Pseudacris nigrita triseriata* COMPARED WITH RATIOS GIVEN BY WRIGHT FOR SPECIES OF *Pseudacris*

Combinations of rows, etc.	Ratios given by Wright (1929)		Ratios obtained in present study
	P. (Raleigh)	*P. ocularis*	*P. nigrita triseriata*
1 U/M	1.50-1.75	2.0	1.55-2.16
1 L/M	1.25-1.60	2.0	1.22-1.91
2 L/M	1.25-1.60	2.0	1.20-1.89
1 L/3 L	3.00-4.00	3.0	2.68-17.00
r&1/m s	2.50-7.00	3.0-4.0	0.82- 2.86

Symbols used for rows of teeth, etc., are the same as in Table V.

The ranges of ratios as determined in the present study of *P. nigrita triseriata* include the respective ranges of ratios of Wright's "Pseudacris (Raleigh)" with one exception, and on the basis of this one ratio (average of right and left parts of second upper row/median space in same) the two species may be separated, provided the range Wright assigns includes actually a "normal" percentage of the tadpoles of the species. *P. ocularis* tadpoles may be distinguished from *P. nigrita* tadpoles by three ratios, provided the ratios as given by Wright for *P. ocularis* are as "exact" or limited as they are listed, which they perhaps are not.

Unfortunately, there is no detailed description of the mouthparts of mature *P. nigrita triseriata* tadpoles with which the present findings may be compared; and the reliability of applying the ratios obtained in this study to "mature" tadpoles must await examination of a series including larger tadpoles before being determined.

Rana pipiens.—The ratios of combinations of rows of teeth, etc., of the tadpoles of the series of this species examined in the present study may be compared with the ratios given by Wright for this species and for *R. sphenocephala, R. palustris,* and *R. clamitans* by examination of Table XVIII. In the case of the ratio of each combination the range established by the present study will include the ranges for all the species compared. It appears, then, that the ranges of ratios as given by Wright for *R. pipiens* must be considerably extended in order to be applicable to young tadpoles, with the result that the ratios of the combinations of rows he uses lose their distinction.

TABLE XVIII.—RATIOS OF *Rana pipiens* COMPARED WITH RATIOS GIVEN BY WRIGHT FOR SPECIES OF *Rana*

Combinations of rows, etc.	Ratios given by Wright (1929)				Ratios obtained in present study
	R. clamitans	*R. palustris*	*R. sphenocephala*	*R. pipiens*	*R. pipiens*
1 U/M........	1.0 (about)	1.0	1.0 or 1.0	1.0 or 1.0 (never 1.5)	1.05-1.52
1 L/M........	....	....	....	1.0	....
2 L/M........	....	....	....	....	....
1 L/3 L.......	2.0	1.49-3.03	1.4-1.49	1.28	0.88-8.60
r & 1/m s......	0.09-0.17	0.25-0.50	1.0-2.00	0.67-1.00	0.07-6.33
3 L/M........	....	....	....	0.75-0.80	....
1 U/2 U......	?	1.0 or 1.0	....	"about" 1.0	1.05-1.56

Symbols used for rows of teeth, etc., are the same as in Table V.

Summary.—From the above comparisons it is first to be concluded that the ratios of combinations of rows as given by Wright for mature tadpoles are not of sufficiently extensive range to be applicable to younger tadpoles, nor, indeed, to be in some instances applicable to all "geographic races" of mature tadpoles of the species in question. And, further, when the ranges are extended to include the cases of younger tadpoles, there is the likelihood of the ratios used by Wright becoming of no specific distinctive value. This might indicate that perhaps ratios between rows of teeth are of little taxonomic value; but such a conclusion will not be drawn at this point for this particular aspect of the question will be further discussed later.

In particular, the tadpoles of *P. nigrita triseriata* examined in this series invariably have the third lower row of teeth after reaching a body length of 3.36 mm., although Wright and Wright (1933) describe the tadpoles of this species as having only two lower rows of teeth and do not mention the possibility of a third lower row being added. Either their identification or description is erroneous or there is a geographical difference in the tadpoles of the species.

Comparison of the Different Species Studied According to Ratios of Combinations of Rows

If the three species of tadpoles studied, i.e., *B. fowleri, P. nigrita triseriata,* and *R. pipiens,* be compared as to restricted ranges of ratios of combinations of rows of teeth or of rows of teeth and upper beak, the more specifically distinctive ratios insofar as the species named are concerned may be determined. In Table XIX are listed the ratios of each combination for the different species; and the ratios may be readily compared by reference to this table. Examination of the table will also readily show which combinations afford ratios that are absolutely distinctive between any two given species of the three species studied.

In the cases of some combinations the ranges of the ratios overlap to a very great extent in the three species studied. However, these ratios are not to be considered as being of no distinctive value because of this overlapping of ranges. If two species cannot be distinguished on the basis of any single ratio, they possibly may be distinguished on the basis of several. Also, although the ranges of the ratios overlap, it is possible

Table XIX.—Comparison of Species Studied According to Criteria Established

Combinations of rows, etc.	Restricted range of ratios			Species* between which the ratio in question affords absolute distinction
	B. fowleri	*P. nigrita triseriata*	*R. pipiens*	
1 U/2 U.......	0.98-1.22	1.02- 1.18	1.05- 1.56	....
1 U/1 L.......	1.00-1.50	1.08- 1.44	1.05- 2.19	....
1 U/2 L.......	1.06-1.52	1.03- 1.37	0.98- 2.47	....
2 U/1 L.......	1.00-1.35	0.98- 1.28	0.81- 3.16	....
2 U/2 L.......	1.03-1.43	0.92- 1.31	0.74- 2.32	....
1 L/2 L.......	0.88-1.22	0.87- 1.08	0.78-10.00	....
1 U/3 L.......	1.30-1.22	3.20-22.33	1.53-14.20	Bf-Pnt
2 U/3 L.......	1.25-2.18	2.65-20.00	0.89-14.33	Bf-Pnt
1 L/3 L.......	1.08-1.85	2.68-17.00	0.88- 8.60	Bf-Pnt
2 L/3 L.......	1.06-1.86	2.76-18.00	1.03- 8.20	Bf-Pnt
1 U/r & 1......	2.18-4.20	2.32- 3.60	3.77-21.50	Pnt-Rp
2 U/r & 1......	2.13-3.46	2.04- 3.21	3.52-15.75	Rp-Pnt, Rp-Bf
1 L/r & 1......	1.79-3.24	1.88- 2.88	1.38-24.33	....
2 L/r & 1......	1.70-3.56	1.91- 3.02	1.53-27.00	....
3 L/r & 1......	1.21-2.18	0.14- 0.80	0.81-18.00	Pnt-Bf, Pnt-Rp
2 U/m s.......	1.98-5.75	2.32- 6.50	1.10- 1.22	Pnt-Rp, Bf-Rp
r & 1/m s......	0.60-2.64	0.82- 2.86	0.07- 6.33	....
1 U/M........	1.48-1.94	1.55- 2.16	1.05- 1.52	Pnt-Rp, almost Bf-Rp
2 U/M........	1.35-1.80	1.43- 1.93	0.84- 1.32	Pnt-Rp, Bf-Rp
1 L/M........	1.17-1.62	1.22- 1.91	0.34- 1.19	Pnt-Rp, almost Bf-Rp
2 L/M........	1.10-1.56	1.20- 1.89	0.50- 1.24	almost Pnt-Rp
3 L/M........	0.80-1.33	0.07- 0.59	0.10- 0.90	Bf-Pnt, almost Bf-Rp
r & 1/M........	0.50-0.79	0.46- 0.82	0.06- 0.38	Rp-Bf, Rp-Pnt

Symbols used for rows of teeth, etc., are the same as in Table X.
*Bf = *Bufo fowleri*; Pnt = *Pseudacris nigrita triseriata*; Rp = *Rana pipiens.*

to distinguish between species if the ratio of the combination in question happens to fall in any particular instance in that part of the range not duplicated. If, for instance, the combination, first upper row/second upper row, be considered, it may be seen that a ratio of less than 1.02:1.00 would, among the three species here considered, identify the tadpole in question as being *B. fowleri*. If the ratio were 1.02-1.04:1.00, the animal could not be *R. pipiens*. If the ratio were 1.05-1.17:1.00, the animal might be either of the three species. If the ratio were 1.18-1.22: 1.00, the animal could not be *P. nigrita triseriata*, and if the ratio were greater than 1.22:1.00, the animal could only be *R. pipiens*. Thus, although the range of this ratio for all three species combined is only from 0.98:1.00 to 1.56:1.00, an "amount of range" of 0.58; this range is overlapped by all three species only from 1.05:1.00 through 1.18:1.00, or an "amount" of the range of 0.14, or about one-fourth of the total amount of range. Now, since the ranges as given in Table XIX are "restricted" ranges and hence include at least 94% of all cases, and since what ranges of ratios are given by Wright for the species involved in the present study are for the most part well within the ranges established by this study, it is safe to assume the ranges in Table XIX as quite reliable and quite apt to include all but exceptional cases (except where some row appears late, which would of itself be a character). Therefore, the ranges as here given are reliable to their limits; and should a ratio fall in the portion of a combined range of several species not overlapped by one or more species, this situation would constitute a valid reason for eliminating the possibility of the animal with such a ratio belonging to such "one or more" species.

Many cases, taken at random, may be properly classified on the basis of a single such ratio that is not absolutely distinctive, and a much greater percentage of cases may be properly classified on the basis of all such ratios. Further, although the ratios of such combinations are not individually nor indeed in the majority of cases distinctive when all are considered, some of them (e.g. ratios of combinations between the four longer rows of teeth) have been shown to be the most nearly constant of ratios of any and all combinations, and are, therefore, most reliable when they do happen to be distinctive.

General Evaluation of the Ratios of the Combinations of Rows

As to the various ratios afforded by all the various combinations of rows and of rows and upper beak, it may be concluded that each is of some value as a distinguishing character. The ratios that are less distinctive compensate by being more nearly constant in each species. The actual combinations affording the ratios of more distinctive character are (1) those involving on the one hand the first and second upper and first and third lower rows of teeth and on the other the upper beak (Compare Charts 4, 7, and 8), (2) those involving on the one hand the first and second upper and first and second lower rows and on the other hand the third lower row of teeth, (3) those involving on the one hand the first and second upper rows of teeth and on the other hand the average of the right and left parts of the second upper row, and (4) that of the second upper row and its median space. The ratios of the other combinations, though individually less distinctive, may in some instances prove to be the deciding character "in favor of" the one or the other species. They are, then, not to be discredited.

Appreciating fully that the number of species here available for comparison is small and that species of the same genus or family would be indeed more difficult to distinguish, it is concluded that this study does indicate that tadpoles may be divided at any stage of existence when the horny teeth and beak are present into relatively small, if not specific groups, on the basis of all the ratios between the rows of teeth and between the rows of teeth and the upper beak, provided the ranges of such ratios are established for all stages of tadpoles of each species. These ratios are not established at present for all ages of tadpoles of the different species except those established in this study. But it is proposed to establish such ratios through the method here introduced to this type of study for tadpoles of all species available from definitely identified parents.

SUMMARY AND CONCLUSIONS

Growth phenomena concerning the rows of teeth in tadpoles, particularly of *Bufo fowleri,* may be summarized briefly. The oral disc increases in size by extension of its radii; these "extensions" may be irregular or disproportionate; and the radii may extend from more than one center of growth. The extension of these radii forces the rows of teeth peripherally, also forcing an increase in length. This obligatory increase in length is brought about by divisions of cells in a plane parallel to the radii of the disc and at right angles to the surface of the disc. These cell divisions ultimately result in divisions of teeth. The rows of teeth also increase in length by addition of tooth-forming cells at their ends, resulting in a circumferential extension of the disc by growth of the rows at either end. The disproportionate extension of the radii of the disc, and the extension of the rows of teeth further around the circumferences, of which they are arcs, result in a changing degree of curvature of the rows of teeth. However, those rows of teeth growing in length more rapidly also increase in arc length/chord length ratio more rapidly, thus making comparisons between chord lengths of rows more nearly constant than comparisons between arc lengths of the same rows.

Arc length of a row of teeth compared with total body length of a tadpole affords the best expression of relative growth of a row of teeth until near the onset of the metamorphic climax. However, chord length of a row of teeth as compared with body (only) length of a tadpole affords a very satisfactory standard for comparison of the different rows of teeth. From examination of such relative growth rates and of percentage increases in length, it has been seen that all rows of teeth and the upper beak have their rates of growth similarly affected by the various conditions of growth, and change growth rates simultaneously and in a similar manner, though possibly to a different extent. In this connection it should also be pointed out that increase in length of a row of teeth is independent of the orginal length of the row, and that increase in length is not a constant fraction of the entire growth complex of the row.

Since growth rates of the rows of teeth are similarly affected by conditions of growth, and since arc length/chord length ratio increases somewhat in proportion to percentage increase in length of a row, it may be concluded that chord lengths of rows of teeth do bear some constant relation to each other and that the use of such relations between rows of teeth and between rows of teeth and the upper beak as taxonomic characters may be justified from the viewpoint of having an explainable basis. It may be further concluded that chord lengths of the rows of teeth and the upper beak are the more frequently comparable measurements.

It should also be pointed out that, since increases in lengths of the rows of teeth are not proportionate to their original lengths, the relationship between the rows of teeth may change. Thus, the combinations of rows of teeth affording ratios more nearly constant for all ages are the rows of more nearly equal lengths. However, ratios of such combinations of rows of teeth are less distinctive of a given species.

Aside from (1) showing that growth phenomena of the oral disc offer an explainable basis for the use as taxonomic characters of ratios between the various rows of teeth and between rows of teeth and the upper beak and (2) showing that the relative constancy of the ratios of the chord lengths of such various different combinations may be determined from a study of these growth phenomena as well as from actual comparison of the different ratios, the results of the present study have some practical application.

Obviously, distinction of a given species can rarely be reliably made on the basis of the ratio afforded by a single combination of rows of teeth. However, if the results from the study of the three species herein concerned may be taken as an indication, it is believed that on the basis of the ratios of all the possible combinations of rows and upper beak tadpoles of all ages may be separated into small, if not specific, groups.

The combinations affording ratios (between chord lengths) more constantly distinctive between the tadpoles of the three species studied (*Bufo fowleri, Pseudacris nigrita triseriata,* and *Rana pipiens*), are (1) those involving on the one hand the various rows of teeth and on the other hand the upper beak, (2) those involving on the one hand first and second upper and first and second lower rows of teeth and on the other hand the third lower row of teeth, (3) those involving on the one hand the various complete rows of teeth and on the other hand the average of the right and left parts of the second upper row.

The combinations affording ratios (between chord lengths) that are less variable with change in age of the tadpoles are (1) those involving the first and second upper and first and second lower rows of teeth, and (2) those involving on the one hand the various rows of teeth and on the other hand the upper beak.

The "graphic" method employed for determining and studying the ratios is a very satisfactory method for such study, since it eliminates endless calculations and shows in a compact and readily interpretable manner the course of ratios of a given combination of rows of teeth throughout all ages of tadpoles. The method also has further applications that cannot yet be made. When the ratios of all combinations of rows of teeth and of rows of teeth and upper beak for tadpoles of all ages or sizes of several species are known, "graphic keys" may be made which will eliminate the necessity of calculating the ratios of rows of teeth of a tadpole to be identified. By drawing on graph paper "lines of equal proportions" to represent the limits of the ratios of the combination of rows in question for different species, and by using such a graph for each possible combination such a "graphic key" may be made. By using the chord lengths of the rows of teeth and of the upper beak as coördinates in all possible combinations the points determined by the various pairs of coördinates will fall within limits (on the different graphs) peculiar to certin species. Although a given range of ratio may be common to several species, it is not likely that the ranges of the ratios of the different combinations would be common to the same group of species in each instance.

As to similarities in growth phenomena, in ratings as to constancy of ratios of the different combinations of rows of teeth, etc., and in actual ratios of the combinations of rows of teeth, etc., there appear to be different correlations between certain of the three species of tadpoles studied. *Bufo fowleri* and *Pseudacris nigrita triseriata* are more nearly similar according to the above-mentioned particulars than are either *Bufo fowleri* and *Rana pipiens* or *Rana pipiens* and *Pseudacris nigrita triseriata.* Although the advisability of attributing systematic significance to any larval character is doubtful, it is of note that the relations as indicated by this study of the larval mouth apparatus coincide with the relations generally conceded to exist between adults of the species.

As to the ratios of combinations of rows of teeth, etc., as given by Wright (1929) for the species involved in this study, the following conclusions may be drawn. (1) The ranges of ratios as given are not of sufficient extent to include ratios in younger tadpoles. (2) The ranges of ratios as given for *B. fowleri* are not of sufficient extent to include ratios of a "normal" percentage of "mature" tadpoles. Also, it has been shown in this study that the description, as given by Wright and Wright (1933), of tadpoles of *Pseudacris nigrita triseriata* as having only two lower rows of teeth is erroneous. Tadpoles from mated pairs known to be *Pseudacris nigrita triseriata* (identification by Dr. G. K. Noble) have the third lower row of teeth added after attaining a body length of from 2.91 to 3.57 mm. There are two possible explanations of the error. (1) There may be a geographical variation in tadpoles of the species. (2) The description may have been made from incorrectly indentified tadpoles.

CHARTS

The data in the tables in the text were gathered from charts similar to those on the following pages. Since it was impracticable to publish the complete set of charts and thus duplicate the data in the tables, eight representative charts have been included as illustrative of the method used.

The charts for the most part serve the purpose of showing ratios between various sets of measurements plotted as coordinates. Each plotted point represents the ratio in a single animal of the two measurements plotted.

The lines on the charts, since each line passes through zero, are lines of equal proportions, the proportion represented by each line being indicated thus: 1.22/1.00, 1.45/1.00, etc. These lines have been drawn so as to include all points and thus represent upper and lower limits of the ratios of the two measurements in question. Lines have also been drawn to exclude extreme ratios (never more than 5-6%).

The numbers giving the values of coordinates are in each case millimeters, with the exception of the values of the abscissas of Chart 3, where they represent numbers of teeth.

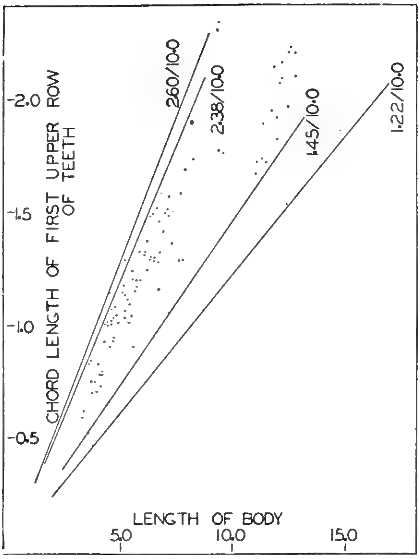

CHART 1.—*Bufo fowleri*

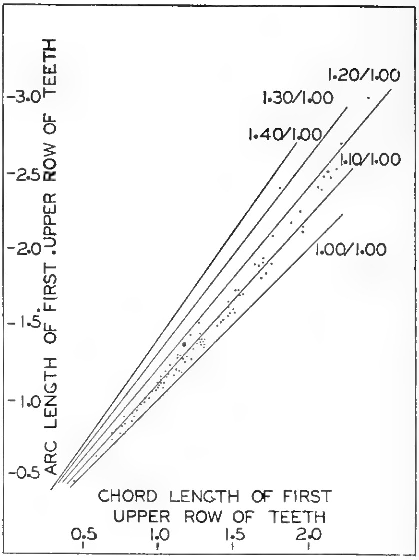

CHART 2.—*Bufo fowleri*

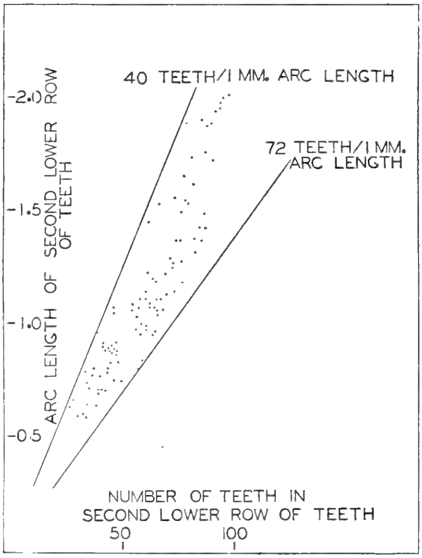

CHART 3.—*Bufo fowleri*

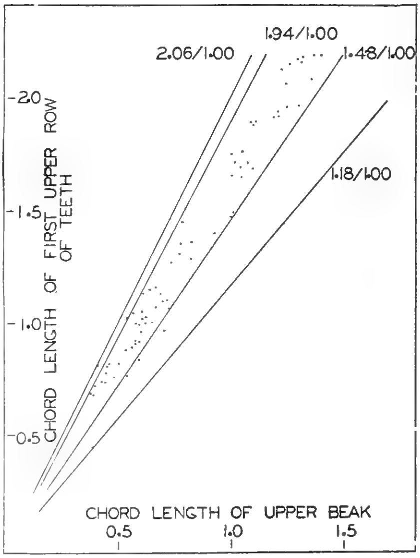

CHART 4.—*Bufo fowleri*

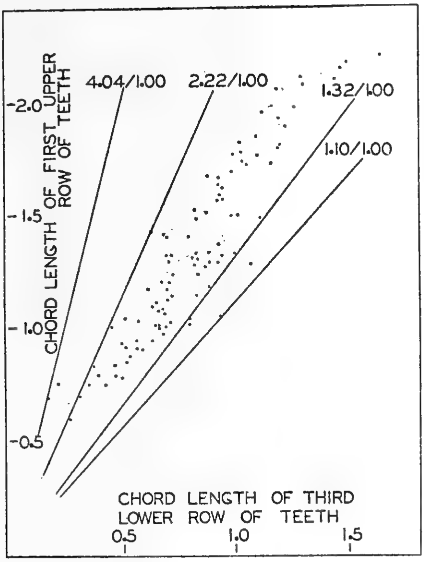

CHART 5.—*Bufo fowleri*

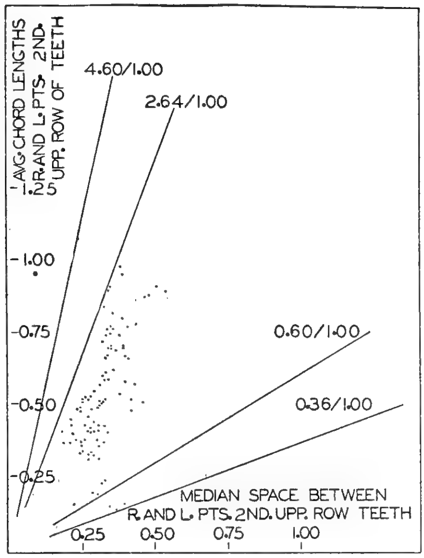

CHART 6.—*Bufo fowleri*

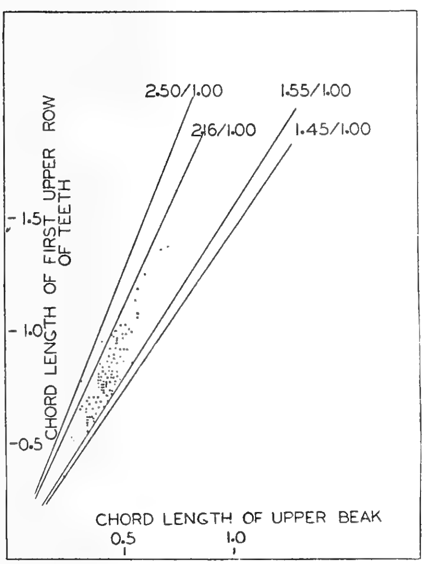

CHART 7.—*Pseudacris nigrita triseriata*

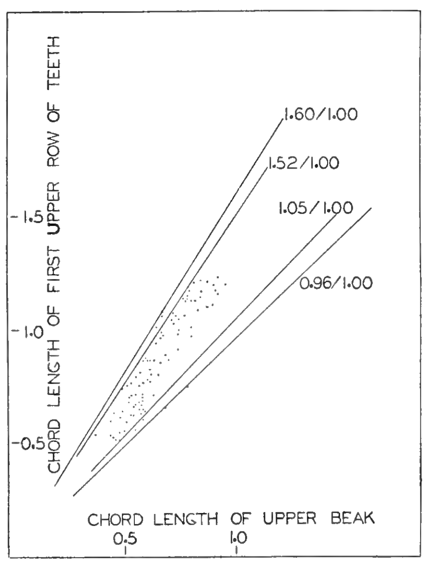

CHART 8.—*Rana pipiens*

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