A Critical Estimate of the Vertebrate Tail with Special Reference to the Frog *Rana tigrina* Daud

By

Beni Charan Mahendra

President of the Academy of Zoology and Head of the Department
of Zoology, Agra College, Agra (India)

Foreword

Professor S. Nishi is known the world over for his outstanding researches in zoology and as leader of a progressive school of anatomists and it is a great privilege to be invited to contribute an article in honor of his seventieth birthday. I am extremely happy to join my Japanese colleagues in paying him homage and to send him the most cordial greetings and wishes not only on my behalf, but on behalf of the Indian zoologists and the Academy of Zoology, of which he is an Honorary Fellow. One of the primary aims of the Academy is to bring zoological investigators together in a brotherhood transcending national and other ideological limitations, and I earnestly hope that the present occasion would help in the establishment of valuable contacts between Japanese zoologists and those of other countries. We wish Professor Nishi all happiness and many more years of scientific work and fruitful service.

Introduction

The term 'tail' is one of those inappropriate popular words which have slipped unobtrusively from the common parlance into the zoological terminology and have never been subjected to a careful scrutiny as to their precise meaning and application. Murray (1919, T, p.27) mentions that the ulterior etymology of this common Teutonic word is "uncertain, but the evidence appears to show that the primary sense was either 'hair' or 'hairy tail', as of the horse, ox, fox, etc., whence it was extended to the tails of other animals. Already in OE it was

applied to the tails of 'worms' or reptiles, and to the sting of the bee. In OE the tail was also called *steort*, start=Du. *staart*." The word means "the posterior extremity of an animal, in position opposite to the head, either forming a distinct flexible appendage to the trunk, or being the continuation of the trunk itself behind the anus. Also, a representation or figure of this part".

As the indiscriminate use of this term together with the other associated words like the *caudal region*, *coccyx* and derivatives from the Greek word '*oura*' (*urostyle*, *anura*, *urodela*, etc.) have led to a great deal of loose thought hampering incisive investigation of this part, I stressed some years back (Mahendra, 1943) the necessity of defining their connotation accurately, and of standardizing their usage. In the present article, the matter is examined with special reference to the common Indian frog, *Rana tigrina* Daud.

General

Before we examine the various concepts mixed up in the term 'tail' as used in the vertebrata, it is advisable to list the various senses in which this word occurs. It is generally employed in the following meanings.

(1) *The end of the body opposite to the head.* The word 'caudad', denoting the direction away from the 'cephalad', is based on this significance. The word is used as a term of orientation and has a relative connotation, as what is *caudad* to the structures situated anterior to it is *cephalad* to those situated behind.

(2) *The postanal part of the body.* This is the common significance of the word 'tail'.

(3) *The region of the body* (particularly of the skeleton) *lying posterior to the place where the ilia are connected with the sacral vertebra (or vertebrae).* The 'caudal vertebrae', for example, are the vertebrae lying posterior to the sacral ones.

Of these, we might leave the first significance out of consideration, as it scarcely if at all bears on our conception of a definitive tail. The other two meanings, however, need careful scrutiny, as the ambiguity in the significance of the term arises mainly from the tacit assumption that the postanal region is identical with the postsacral. That is, however, far from the truth. Although in many vertebrates the two regions appear to be more or less co-extensive in the adult, they never exactly correspond with each other. Moreover, they arise

as a result of different functional requirements in different manners and at different stages of development, and have evidently evolved at different times in the phylogeny of the Vertebrata.

In view of the foregoing facts, it is essential to replace the loose concept of a tail by precisely defined terms. We have four words (with their derivatives) for the tail: the tail, the *cauda*, the *coccyx*, and the *ura* (variant of the Gk. *Oura*). As the words 'tail' and '*cauda*' (in the adjective *caudal*) have been vaguely employed for centuries, any attempt to restrict their connotation and to standardize their usage is apt to be unsuccessful. It seems expedient, therefore, to leave them as they are as semi-popular words and to define the other two terms accurately so as to limit them each to a precise anatomical concept.

The word '*coccyx*' (L. *coccyx*, Gk. *kokkux* Cuckoo, also in Galen the *os coccygis* or cuckoobone, so called because in man it was supposed to resemble the bill of the cuckoo) means, according to Murray (1893, II, p, 564), "the small triangular bone appended to the point of the sacrum and forming the termination of the spinal column in man, formed by the coalescence of four rudimental coccygeal vertebrae; also, an analogous part in birds or other animals." In support of this connotation, Murray (1893, *l.c.*) gives the following illustrations.

1615. Cooke *Body of man* 493. In Dogs and Apes there are three coniugations preceding out of the Coccyx or rump-bone.
- 1754-64. Smellie *Midwif.* I. 75. The *Coccyx* is moveable at its connection with the *Sacrum* as are also the four bones that compose it.
1879. tr. De Quatrefages' *Human Species* 52. In the sheep of Central Asia the tail disappears and is reduced to a simple coccyx.

It is evident from the examples that the term '*coccyx*' was originally applied to the more or less compact structure formed by the fusion of the postsacral vertebrae in some vertebrates. It may be retained in that significance, while for the postsacral region of the body in tetrapod vertebrates, we might coin a new word '*coccygeum*' to fit in with the adjective '*coccygeal*' which is already in use. For the terminal piece of coalesced coccygeal vertebrae found for example in certain fishes and Urodela, the term urostyle (Gk. *oura*, tail; *stylos*, pillar), *sensu strictu* (*vide infra*) is available, and for the peculiar terminal bony expansion of the last few vertebrae in Birds, the term 'pygostyle' (Gk. *pyge*, rump; *stylos*, column) is already in use.

The word *ura* (Gk. *oura*, tail) has not been used so far as an independent term, although it occurs as part of several compound words such as *anura*, *urite*, *urodela*, *urochord*, *urogastric*, *urohyal*,

uromere, uroptagium, uropod, uropygium, urostyle, etc. It is available, therefore, for use as a technical term, provided that its indiscriminate use in compound words should be stopped. It may preferably be confined consistently to what has hitherto been regarded as the postanal part of the body.

The Development of the Ura in the Frog *Rana tigrina*

In order to comprehend the various implications of the word 'tail' in the Chordata, the common frog might be taken as an example, particularly as it is a highly evolved tetrapod vertebrate with an active tailed larva living in water and a so-called 'tail-less' adult living virtually on land.

As the tail has been generally regarded as a postanal structure, we might begin our study from the stage at which the proctodeum makes its appearance. Ziegler (1892) and Marshall (1893) have figured the relevant stages on the basis of a series of wax models, and my examination of the development of *Rana tigrina* confirms them.

After the blastopore is reduced to a nearly circular appearance with the whitish yolk-plug filling it up (Text-fig. 1, A), its lateral lips meet together and fuse to form the "primitive streak" (Text-fig. 1, B), which bears a slight vertical groove (the *primitive groove*) with a pin-hole depression both at the upper and the lower end. The lower depression is the beginning of the proctodaeal invagination, while the upper one is the open part of the blastopore. Above the "primitive streak" and in alignment with it is the neural groove which gradually deepens (Text-fig. 1, C), while the neural folds bordering it become more prominent and grow medianwards. As they meet each other

Text-fig. 1. Successive stages in the development of the frog, showing the closure of the blastopore, formation of the anus and the appearance of the tail-bud. (After Ziegler.)

(Text-fig. 1, D) the tail-bud makes its appearance at first indistinctly, but later on perceptibly as an elevation growing backwards. In the meantime, the "primitive streak" disappears, leaving only a minute aperture (the proctodaeum) below the tail-bud (Text-fig. 1, E). As the neural tube is completed, the tail begins to increase in size.

Sagittal sections passing through the later stages of the closing blastopore reveal five facts of great significance. In the first place, the neural tube is bent at its hind end downwards in a broad round curve, more or less as at its anterior end. Secondly, its central canal, which at first (Text-fig. 2, A) opens to the outside at the point where the blastopore leads into the archenteron, retains after the complete closure of the blastopore (Text-fig. 2, B) communication with the archenteron by a vertically disposed canal, the *canalis neurentericus*. Thirdly, the notochord at this stage (Text-fig. 2, B) ends abruptly in front of the neurenteric canal. Fourthly, the proctodaeal invagination (Text-fig. 2, A) lies at some distance beneath the neurenteric canal and the termination of the notochord. Fifthly, the anlage of the tail (Text-fig. 3) appears immediately posterior to the neurenteric canal and is thus dorsal to the proctodaeum. It grows at first obliquely upward and backward, and later on in a posterior direction. It is clear, therefore, that the tail is primarily not postanal (=post-proctodaeal), but post-blastoporal or more strictly post-neurenteric.

The neurenteric canal soon disappears and the neural tube grows straight posteriorwards, accompanied by the notochord and the gradually differentiating mesoblastic somites. Thus the elevation-like small tail-bud soon elongates into the tail of the tadpole.

Text-fig. 2. Sagittal sections of the posterior part of Frog Embryos: (A) shortly before, and (B) soon after the closure of the blastopore. A corresponds to the stage D, and B to the stage E of Text-fig. 1.

Text-fig. 3. Sagittal section through the growing tail of a Frog Embryo after the closure of the canalis neurentericus.

In order to elucidate the changes leading to the differentiation and further development of this region as well as to form a basis for comparison with other animals, we might call the transverse vertical plane passing through the neurenteric canal and the proctodaeal invagination the *blastoporal plane*, as the neurenteric canal and the proctodaeal invagination arise very nearly at the place occupied by the blastopore.

As the tail in the frog arises from and behind the neurenteric region, we might imagine the blastoporal plane as dividing the tadpole's body into two parts—an anterior part in which the successive mesoblastic somites develop (or developed) from the distal region towards the blastoporal plane, and a posterior part in which the mesoblastic somites differentiate successively from near the blastoporal plane distalwards. The former, which forms the head and the trunk in the Chordata, may be called the *pars ad-blastopora* (L. *ad*, to), as the new somites in it are added from the distal end proximalwards towards the blastoporal plane. The latter, which forms the ura or the so-called tail, may be designated as the *pars ab-blastopora* (L. *ab*, from) since the new somites in it are formed from near the blastoporal plane distalwards. The surface of the larva along which the neural (medullary) plate develops is the *neural surface*, while the surface opposite to it is the *ab-neural*.

While it is beyond the scope of the present paper to deal with the intricate problem of orientation of the body in animals, it may be pointed out that the commonly used terms 'dorsal', 'ventral', 'anterior', 'posterior', 'cephalad', 'caudad', etc., have led to a great deal of confusion. Adopted originally from the orientation found in adult vertebrates, they neither express comparable surfaces or directions in various phyla, nor have the same value from the early stages to the adult. It is suggested, therefore, that a more precise set of terms based on embryological facts be adopted instead.

If we recognise the importance of the blastoporal area as a starting point for determining comparable surfaces in animals, we have to consider the fact that in some of them (the Platyhelminthes, Nemat-

helminthes, Rotifera, Molluscoida, Annelida, Mollusca and Arthropoda) the blastopore persists as the adult mouth, while in others (the Echinodermata, Hemichordata, Urochordata, Cephalochordata, and Vertebrata) the anus is formed by it or near it. The former subdivision is called by Grobben (1908) the *Proterostomia*, and the latter the *Deuterostomia*. To take an example, a blastopore-based terminology of orientation would perhaps indicate that the mouth of the Annelida is the homologue of the anus of the Vertebrata; that the Annelid prostomial region presumably corresponds to the vertebrate ura; and that the ventral surface of the Annelida is the equivalent of the dorsal surface of the Vertebrata.

The full implications of such a suggestion will be explained elsewhere in detail.

The Development of the Coccygeum in *Rana tigrina*

As we examine the successive transverse sections of a horny-jawed tadpole of *Rana tigrina* bearing the bud-like rudiments of hind-limbs, we find that the dorsal and ventral fins (Fig. 1, Plate) are prominent folds of the epithelium enclosing a loose mass of connective tissue; while the remaining part of the ura consists the musculature, nerve-cord, notochord and caudal blood-vessels. The notochord in this region is not cylindrical as is usually believed, but is laterally compressed, raised up on either side at its dorsal and ventral surfaces to form horn-like projections bounding a semicircular dorsal and a similar ventral groove. In the upper groove lies the nerve-cord; and in the lower, the haemal blood-vessels. There are no vertebral chondrifications.

This type of structure persists with almost no change up to the anal orifice, just behind which (Fig. 2, Plate) the ventral fin divides at its free end to form two branches—a lower branch, curved crescentically upwards and an upper one curved at its distal end downwards. By the coalescence of these branches of the fin, a short spout-like orifice (the *anus*) is formed underneath the main mass of the ura. In sections anterior to it (Fig. 3, Plate) are seen the rudiments of the hind-limbs projecting on either side of the rectum. The notochord even here has the peculiar laterally-compressed, dorsally and ventrally grooved appearance. There is no anlage of the vertebral or pelvic chondrifications, although slightly anterior to it traces of the basidorsals can be made out.

As the hind-limbs develop fully, several important changes take

place. The notochord loses the dorsal and ventral grooves (Fig. 4, Plate). The ventral fin gradually becomes lower and lower, and forms a slight obtuse prominence as the proximal end of the ura is reached. The anal aperture is no longer enclosed by the bifurcations of the ventral fin, but is formed rather posterior to that site out of the laterally compressed vertical space between the bases of the thighs (Figs. 5 and 6, Plate). Farther forwards (Fig. 7, Plate), beneath the rectum are the ventral ends of the paired pelvic cartilages, closely applied to each other. Each of these cartilages, when traced forwards (Figs. 8 and 9, Plate), is seen to extend obliquely upwards and forwards on the side of the body so that its anterior end comes to lie slightly above the notochordal level ventrolateral to the cartilaginous parapophysis of the sacral vertebra, with which it is united by ligament. The basidorsals have developed in the region anterior to the proctodaeum, although they are absent in the ura; and a cylindrical procartilaginous structure (the *hypochord* of Mookerjee) has appeared in close contiguity with the lower surface of the notochord from the proctodaeal region up to the place of the iliosacral connection. The 'urostyle' has not yet formed, but careful scrutiny of the post-sacral axial skeleton establishes the fact that, behind the pair of those basidorsals that give rise to the sacral vertebra, are developed only two pairs of basidorsals—a fairly well formed tenth and a vestigial eleventh. Behind these is only the notochord with the underlying hypochordal cartilage.

The examination of this stage shows that the coccygeum can be divided into two regions—the *pre-coccygeum*, which lies anterior to the anus between it and the ilio-sacral connection, and the *post-coccygeum* which lies behind the anus and is almost equivalent to the *ura*, as already defined. The pelvic cartilages arise in the precoccygeum just anterior to the anus and their conjoined ventral ends lie underneath the rectum. The hypochordal cartilage develops only in the precoccygeum; it extends forwards from in front of the anus up to the level of the tenth pair of basidorsals.

The So-called 'Urostyle' of the Frog

Mookerjee (1931 and 1936) has described the development of the 'urostyle' in *Rana temporaria*, *Bufo melanostictus*, *Bombinator igneus* and *Xenopus laevis*, and Green (1931) has shown that it does not chondrify completely until the M. pyriformis attaches to it. Alizarin-

stained preparations and serial sections of later stages of *Rana tigrina* Daud. seem to confirm these observations. The so-called 'urostyle' of *Rana tigrina* is formed by the coalescence and ossification of the two pairs of postsacral basidorsals, the perichordal tube and the hypochordal cartilage, whilst the notochord is almost completely obliterated in this region. It is important to note that at no stage of its development the notochord of the ura (post-anal region) takes part in its formation. The term 'urostyle' (Gk. *oura*, tail; *stylos*, pillar) is, therefore, singularly inappropriate.

How misleading the use of this term has been during the past several decades, may be exemplified by reference to several standard authors. Gegenbaur (1878, p. 433) says about the vertebral column of the Anura that "the connection between the pelvic girdle and the vertebral column does distinctly mark off the caudal portion from the region of the trunk". Huxley (1871, pp. 151-152) observes that "the coccyx consists of a long, cylindroidal, basal bone proceeding from the ossification of the sheath of the termination of the notochord, and corresponding with the urostyle of the Teleostei". Wiedersheim (1907) notes that "in Anura, the caudal portion is modified to form a urostyle" (p. 54), and "the long caudal portion of the vertebral column in Anuran larvae, which is very similar to that of Urodeles, undergoes during metamorphosis a gradual retrogressive modification, and the vertebrae of its proximal end become fused and co-ossified to form a long, unsegmented, dagger-like bone, the *urostyle*" (p. 56). Abel (1919, pp. 311-313) lays stress on the tail-less depressed body of the Anura, "dessen Schwanzwirbel zu einem dolchförmigen, in der Mittellinie des Körpers zwischen des langgestreckten Hüftbeinen liegenden Knochen (Coccyx oder Urostyl) verschmolzen sind". Kingsley remarks that "the caudals of Anura are fused to a single bone, the *urostyle* or coccyx" (1925, p. 36), and that "a striking feature" of the Anuran vertebral column "is the fusion, in the adult, of all the caudal vertebrae into the well-known rod, the *coccyx* or *urostyle*" (1926, p. 59). Parker and Haswell (1930, p. 290) say that "in the Anura the caudal region is represented by a single rod-shaped bone, the *urostyle*". Such examples may be multiplied by the score.

While many text-book writers seem to have assumed from the erroneous implication inherent in the term 'urostyle' that the bone in the Anura consists of the caudal vertebrae fused together, it is refreshing to quote Gadow's observations:

"The tail proper, namely that portion which is absorbed during

the metamorphosis, remains throughout its existence in an apparently primitive condition. The chorda dorsalis and the spinal cord extend through its whole length, surrounded by continuous connective tissue without any cartilage; in fact it represents a piece of typical vertebral column before the appearance of cartilage. The reduction of the swimming organ begins at the hind end" (1909, p. 21).

"The disappearance of both notochord and spinal cord, and the conversion of the cartilaginous elements into a continuous rod in the case of the os coccygeum, find an analogy in the hinder portion of the tail of Dipnoi and Crossopterygii, and in the tail-end of most Urodela, portions which are not homologous with the os coccygeum. The term 'urostyle' should be restricted to such and similar modifications of the tail-end, and this latter happens to be lost by the Anura during metamorphosis" (1909, p. 23).

"The term 'urostyle' is scarcely applicable, since the composing bony units never were caudal" (1933, p. 168).

"Beyond the coccyx comes of course the true tail, which is absorbed during metamorphosis" (1933, pp. 168-169).

In view of these facts, it is necessary to give up the term 'urostyle' completely in this connection and always to call the postsacral bone of the Anuran vertebral column the '*os coccygeum*'. The term 'urostyle' may, however, be retained for the styloid termination of the vertebral column in Teleosts, Urodela, etc., as pointed out above by Gadow, (1909) and indicated by Niemann and Honigmann (1919, p. 215).

Summary

The author has carefully examined the conception of the vertebrate tail on the basis of a developmental study of the Indian frog *Rana tigrina* Daud., and has shown that the postanal part of the body does not coincide with the postsacral developmentally and functionally. It is suggested, therefore, that the former region be called the 'ura' and the latter the 'coccygeum', while the region between the anus and the ilio-sacral connection be designated as the 'pre-coccygeum'. The term 'urostyle', as far as the Anura is concerned, is a misnomer and should be given up in favour of the '*os coccygeum*'.

In order to build up a more rational terminology of the orientation of the body in the adult, the author feels that the blastoporal plane of the larva and its subsequent fate should be taken into account, and the body divided into two regions—the *pars ad-blastopora* and the

pars ab-blastopora.

The other new features discovered are as follows :

(1) The tadpole's tail is primarily not post-proctodaeal, but post-neurenteric, as it arises dorso-posterior to the proctodaeal invagination behind the place where the canalis neurenteric closes.

(2) In the horny-jawed tadpole of *Rana tigrina* bearing the bud-like rudiments of the hind-limbs, the notochord of the ura bears longitudinal grooves along its upper and lower surfaces; the anus is formed by the coalescence of branches of the ventral fin, and there are no anlagen of the vertebral and pelvic chondrifications.

(3) When the hind-limbs develop, the anus becomes enclosed between the bases of the thighs, and a hypochordal cartilage arises in the precoccygeum.

(4) The os coccygeum is formed by the coalescence and ossification of the two pairs of postsacral basidorsals, the perichordal tube and the hypochordal cartilage. It has no component belonging to the ura, and should not, therefore, be called the 'urostyle'.

References

1. Abel, O.: Die Stämme der Wirbeltiere. Berlin und Leipzig, 1919, pp. 311-313.
2. Gadow, H.: Amphibia and Reptiles. Camb. Nat. Hist., 1909, pp. 21, 23.
3. Gadow, H. F.: The Evolution of the Vertebral Column: A Contribution to the study of Vertebrate Phylogeny. Cambridge, 1933, pp. 167-169.
4. Gaupp, E.: Ecker und Wiedersheim's Die Anatomie des Frosches, Abt. 1. 1896, pp. 24-25 and 29-30.
5. Gegenbaur, Carl: Elements of Comparative Anatomy (translated by F. Jeffrey Bell and revised by E. R. Lankester). Macmillan & Co., London, 1878, p. 433.
6. Green, T. L.: On the Pelvis of the Anura: a Study in Adaptation and Recapitulation. Proc. Zool. Soc. Lond., 1931, pp. 1259-1290.
7. Grobben, Karl: Die Systematische Einteilung des Tierreiches. Verh. Zool. Bot. Ges., Wien, 58, 1908, pp. 491-512.
8. Henderson, I. F. and Henderson, W. D.: A Dictionary of Scientific Terms. Edinburgh, 1953.
9. Huxley, T. H.: Manual of the Anatomy of Vertebrated Animals London, 1871, pp. 151-152.
10. Keibel, F.: Die Entwicklung der äusseren Körperform der Wirbeltierembryonen, insbesondere der menschlichen Embryonen aus den ersten 2 Monaten. Hertwig's Handb. d. vergl. u. experim. Entwickl. d. Wirbeltiere, Bd. 1, Tl. 2, 1906, pp. 69-72.
11. Kingsley, J. S.: The Vertebrate Skeleton from the Developmental Standpoint. London, 1925, p. 36.
12. Kingsley, J. S.: Outlines of Comparative Anatomy of Vertebrates. Philadelphia, 1926, p. 58.
13. Mahendra, B. C.: Conception of the Tail in the Craniata. Nature, 152, 1943, p. 163.
14. Marshall, A. M. Vertebrate Embryology. London, 1893.

15. Marshall, A. M.: The Frog: An Introduction to Anatomy, Histology and Embryology (edited by F. W. Gamble). London, 1914.
16. Maurer, E.: Die Entwicklung des Darmsystems. Hertwig's Handb. d. vergl. u. experim. Entwickl. d. Wirbelt., Bd. 2, Tl. 1, 1906, pp. 212-214.
17. Mookerjee, H. K.: On the Development of the Vertebral Column of Anura. Phil. Trans. Roy. Soc. London, B. 219, 1931, pp. 165-196.
18. Mookerjee, H. K.: The Development of the Vertebral Column and its Bearing on the study of Organic Evolution. Ind. Sc. Congr., Zool. Sect., Indore, 1936.
19. Morgan, T. H.: The Development of the Frog's Egg. Macmillan Company, New York, 1897.
20. Murray, James A. H.: A New English Dictionary on Historical Principles; founded mainly on the materials collected by the Philological Society. Oxford, Vol. II, 1893, p. 564, and Vol. IX, Pt. II, 1919, T. p. 27.
21. Nicholls, G. E.: A Note on the Urostyle (*Os Coccygeum*) of the Anurous Amphibia. Proc. Zool. Soc. London, 1915, pp. 239-242.
22. Niemann, G. and Honigmann, H. L.: Zoologisches Wörterbuch. Osterwieck-Harz, 1919.
23. Parker, T. J. and Haswell, W. A.: A Text-book of Zoology, Vol. II (revised by C. Forster Cooper), London, 1930, p. 290.
24. Pasteels, Jean: Fermeture du blastopore, anus et intestin caudal chez les Amphibiens Anoures. Acta Neerland. morphol. 5, II, 1943.
25. Remane, A.: Wirbelsäule und ihre Abkömmlinge. Bolk, Göppert, Kallius, and Lubosch's Handb. der vergl. Anat. 4, 1936.
26. Rugh, Roberts: The Frog: Its Reproduction and Development. Philadelphia, 1951.
27. Schauinsland, H.: Die Entwicklung der Wirbelsäule nebst Rippen und Brustbein. Hertwig's Handb. d. vergl. u. experim. Entwickl. Wirbelt, Bd. 3, Tl. 2, 1906, pp. 501-507.
28. Shumway, W.: Vertebrate Embryology, New York, 1930, pp. 210-229.
29. Wiedersheim, Robert: Comparative Anatomy of Vertebrates (adapted by W. N. Parker). London, 1907, pp. 54 and 56.
30. Ziegler, F.: Zur Kenntniss der Oberflächenbilder der Rana-Embryonen. Anat. Anz., 7, 1892.

Explanation of the Plate

- Fig. 1. Transverse section of a horny-jawed tadpole of *Rana tigrina*, passing through the middle of the tail. ($\times 30$).
- Fig. 2. Transverse section of a horny-jawed tadpole of *Rana tigrina* immediately behind the anus. ($\times 30$).
- Fig. 3. Transverse section of a horny-jawed tadpole of *Rana tigrina* at the base of the hind-limb buds, immediately anterior to the anus. ($\times 30$).
- Fig. 4. Transverse section of an advanced tadpole of *Rana tigrina*, slightly behind the thighs. ($\times 30$).
- Fig. 5. Transverse section of an advanced tadpole of *Rana tigrina* passing through the thighs immediately behind the anus. ($\times 30$).
- Fig. 6. Transverse section of an advanced tadpole of *Rana tigrina* at the level of the anus. ($\times 30$).
- Fig. 7. Transverse section of an advanced tadpole of *Rana tigrina*, showing the lower ends of the pelvic cartilages. ($\times 30$).

Fig. 8. Transverse section of an advanced tadpole of *Rana tigrina*, passing through the acetabular region. ($\times 30$).

Fig. 9. Part of a transverse section, showing the ilio-sacral connection in an advanced tadpole of *Rana tigrina*. ($\times 55$).

Abbreviations Used in the Figures

- a anus.
- ab.p. ab-blastoporal part.
- ad.p. ad-blastoporal part.
- ar archenteron.
- bd basidorsal.
- bl.p. blastoporal plane.
- bp blastopore.
- cn canalis neurentericus.
- db dorsal branch of the ventral fin.
- d.f. dorsal fin.
- dg dorsal groove on the notochord.
- dp diapophysis.
- ex. nc. extension of the notochord into the ura.
- ex. nt. extension of the neural tube into the ura.
- f. femur.
- h.c. hypochordal cartilage.
- h.l. hind-limb bud.
- i.pc. iliac part of the pelvic cartilage.
- lg ligament.
- m musculature of the ura.
- n neural (medullary) folds fused together.
- nc notochord.
- nf medullary (neural) folds.
- ng neural groove.
- nt neural tube.
- p proctodaeum.
- p.c. pelvic cartilage.
- pr proctodaeal pit.
- ps "primitive streak".
- p. vf. proximal end of the ventral fin.
- r rectum.
- t tail.
- tb tail-bud.
- vb ventral branch of the ventral fin.
- v.f. ventral fin.
- vg ventral groove on the notochord.
- v. sp. vertical space between the thighs.
- yp yolk-plug.