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MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD
COLLEGE. E. L. MARK, DIRECTOR.

No. 150.

THE DEVELOPMENT OF THE MESONEPHROS AND THE
MÜLLERIAN DUCT IN AMPHIBIA.

By ROBERT W. HALL.

With EIGHT PLATES.

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I. Introduction.

THE present investigations deal with the early development of the mesonephros and of the Müllerian duct. As these organs are in a measure independent of each other in their development, the introductory remarks on the Müllerian duct may best be left for the portion of the paper dealing with the development of that organ.

As is well known, the mesonephros consists essentially of a mass of tubules, each of which, in its typical form, may be divided into three regions: (1) a short duct leading from the body cavity into (2) a dilatation which contains an invaginated vascular mass (the glomerulus) and is in communication with the Wolffian duct by means of (3) a long, coiled duct. These three parts may together be called a *mesonephric unit*. According to their position, structure, and connections, the units fall into various sets. In the higher Amphibia two chief sets can be distinguished: a ventral set, in which the units (primary units) connect directly with the Wolffian duct, and a smaller or greater number of dorsal sets, which form connections with the Wolffian duct *indirectly* by opening into the primary set. The dorsal sets are arranged in longitudinal rows above the ventral set, and are designated as secondary, tertiary, etc.

Among the problems presented by the development of the mesonephros in Amphibia three stand out at present as of greater importance than the others; it is to these three that I have given most attention. They are: (1) the origin of the tissue which forms the fundamentals of the mesonephric units, (2) the origin of the dorsal sets of units, and (3) the dysmetameric condition of the primary units, — supposing them to have been originally metamerically arranged.

Before considering the views that have been held in regard to the origin of the mesonephric units, it is necessary to have a clear understanding of the condition of the mesoderm (mesothelium) at the time when they make their appearance. The mesoderm on either side of the body presents two layers, the splanchnoderm¹ mesially (ventrally) and the somatoderm¹ laterally (dorsally). These layers are separated by the

¹ I have coined these two words to fill a real need, the expressions "splanchnic layer of the mesoderm" and "somatic layer of the mesoderm" being awkward terms with which to designate these layers as compared with single words. The terms "splanchnopleure" and "somatopleure" have been used in this sense, but incorrectly, since the latter properly includes ectoderm as well as mesoderm and the former entoderm as well as mesoderm.

primitive coelom. While ventrally the coelom is uninterrupted, dorsally it exists in the shape of separate pockets, so that the mesoderm has the form of separate, hollow processes whose median walls are composed of splanchnoderm, the lateral walls of somatoderm. These processes are the somites. A diagrammatic cross-section of one is shown in Figure A. They seem to be represented in their most primitive condition in the elasmobranchs, where, according to Van Wyhe ('89), the segmentation extends ventrad even through the region of the germinal epithelium. Three regions may be more or less distinctly recognized

FIGURES A-D.

Four figures to illustrate the relation of the mesomer to the rest of the mesoderm. For explanation see Introduction (page 32). The median plane of the body is at the right in each case.

in each somite. The most dorsal, to adopt the nomenclature of Van Wyhe, is the *epimer* (*e'mer.*, Fig. A), generally designated as the myotome because the main trunk-muscles are derived from it. Its cavity is the epicoelom. Passing ventrad, the next region is the *mesomer* (*ms'mer.*), enclosing the mesocoelom. The mesomer has been designated by the terms middle plate, intermediary cell-mass, "Urwirbelkommunikation," etc. The sclerotome may be considered as arising from the upper portion of its median wall, but the major part of both walls seems to enter into the formation of the nephric fundaments. For this reason

it has also been termed the nephrostome. The third, most ventral, portion of the somite is the *hypomer* and gives rise to the germ cells (*cl.g.*). These originally arose from both layers,¹ but now seem usually to be confined to the splanchnoderm. Following on the hypomer comes the unsegmented portion of the mesoderm, "lateral mesoderm," consisting of the lateral plates enclosing the true body cavity (*coel.*). It must be borne in mind that the three portions of the somite are distinguishable rather from their fate than by any early differences in shape or histological structure.

The various views held in regard to the origin of the mesonephric units may be arranged in five categories as follows: the cells composing the fundaments of the units are derived from (1) the Wolffian duct, (2) the myotome, (3) the intermediary cell-mass, (4) the peritoneal epithelium, (5) mesoderm cells of unknown origin.

The first view, that the Wolffian duct furnishes the fundaments of the mesonephric units, we may safely exclude, for there is but one group of vertebrates (Teleosts) in which such an origin has been claimed of late years (Felix, '97), and in this group it seems questionable not only whether the organ described is really a mesonephros, but also whether the Wolffian duct is truly homologous with that of other groups.²

In regard to the second, third, and fourth views, they are all reconcilable with the theory that the mesonephric tissue is always derived from a portion of the mesothelium, the mesomer, which is homologous throughout the vertebrate phylum. If the severance of the ventral (lateral) portion of the mesoderm from the dorsal portion takes place between mesomer and hypomer (Fig. *B*), the former may appear as an integral part of the epimer, and on developing give rise to the impression that the sclerotome and mesonephros arise from the myotome. If the division takes place between mesomer and epimer, the mesonephric fundament will appear either as if derived from the intermediary cell-mass (Fig. *C*), or, in case that structure has flattened out, as if from that portion of the peritoneal epithelium immediately lateral (dorsal) to the gonad (Fig. *D*). That the sclerotome never seems to arise directly from the peritoneum is due to the fact that it is given off at too early a stage.

¹ Rabl ('96) states that primitive germ cells are found in the somatoderm as well as in the splanchnoderm in early stages of elasmobranch development, and I find the same condition in Amphibia.

² Felix states that both somatoderm and splanchnoderm enter into the formation of the Wolffian duct in the trout.

In the diagrammatic figures *A-D* it will be noticed that I have represented, in every case, the mesomer as containing tissue from both splanchnoderm and somatoderm, — thus making its cavity a true part of the primitive coelom. This important conception we owe to Adam Sedgwick ('81). Having come to the conclusion that the middle plate of the chick represented a portion of the splanchnoderm and somatoderm, he proceeded to verify it in the elasmobranchs.

The condition he described in these animals is briefly this: The middle plate is in the form of a tube connecting the coelom of the lateral mesoderm with the cavity of the myotome. This tube becomes cut off from the myotome and its dorsal end curves downward and outward¹ to join the pronephric (Wolffian) duct.² At a point near its connection with the lateral plates, the dorsal wall of the tubule is invaginated to form a glomerulus. The portion between the Malpighian body thus formed and the lateral plates is the outer tubule; that between the Malpighian body and the duct is the inner tubule. The nephrostome is thus formed by the persistence of an opening already present, and the cavities of the outer and inner tubules, as well as that of the Malpighian body, are a portion of the primitive body cavity.

I believe Sedgwick's description is correct except in one important detail; instead of the inner tubule arising by a bending downward of the blind pocket, which — as it contains both splanchnoderm and somatoderm — would cause the lumen of the inner tubule to represent primary coelom, the inner tubule is formed *entirely by means of the evagination of the somatic layer*. This would make the lumen of the inner tubule, in a way, a secondary one. Field ('91) lays stress on this point, and it has been vaguely recognized by other authors.

Sedgwick's conception, with more or less modification, has been found to apply to most of the vertebrate groups which have been studied since 1881. In the Amphibia, however, two of the authors who have expressed an opinion on the subject since that date have derived the mesonephric elements from evaginations of the peritoneum.³ Hoffmann ('86) describes their origin in Triton and states that the serial evaginations (in the form of solid outgrowths) retain their connection with the peritoneum to form the nephrostomes. Field ('91), in a work on the pronephros of *Amblystoma*, simply mentions that he could not be certain as to the mode of

¹ A glance at Figure *C*, page 33, may aid in understanding this process.

² No distinction will be made in this paper between pronephric and Wolffian ducts.

³ I leave out of account, for the present, that primitive amphibian, *Ichthyophis*.

origin of the mesonephric elements, but is inclined to think that they are derived from the peritoneum.

As was pointed out above, such an origin of the mesonephric units would not be incompatible with the existence of a mesonephric fundamen-
ment (the mesomer) homologous throughout the vertebrate series, and would even seem to be fairly well established for *Petromyzon* (Wheeler, '99). The *fact* of such an origin in *Amphibia* has, however, been disputed by Marshall and Bles ('90). Although they were unable to decide as to the true origin of the mesonephric fundaments, they were certain that these do not arise from the peritoneum and that the nephrostomes join them secondarily.

The first problem, then, is that of the origin of the mesonephric fundaments and the question as to whether or not both layers of the mesoderm enter into it.

The origin of the dorsal sets of units seems never to have been carefully investigated. Spengel ('76) thought they arose by a splitting of the Malpighian body of the primary units. Fürbringer ('78) states that their origin is similar to that of the primary, which he describes as developing (at least in the case of the more anterior units) from solid peritoneal outgrowths. Hoffmann ('86) came to the conclusion that they are derived from the primary units because they equal them in number.

MATERIAL AND METHODS.

I have no reason to doubt that all of the urodele material on which the investigation of the mesonephros is based consists of *Amblystoma punctatum* Linn., as that is the only species of *Amblystoma* at all common about Cambridge, Massachusetts, where the eggs were collected. The male and female animals of this species were often found in the ponds where the eggs were collected. Two females of the species named, when brought home, laid freely in captivity; and the developing embryos and larvae differed in no respect from any of those collected from the ponds. The large translucent masses of jelly containing the eggs are attached to twigs and rushes about a foot beneath the surface of the water. In the near neighborhood, the white, fungus-like spermatophores can generally be seen dotting the twigs and leaves of the bottom. The eggs are laid as soon as the ice is well out of the ponds.

The *Amblystoma* material which was used in the study of the Müllerian duct was mostly collected at New Haven, Connecticut. It consists of larvae in their second year. The majority were caught early in May

and raised in captivity. Although well fed, these were shorter by about ten millimetres at the time of their metamorphosis than those which were not kept in captivity. This difference in size is already observable at the time when the Müllerian duct begins to develop. For this reason the length of the specimen has little significance. In the case of animals raised in captivity the fundament of the duct first appears when they have reached a length of thirty-five millimetres; in the others, when they are about forty-five millimetres long.¹

Some of my specimens were given me by Professor J. S. Kingsley, who also loaned me some of his slides. I wish here to express my gratitude for his kindness, and that of Doctors F. D. Lambert, H. V. Neal, and J. H. McGregor, who also put their material at my disposal.

My anuran material consists of specimens of *Rana sylvatica* Le Conte, which were all raised from the egg. The eggs of this species can be distinguished from those of any other New England anuran by the early date at which they are laid. They are deposited quite as early as those of *Amblystoma punctatum* and are often found with the eggs of that species in cold shaded pools, where they are attached in a similar manner to twigs, etc. The jelly in which they are imbedded forms rounded masses of a tougher consistency than the egg masses of any other New England frog. The development of the Müllerian duct was also investigated in *Hyla versicolor* Le Conte. The larvae were collected at Wood's Hole, Mass., in July and kept in captivity. They are distinguished from other tadpoles by their crimson tails and blunt snouts.

I tried a number of killing reagents. The most serviceable one for the younger stages seems to be a saturated aqueous solution of corrosive sublimate with five per cent acetic acid. Kleinenberg's picro-sulphuric mixture gave good results when the embryos were imbedded in paraffin soon after hardening. By far the best results with embryos from ten millimetres up were obtained with Zenker's fixing reagent. Unfortunately this was not learned early enough to try it on younger stages. Felix found it unsuitable for trout which still had the tissues loaded with yolk and this might also prove to be the case with amphibian material. I kept some of the hardened embryos in 82 per cent alcohol, some in 90 per cent. After five or six months I was much chagrined to find that none of the material so preserved except the older larvæ was of any value for finer details. I hear from various sources the

¹ Thinking that I might be dealing with two different species, I took one of the smaller larvæ which had metamorphosed to Mr. Samuel Garman. He tells me that he sees no reason to doubt that it is a specimen of *Amblystoma punctatum*.

same report in regard to the early stages of amphibian material and conclude that the only safe way is to imbed and preserve in paraffin. Much difficulty was encountered at first in cutting the younger specimens. The yolk crumbled under the knife and utterly destroyed the tissues. This trouble later disappeared. I believe the change in method which brought about the amelioration was a shorter sojourn of the objects in the higher grades of alcohol, xylol, and paraffin. I generally found it sufficient to leave the smaller embryos but five minutes in each of the following: absolute alcohol, xylol, soft paraffin, hard paraffin. A number of stains were tried. I finally restricted myself to Delafield's haematoxylin followed by orange G. A weak solution of Delafield's haematoxylin in water was employed, of such a strength that the nuclei stained to the proper shade in about thirty minutes (staining was always done on the slide). Treated in this way this stain is so selective that no decolorizing is necessary. The slides were then washed in tap-water and passed through ascending grades of alcohol, in one of which (preferably 70 per cent) some crystals of orange G had been dissolved. The latter does not overstain the yolk, as most plasma stains do. This process makes the nuclei blue, in sharp contrast with the orange yolk and paler yellow cytoplasm. In the older stages the cytoplasm usually stains a faint blue.

In describing the mesonephric development I shall make use of the following terms: blastulae (the "Bläschen" of German writers), inner tubule (main tubule, *canalis principalis*), inner funnel, outer tubule or nephrostomal tubule (*canalis nephrostomalis*), outer funnel or nephrostome, Malpighian body, and glomerulus. The "visceral layer" of the Malpighian body (Semon) I shall call the glomerular covering, reserving the term "Bowman's capsule" for the "parietal layer."

The work was begun and the part relating to *Amblystoma* practically completed at the Museum of Comparative Zoölogy of Harvard University at the suggestion and under the direction of Dr. E. L. Mark. It gives me pleasure to express my gratitude to him for his constant aid. I wish also to thank Doctors W. E. Castle and G. H. Parker for their interest and suggestions. The work was completed at the Sheffield Biological Laboratory of Yale University, and I am indebted to Professors S. I. Smith and W. R. Coe of that institution for many favors.

II. Development of the Mesonephros.

A. AMBLYSTOMA.

Stage I.

In embryos of Stage I, the head and tail are already slightly differentiated from the oblong mass of the body. The eye is visible, although sections do not show any sign of the lens.

About nine body somites are already established, — two in front of the pronephric thickening, two in the region of that thickening, and five posterior to it. In order to make my account more readily comparable with that of Field ('91), I shall call the somites in connection with which the pronephros is developed somites three and four, ignoring the head segments.

In cross-sections the somites have in outline the form of triangles (Figure 1, Plate 1), the median sides of which abut on the neural tube and chorda. In the middle of the somite there is a lumen. The walls are thick and composed of a single layer of slender columnar cells heavily pigmented in the ends bordering on the lumen. From Figure 1 it will be seen that the lateral plates (*so'drm. l.* and *spl'drm. l.*) are considerably thinner than the walls of the somite, and that the lateral extension of the lumen of the somite between them is indicated by cell-boundaries only, there being, generally, no real cavity. On following the lateral plates ventrad they are seen to become still thinner.

Frontal sections show the somites as rounded rectangles, somewhat elongated laterally and flattened against each other. Segmentation of the mesoderm extends as far laterad as the point *nph'tm.* in Figure 1; that is, to a point about on a level with the dorso-median boundary of the Wolffian duct (*dt. Wf.*). The only clue to the position of the mesomer is the pronephric thickening, which, as it is the fundament of the pronephric tubules, must lie in the mesomeric somatoderm. The section from which Figure 1 was taken passed through the seventh somite. Superposition of camera drawings of that section and those anterior to it shows the pronephric thickening to occupy a position corresponding to that portion of the somatoderm marked *nph'tm.* in Figure 1. How much of the ventral (splanchnic) wall of the somite is to be assigned to the mesomer, is not to be determined at this stage. The Wolffian duct has reached the middle of the eighth somite.

Stage II.

Embryos of Stage II have increased considerably in length over those of Stage I. The head and tail are clearly marked off from the body. The optic vesicles still communicate widely with the forebrain, and there is no sign of a lens-thickening.

The chief difference in the structure of the somite between this and the previous stage, as may be seen from Figure 3, is a great increase in its dorso-ventral diameter. Its lumen in that diameter has increased even more than has the somite, but it has decreased in its antero-posterior diameter, so that the anterior and posterior walls of the somite now almost touch each other. Figure 3 does not fully show this increase in the vertical diameter of the lumen, because the somites are oblique both to the frontal and slightly to the sagittal plane of the body, their anterior and posterior walls sloping backward both dorsally and laterally. Sections in the three planes, transverse, sagittal and frontal, show the anterior, posterior, and median walls of the somites to be thick, the ventral and dorso-lateral walls thin. The somites are more closely applied to each other than in the preceding stage, and fit together like opistho-coelous vertebrae. The lateral mesoderm is more distinctly differentiated from the somite than in Stage I.

The duct has reached somite 14. *Germ cells* are present and rather conspicuous opposite somite 11. They are differentiated out of the *most dorso-median portion of the lateral mesoderm*¹ by the increase in size of cells of *both splanchnoderm and somatoderm* (cf. g., Fig. 5, Plate 1). These cells form a rod parallel with the lateral edge of the somite and enclose a small lumen which is a portion of the coelom. They are still connected with the rest of the lateral mesoderm and with the mesomer. At *ca. snj.* (Figure 3) are seen cells which apparently give rise later to blood-vessels. Their origin is unknown.

Stage III.

The embryos of Stage III possess about twenty somites and measure from 5 to 5.5 mm. in length. The fundamentals of the gills are beginning to show as external protuberances. The cavity of the optic vesicle is nearly obliterated, and the lens-thickening is beginning to appear.

A comparison of Figure 13 (Plate 2), with Figure 3 shows the main points of advance in the development of the somite between this stage

¹ This tissue represents, of course, the hypomer, but segmentation is rather indistinct and very transitory.

and Stage II. The changes will be seen to consist in an alteration in shape and in an increased difference in the relative thickness of the walls. In Figure 3 it will be noticed that the lateral wall is bent outward to a slight extent just above the duct (at the point marked *so. v-l.*). In Stage III this bend is so pronounced that the junction of mesomer and lateral plates (Figure 13, *nph'tm.*) lies ventral to the edge of the somite. The ventral wall of the somite thus contains a small amount of somatoderm. By the increased thickening of the anterior, posterior, and median walls, the cavity of the somite has become nearly obliterated. There is left only a narrow fissure-like lumen extending from the ventro-median to the lateral and thence to the dorsal angle.

One of the most important points to be noticed in this stage is the beginning of the differentiation of the sclerotome, the first indication of which may be seen in Figure 13, in the slight extension (*sc'l'tm.*) of the ventral wall of the somite toward the chorda. The tissue which forms the sclerotome is certainly derived from the splanchnoderm of the ventral wall of the somite, but at precisely what point or points the cell multiplication takes place, I have been unable to determine. The peculiar form and arrangement of the cells of the median portion of this ventral wall (see Figure 13) suggest, however, that this cell-layer is being shoved mediad, and I suspect that the increase of cells takes place quite near the point of union of mesomer and lateral plates, perhaps near the point *a*. However this may be, I think we are justified in considering all of the splanchnoderm of the ventral wall *lateral* to the point *a*, as belonging to the mesomer. The mesomer thus consists of a splanchnic portion, just described, extending mesiad from the point of union with the laterad mesoderm at least as far as the point *a*, and a somatic portion, which, beginning at the point of union with the lateral mesoderm, extends laterad toward the outer angle of the somite (see the discussion of the position of the pronephric thickening in the description of Stage I).

The Wolffian duct at Stage III has joined the cloaca opposite the anterior end of somite 19. In the anterior half of the embryo it already possesses a small lumen.

Germ cells are conspicuous from the posterior end of somite 11 to the posterior end of somite 15. They are most conspicuous intersegmentally, but extend a short distance beneath the two adjacent somites. In the last segment in which they are seen (somite 15), they extend along the entire somite. Although partially forced into an intersegmental position, the germ-cell masses do not lose their connection with the mesomers.

The loose tissue shown at *va. sng.* in Figure 3 has in this stage developed into the walls of blood spaces (Plate 2, Figure 13, *va. sng.*), which as yet contain no corpuscles.

Stage IV.

This stage may be considered rather briefly. The embryos measure from 6 to 6.5 mm. in length. The deeper layer of the ectoderm over the optic vesicle has invaginated to form a conical lens-thickening of high columnar cells.

The cells of the splanchnic layer of the epimer have increased in number and are beginning to take on the form of muscle cells, but there is no indication of fibrillae.

Figure 2 (Plate 1) shows the main features to which I wish to call attention. These are the further migration of the duct (*dt. Wf.*) inward under the somite, and the growth of the sclerotome (*sc'ltm.*), which has now extended dorsad between epimer and neural tube and encountered the sclerotome of the opposite side of the body. Loose cells of unknown origin lie where the aorta later appears and presumably contribute to its formation. Similar scattered cells are commonly found beneath the whole of the ventral wall of the somite, where they later become much more numerous. In sections posterior to the one figured, the lumen of the somite (*coel. so.*) extends up to its dorsal angle.

Stage V.

I take as a type of this stage an embryo 9.25 mm. in length. A considerable advance over the last stage has been accomplished in the specialization of tissues. The main mass of the epimer is composed of longitudinally directed muscle cells whose nuclei occupy a central position. In frontal sections the non-nucleated ends of the cells are seen to form broad, clear bands at either end of the somite. The clear bands of successive somites are separated by a thin layer of connective tissue, the myocomma (Plate 1, Fig. 7, *my'cm.*, and Fig. 9). Muscle fibrillae are clearly distinguishable. The sclerotome has only occasionally the form of a continuous layer of cells, having been for the most part transformed into finely branching, mesenchymatous tissue with scattered nuclei, which fills the space between the somites, the neural tube, chorda, etc. Between the ventro-median side of the somite and the entoderm the sclerotome seems to retain some of its continuity with the somite, but how much of that tissue (Fig. 8, β) is sclerotome and how much has arisen from the loose cells mentioned in the description of

Stage V it is impossible to decide. The more dorsal portion of the somatic layer of the epimer has also been converted into mesenchyme. Of the two thinner walls of the somite, the lateral and the ventral, there thus remain only the mesomer and a small adjacent part of the somatic layer of the epimer (*so'drm. t.*, Fig. 7). The latter bounds the ventral and lateral sides of the remnant of the epicoelom.

To understand Figures 7, 8, and 9, it is necessary to bear in mind the opisthocoelous character of the somites and their oblique position. Not only are they placed obliquely, but their ventro-lateral portion, with the enclosed lumen, has been stretched backward, so to speak, until the most posterior point of each somite lies well back on the next following. Figure 8 represents a section through the middle of a somite; Figure 7 shows one passing back of the middle of one and barely cutting the anterior end of another (which would be seen above and to the right of the myocomma, *my'cm.*); the section represented in Figure 9 passes through the posterior end of a somite. The overlapping of the somites causes the mesomer to extend obliquely outward and backward, so that in the anterior portion of the somite it lies some distance from the duct and mesad of the postcardinal vein, while toward the posterior end it lies against the duct (Fig. 9, *ms'mer.*).

The point to which attention is to be especially directed is the appearance of the mesomer, for it is in the mesomer and at this stage that the *fundaments of the mesonephros* are first discernible. These fundaments arise in the embryo under consideration in the posterior fourth of each mesomer from somite 9 to somite 18, inclusive. Without doubt the one or two remaining somites anterior to the cloaca give rise in a similar manner to mesonephric fundaments, as the blastema¹ is seen to extend in older larvae to the posterior end of the duct. This question could not be decided definitely, as that part of the body in the particular embryo described above was lost, and it was found that in other specimens (and presumably this would have been likewise true of that specimen) the curving of the body renders all processes in the posterior region obscure.

The differentiation of the mesonephric fundaments may be described as follows: the posterior fourth of each mesomer (Figs. 7, 9, *ms'mer.*) distinguishes itself from the remaining portion (and from the *entire* mesomer of somites anterior to the ninth) by three peculiarities: the

¹ The term "blastema" has been employed to designate the continuous cell-mass from which the mesonephros arises in Amniota. As will be shown in the description of the next stage, the term applies equally well to Urodela.

crowding of the nuclei, the intensity of the nuclear stain, and the presence of a large amount of pigment throughout the cells. These three peculiarities combine to give these earliest fundamentals of the mesonephros that conspicuousness which characterizes the organ until it becomes functional.

That both somatic and splanchnic layers of the mesomer participate in the formation of these fundamentals seems unquestionable from the appearance of such sections as that shown in Figure 7, where two groups of nuclei will be noticed, one on each side of the point marked *ms'ner*. Although such a favorable fundament (that is, one showing a clear separation into two masses, a somatic and a splanchnic) is rather rare, I have seen, nevertheless, such a condition often enough to justify the belief that it is not without significance.

The only additional points to be noted in this stage are the presence of a distinct aorta (Fig. 7) and postcardinal vein (*va. snj.*, Fig. 8), the open lumen of the duct, and the coalescence of the germ-cell masses to form a more or less continuous ridge, no longer showing any sign of segmentation. This ridge extends from the posterior end of somite 10 to somite 16 (see Diagram 1, page 56, column A).

The earliest traces of the mesonephros thus appear as specialized masses of cells differentiated from the posterior portion of the mesomers from somite 9 back to, presumably, the posterior end of the duct. The fundamentals are metameric, there being one for each segment. They are derived from both splanchnoderm and somatoderm.

Stage VI.

The larva described as illustrating this stage measured 10 mm. in length. The development of the mesonephric fundament is very rapid in larvae from 9 to 10 mm. long, which explains the fact that among the many specimens sectioned, I have been able to find but one good example of each of the Stages V. and VI.

Figures 10, 11, and 12 (Plate 1) illustrate the changes which the somites have undergone. The mesomer, duct, and dorso-median angle of the lateral mesoderm have migrated still farther mediad. The remaining portion of the somatic layer of the epimer has been more or less completely converted into mesenchyme, thus obliterating the remains of the epicoelom by depriving it of one of its walls. In the section represented by Figure 12 this process has been nearly completed. In that shown in Figure 10 it is still in progress, the outer wall being very thin. That portion of the somatoderm directly over the duct has

also become very thin, or has entirely disappeared. Occasionally, however, as at *so'drm. t.*, Figure 12, this layer is still visible as a thin membrane connecting the mesomer with the *lateral* portions of the epimeric somatoderm. Aside from this slender connection, the mesomer has been completely severed from the overlying epimer. The all-important change to be noted is the *fusion of the successive mesomers to form a continuous cord*. That portion of the cord extending from somite 9 to somite 19 or 20 is the *mesonephric blastema*. This blastema is not of uniform diameter throughout its length, but presents swellings extending from the posterior third of each somite backward to a point opposite the anterior third of the following one. These swellings present all the characteristics of the mesonephric fundaments described in the preceding stage, and are presumably identical with them. That each has moved slightly backward from the position in the posterior part of each somite where it arose, thus bringing its greatest diameter into an intersegmental position, is not strange, as the mesomer is now practically free from the rest of the somite. Cross-sections of two of these swellings are shown in Figures 10 and 11 (*fund. ms'nph.*). In Figure 10 may still be seen a condition suggestive of an origin from the two layers, splanchnoderm and somatoderm (compare Fig. 7).

Opposite the middle of each somite, from the ninth to the twelfth, there is an additional swelling which is quite evident, though much smaller than the ones just described. Opposite somite 13 there seem to be at least two of these smaller thickenings.¹ For convenience I shall refer to all of these smaller swellings as swellings or units of the "*second order*," to the larger ones as those of the "*first order*." Figure 12 (*fund. ms'nph.*) shows a cross-section of one of the most distinct of the former, that opposite the middle of the twelfth somite. The units of the second order are probably developed from the tissue of the anterior portion of the mesomer just before or shortly after the fusion of the mesomers to form the continuous blastema.

A word should be said in respect to the relation of the blastema to the lateral plates. In Figures 11 and 12 there is shown an intimate fusion between the blastema and the lateral plates, here represented by the germ-cell mass. This is true only as far forward as the germ-cell mass extends, — to somite 11. There are about six thickenings anterior to that point, which seem in this larva to have no connection with the lateral plates.

¹ Unfortunately I do not possess the portion of this larva back of somite 13.

Stage VII.

The larvae of this stage measure from 10 to 10.5 mm. in length. The duct, the median angle of the lateral mesoderm, and the mesonephric blastema have migrated still farther mediad, so that the blastema now lies at the ventro-median angle of the epimer. The most noteworthy change is the transformation of the thickenings of the blastema into more clearly cut masses, which from this stage on I shall call *blastulae* (the "Bläschen" of German authors). These, although still elongated antero-posteriorly, are shorter than in the preceding stage and more rounded in cross-section. Their nuclei have begun to place themselves radially about the long axis of the blastula, leaving a clear protoplasmic area in the centre. The first indication of this arrangement is to be seen in Plate 2, Figure 17, *fncl. ms'nph.* As will be seen in columns *C* and *D* of Diagram 1 (page 56), the blastulae are distributed as in Stage VI (column *B*, Diagram 1), one of the first order and one of the second order for each segment. As before, this statement is true only for the more anterior somites. From somite 13 or 14 caudad those of the second order become more numerous. Those lying in the regions where the germ-cell mass exists are in close contact with it. The fact that those anterior to it are invariably connected with the lateral plates makes it doubtful whether the separation mentioned in the preceding stage was artificial, or the continuity in the present stage is due to a secondary fusion.

Posterior to somite 15 the blastema becomes more slender and more uniform in diameter. Although there are occasional swellings in it, they are ill defined and irregularly placed, and may possibly not represent blastulae.

Stage VIII.

The larva on which I base my descriptions of Stage VIII measures 12 mm. in length. Figure 19 (Plate 2) represents a portion of a cross-section through the posterior end of somite 11 of both right and left sides, and cuts a pair of blastulae near their centres.

The epimers, as the result of the great increase in their dorso-ventral diameter, now project far below the chorda, and those of the opposite sides of the body have approached each other so that they now compress the aorta slightly. In this stage the body cavity (*coel.*) is represented by an actual lumen immediately ventral and lateral to the germ-cell mass, the lumina of the opposite sides of the body being separated by a thin layer of tissue, the mesentery.

The mesonephric blastulae are very conspicuous, being considerably larger than in Stage VII. They are more rounded in cross-section, and the radial arrangement of the nuclei, which began to be noticeable in the last stage, is well established. This radial arrangement is seen not only in cross-sections, but in frontal and sagittal sections as well, which proves that the nuclei all point toward a common centre. In frontal sections the blastulae are seen to be elongated masses, two or three times as long as they are broad, each one just touching its neighbors. While the median wall of the blastula appears nearly straight and is parallel with the long axis of the body, the lateral wall appears quite convex, projecting outward over the Wolffian duct. *This wall is also thicker than the median and has more elongated nuclei.*¹

It is a point of importance that in this stage the enlargements which I have termed "blastulae of the second order" are no longer to be distinguished by their size. They have overtaken those of the first order in their development, and the two sets are henceforth indistinguishable except by their position, and even that criterion does not long serve to distinguish them.

The Dorsal Extent of the Somatic and Splanchnic Layers of the Lateral Mesoderm.

Before proceeding further with the description, I wish to make a slight digression to discuss the question of the dorsal extent of the somatic and splanchnic layers of the lateral mesoderm. The study of such a stage as that represented by Figure 19 would lead one to think that the junction of the two layers lay directly over the point marked *coel*. It really lies a little mesad of the duct, at the point designated *nph'stm*. In order to justify this statement it is necessary to revert to the description of Stage II. It was there shown that the germ cells were differentiated from both layers of the lateral mesoderm in the region of their junction with the corresponding layers of the mesomer. In all of the later stages the mesomer (represented by the mesonephric blastema or blastulae) has remained closely connected with the germ-cell mass and has migrated with it toward the median plane of the body. As the morphologically dorsal angle of the body cavity must be at the junction of mesomer with lateral mesoderm, it lies, in such a section as that represented by Figure 17, *in the germ-cell mass near the point nph'stm*. How, then, has the apparent dorsal angle in Figure 19 (*coel*.) arisen?

¹ This characteristic, so noticeable in frontal sections, is shown only to a slight extent in the particular cross-section figured (Fig. 19).

The arrangement of the nuclei at the point *coel.* in Figure 17 seems to indicate that it has arisen as an outfolding of the splanchnic layer of the lateral mesoderm toward the median plane. In the elasmobranchs such an outfolding is very evident (Rabl, '96, Taf. 15, Fig. 8; Rückert, '88, Taf. 15, Fig. 21). In those animals the mesonephric nephrostomes unquestionably mark the morphologically dorsal angle of the body cavity, and they lie just mesad to the duct, while the apparent dorsal angle is much nearer the median plane, and is formed by an outfolding of the splanchnic layer of the lateral mesoderm.

In Figure 19 the ventral angle of the blastula (directly above the point *nph'stm.*), which is to form the nephrostome, seems to have moved ventrad into a position between the duct and the germ-cell mass. Such a shifting of the fundament of the nephrostome would seem to necessitate a severance of its connections with the two layers of the lateral mesoderm and the re-establishment of a connection exclusively with the somatic layer of the lateral mesoderm. Such a condition would exclude a strict parallel between the nephrostome development in *Amblystoma* and that in elasmobranchs, where, as above stated, the original connection between the lumen of the mesomer and that of lateral plates is retained as the nephrostome, which consequently opens at the point of union of the two layers of the lateral mesoderm. But such an interruption of the connection between the fundament of the nephrostome and the lateral plates in *Amblystoma* is not the only possible interpretation of the condition shown in Figure 19. The indicated migration of the ventral region of the blastula, *without loss of continuity between the layers of the mesomer and those of the lateral plate* might be brought about by a degeneration of the germ cells of the somatic layer into ordinary epithelial cells. Rabl ('96) assumes precisely such a degeneration in elasmobranchs, where, in early stages, he finds germ cells present in *both* layers, whereas later they are confined to the splanchnoderm. In *Amblystoma* the degeneration of the cells in question is rendered probable not only by the fact that *all* of the germ cells disappear from posterior somites (see Diagram 1), but also by the additional fact that, in the larva from which Figure 19 was taken, there were frequently seen, lying just ventral to the blastula cells, which are far too small to be germ cells, yet resemble them in containing a conspicuous amount of yolk.

There is probably, then, a persistent connection between the two layers of the blastula and the corresponding layers of the lateral mesoderm, which brings the condition in *Amblystoma* into close conformity with that in elasmobranchs, and, what is of even greater importance,

with that found by Semon ('92) in *Ichthyophis*. (See Figures *F* to *H*, page 72.)

What has been said in regard to this persistent connection applies only to the somites anterior to the sixteenth. Posterior to the sixteenth the blastulae are separated more and more widely from the peritoneum by loose, mesenchymatous tissue (compare Figure 20, a section through somite 16 of a larva 21 mm. long). The nephrostomes of these posterior units, as well as those of all secondary units, must therefore join the peritoneum secondarily. Whether those of the posterior primary units join the peritoneum at the point of junction of somatic and splanchnic layers or not, is impossible to determine. It is certain that these and the nephrostomes of secondary units cannot both open at the line of junction, for both sets of nephrostomes are often seen in one cross-section, opening at some distance from each other (see Fig. 24, Plate 3, *nph'stm.* 1 and *nph'stm.* 2).

Development of a Mesonephric Unit in Amblystoma compared with that in Pristiurus.

In resuming the description of the mesonephros I shall no longer describe larvae at successive stages of development, but instead briefly describe the *development of a blastula* into a functional unit,¹—briefly, because these changes have been well described, in the main, by Fürbringer ('78) and others.

In order the better to compare the course of development in *Amblystoma* with that in elasmobranchs, it will be well to trace the history of such a unit in *Pristiurus* as described by Rabl ('96). According to that author the blastula is formed in the following manner. The mesomer, which is in the form of an epithelial tube connecting the lateral plates with the epimer, is early rendered incomplete by the breaking up of the dorsal portion of the splanchnoderm to form the sclerotome. The gap thus formed is again closed by the growth mesad and ventrad of the dorsal edge of the somatoderm, which has already freed itself from the epimer. There is thus formed a blind pocket opening into the coelom. Of the median wall of this pocket, a portion adjoining the lateral mesoderm is thus formed of splanchnoderm. The rest of the pocket is composed of somatoderm. The splanchnic portion is thin; the somatic portion, especially on the lateral side of the blastula, is thick. The

¹ The development can be followed by examining successive units in the same larva, beginning at the caudal end of the series, where they are less differentiated, and progressing cephalad.

pocket then becomes differentiated to form a wider portion distally and a narrower portion proximally. The latter becomes the outer tubule, while from the much-thickened lateral wall of the former the inner tubule is differentiated and grows outward and downward to join the duct. The median wall, or sometimes the dorsal wall, of the distal portion becomes invaginated to form the Malpighian body.

As far as we have progressed in our description of the development of a unit in *Amblystoma*, it will be seen that there is a rather close similarity to the development in *Pristiurus*. As will be remembered, the blastula in *Amblystoma* is composed of cells from both splanchnoderm and somatoderm. These layers probably retain their original relative position, the somatoderm giving rise to the thick lateral wall of the blastula, the splanchnoderm forming at least a portion of the thinner median wall. In the anterior units, where the blastula retains its connection with the lateral mesoderm, this is undoubtedly the case.

Later Development of the Mesonephric Units.

Turning to the later development of the mesonephric unit, I have figured four stages (Plate 2, Figs. 20-23), all from the posterior half of the sixteenth somite of a larva 21 mm. in length (see Explanation of Plates). The first change in such blastulae as are shown in Figure 19 is the shortening of each to form a more nearly spherical mass (Fig. 20), which thus becomes larger in cross-section and more widely separated from its neighbors. Then there is formed a process which grows ventrad to touch, and later to fuse with, the peritoneum (Fig. 21, *nph'stm.*). In those anterior somites in which contact between blastula and peritoneum is present from the beginning, the same appearance is produced by a slight dorsal migration of the blastula, leaving a cone of cells joining it with the peritoneum. The thinness of the median wall of the blastula (Fig. 21) has become more marked than in previous stages. As above stated, this thinner median wall probably represents the splanchnic layer of the mesomer. The thickened lateral wall (presumably all somatic) sends out a conical proliferation of cells, which bends ventrad and presses its point against the dorsal wall of the duct (Fig. 22).

In the stage represented by Figure 23 the inner tubule has fused with the duct, and the dorso-median portion of the blastular wall has bent inward (*tbl. ms'nph.* and *cps. Bow. i.*). The mesonephric unit now presents in cross-sections of the body the form of a sigmoid curve. The incurved portion, just mentioned, has sometimes been described as

forming the covering of the glomerulus. In *Amblystoma*, at least, it is only the median portion of the wall of the invagination (*cps. Bow. i.*) which forms the glomerular covering, the lateral wall (*tbl. ms'nph.*) allying itself entirely with the inner tubule.

The further development of the Malpighian body is as follows: the median wall of the infolding (*cps. Bow. i.*, Fig. 23), which is conspicuous as the most darkly staining portion of the entire unit, grows dorsad, stretching the tissue of Bowman's capsule (*cps. Bow.ex.*) to a very thin membrane. It then becomes curved to form a hollow hemisphere with the convexity directed toward the capsule, thus reducing the lumen of the latter to a narrow slit. The cavity of the hemisphere then becomes filled with cells, which increase in number until the whole forms a compact, darkly staining mass, the glomerulus. I am not certain as to the origin of the cells which fill the glomerulus. They may arise *in situ*, but I am inclined to think they are derived from small masses of cells which lie beneath the aorta, as there is often seen a connecting cord of cells between these masses and the glomerulus.

In Figure 23 the curves of the inner tubule all lie approximately in one plane. With increase in length, its curves become more complex and are no longer confined to the transverse plane. Figures 34 and 35 (Plate 3), drawn from a wax reconstruction, show a stage in which the curves are still rather simple. The mesonephric unit in this case is from the eleventh somite of a larva 16 mm. in length and is almost functional (see Explanation of Plates). A comparison of Figure 34 with Figure 23 will show that the cone of cells (*nph'stm.*) connecting the unit with the peritoneum becomes the outer tubule. This later elongates somewhat.

At the point *crv. cp. Mpg.* (Fig. 23) the outer and inner tubules communicate with the lumen of the Malpighian body. In forms more primitive than the Amphibia, this condition persists. In *Myxine* (Maas, '97) the outer tubule may even open into the cavity of the Malpighian body at a point *opposite* the opening of the inner tubule. In *Amblystoma*, however, as in *Ichthyophis* (Semon, '92), the outer tubule *apparently* loses its direct connection with the Malpighian body and opens into the inner tubule at a short distance from the opening of the latter into the Malpighian body (Plate 3, Fig. 24, *crv. cp. Mpg.*). This is brought about by a constriction of the Malpighian lumen just mesal to the point marked *crv. cp. Mpg.* in Figure 23, combined with a lengthening of the constricted region. The short, ciliated tube thus formed, which I shall call the *neck of the Malpighian body*, has generally been considered a

part of the inner tubule. Viewed from the standpoint of its embryonic development, I do not see how it can rightly be so considered. Functionally, of course, it serves as an inner funnel, but, if my view of the extent of the two mesomeric layers is correct, it contains tissue from the splanchnic layer, — which no part of a true inner tubule does.

The differentiation of the blastula to form a complete mesonephric unit, as outlined above, will be found by comparison to agree quite closely with the similar processes in *Pristiurus* as set forth on page 49.

The further changes which take place in the mesonephric unit to fit it for functioning have been too well described for Urodela to necessitate a redescription. These changes consist in a widening of the various lumina, a great increase in the length and tortuousness of the inner tubule combined with a differentiation of its parts, and the establishment of a blood supply to the glomerulus.

Origin of the Dorsal Sets of Units.

In larvae about 20 mm. in length, the blastulae which develop into the primary units have become distinct as far back as the region of the opening of the duct into the cloaca. Soon after these blastulae have become well defined they are seen to be accompanied by smaller ones (*fund. mes'eph. 2*, Fig. 26, Plate 3), which are found from about the anterior end of the eighteenth somite caudad. These smaller blastulae are the *fundaments of the secondary units*. They are sometimes slightly removed from the primary blastulae, but generally in close contact with them. In the former case they may lie mesad to the primary ones, in the latter case they are always dorsad to them. *There is a single secondary blastula to each primary one.* Although these secondary blastulae may possibly develop from residual portions of the mesonephric blastema, they have every appearance of arising by a division of the primary blastulae.¹

Cephalad, the secondary blastulae are generally considerably smaller than the primary, whereas caudad they may nearly equal the latter in size. This fact is apt to give the impression that the mode of division of the primary blastulae to give rise to the secondary ones (assuming that the secondary do so arise) alters as one passes caudad, but I think the true explanation is, that by the time the more posterior blastulae have divided, the growth of the *primary* units farther forward has out-

¹ As will be shown later, there is no possible doubt as to the origin of the secondary units from the primary ones in *Rana sylvatica*.

stripped that of their secondary companions (Fig. 25, *fund. ms'nph. 2*), — since the latter remain almost unaltered for a considerable period during the metamorphosis of the primary units.¹

All that has been said in regard to the origin of the secondary units applies to that of the tertiary, with the exception that the latter arise by a splitting of, or proliferation from, the secondary blastulae, instead of from the primary. In Figure 27 one of these tertiary blastulae is represented in the process of splitting off from a secondary one. The section figured is especially significant from the fact that a dividing cell is seen between the secondary and tertiary blastulae.

The tertiary blastula, in its turn, remains unaltered for some time and then gives rise to a fourth blastula. As one passes caudad, the first tertiary fundament appears about half a somite behind the first secondary; the first quaternary a short distance behind the first tertiary, and so on (see Diagram 1, page 56, column *S*).

Later Development of the Dorsal Sets of Units.

Figure 25 is drawn from a section anterior to the region of the tertiary units. The primary unit presents the form of a sigmoid curve. The secondary blastula (*fund. ms'nph. 2*) always lies against this curve at the upper limit of its lateral arm, which I shall call the collecting trunk (*trn. clg.*). The secondary blastulae which were described as lying dorsal to, and in contact with, the primary blastula have evidently simply retained that position, whereas those which were median to the primary blastula must have moved upward and outward to their present position. This change of position might be brought about by the growth of the Malpighian body of the primary unit, which would tend to force the secondary blastula upward and outward. In the development of the primary unit, the collecting trunk increases in length without becoming coiled, — the great mass of the unit being formed by the lengthening and coiling of the median arm of the curve (*tbl. ms'nph.*, Fig. 25). This fact allows the secondary blastula to retain undisturbed its position against the collecting trunk at the periphery of the mass.

With the increasing complexity of the primary unit, its Malpighian body and outer funnel, as well as the Wolffian duct, are shoved ventro-laterad until they lie at some distance from the mesentery (Fig. 24).

¹ The early appearance of the secondary fundaments was a surprise to me, as all previous authors have stated that they are first visible when the primary units are far along in their development.

The Malpighian body is squeezed against the peritoneum, and the outer funnel opens slightly posterior and generally mesad to it.¹

Nephrostomes of Secondary Units.

Soon after the primary unit has become functional, the secondary begins to go through the same process of development. Its behavior differs from that of the primary in two respects, however: its lateral arm empties into the collecting trunk of the primary unit instead of into the Wolffian duct; its outer tubule is not formed until the rest of its development is nearly completed. The development of this outer tubule is very difficult to decipher from the fact that, at the period when it begins, the Malpighian body has become imbedded in a mass of primary-tubule coils. I think, however, that I am not mistaken in saying that a hollow evagination, tipped with a solid, conical, deeply staining point, grows out from the neck of the Malpighian body, and, pushing its way through the mass of tubules, opens on the peritoneum mesad to the primary Malpighian body (Fig. 24, *nph'stm.* 2). This process begins in larvae about 45 mm. in length.

The later, more dorsal sets of units develop precisely as do the secondary. Each opens into the collecting trunk of the next ventral, so that there is formed a long *compound collecting trunk* reaching from the most dorsal set down to the duct.

Whether or not any or all of the units dorsal to the secondary one produce outer tubules, I do not know. In my oldest specimen² (from which Figure 24 was drawn), which had lost its gills, having left the water and assumed the adult markings, there are occasionally three outer funnels cut in one cross-section. In these cases the two younger nephrostomes are closely approximated to each other. This would seem to suggest that some of the tertiary units had developed outer tubules. The only way to settle this point with absolute certainty would be to follow each unit from its outer funnel to the common collecting trunk. This is practically impossible. A less certain but fairly satisfactory way would be to plot the outer funnels and all those glomeruli which, from their position, seem to belong to primary and secondary units. By comparing the number of outer funnels thus obtained with the sum of primary and secondary units, an inference could be drawn as to whether these two sets alone

¹ The section figured passes tangentially through the posterior wall of Bowman's capsule (*glm.* 1), which touches the peritoneum in the next anterior section.

² I unfortunately have no record of the length of the specimen, but should estimate it at about 50 mm.

possess outer tubules or whether some of the tertiary also possess them. This I did throughout two somites in my oldest specimen with the following results: The number of outer funnels was somewhat *less* than the sum of the primary and secondary glomeruli, which points to the conclusion that only primary and secondary units possess outer funnels at this stage, — and possibly the same is true in the adult.¹ The fact that the sum of the primary and secondary glomeruli exceeds the number of outer funnels does not necessarily mean that some lacked outer tubules, but rather that some tertiary glomeruli were included in the enumeration. In fact, before comparing the numbers, I had marked some as possibly belonging to the tertiary set. The position of the glomeruli of the different sets is so variable at this stage that I was compelled to plot the openings of the collecting trunks into the duct in order to assure myself that what I took to be secondary glomeruli were not merely primary ones which had shifted their position dorsad. The number of openings found differed by only two from the number of those which I had considered as primary.

The plotting also brought out the fact that, at this late stage, there has been no change in the relative number of units in the different sets. There is still one secondary for each primary (in the region of the secondary), one tertiary for each secondary, etc. Six or seven sets are present. All are functional except the two dorsal sets, of which the most dorsal consists of small, spherical, darkly staining blastulae.

Description of Table 1 and Diagram 1.

I wish now to call attention to Diagram 1 and Table 1, pages 56, 57. In the diagram I have plotted for the right side of the body in twenty-one individuals the position of the mesonephric units, the extent of the germ-cell mass, and the position of the opening of the duct into the cloaca. In the earlier stages the position of the units was determined by the point of greatest diameter in the blastula; in the later ones the glomeruli were taken as representing the units. In the case of the secondary, tertiary, etc., units, only the most anterior one is indicated. In Table 1 (page 57) I have translated the plotted units into numbers-per-somite for more ready comparison. By examining the diagram and table, the following questions can be answered: —

(1) Do any units degenerate and disappear?

¹ Fürbringer ('78) states that in *Salamandra maculosa* the secondary units send outer tubules to the peritoneum. Hoffmann ('86), on the other hand, states that in *Triton* they do not.

DIAGRAM 1. (For explanation see opposite page.)

EXPLANATION OF DIAGRAM 1.

Mesonephric units of *Amblystoma* plotted according to position in the somite. Individual larvae denoted by the letters *A* to *U*, with their lengths in millimetres immediately below. Somites 9 to 20 are numbered in the extreme right-hand and left-hand columns. The units are represented by solid circles or ovals,—*rings* indicating indistinct fundaments, whose number is uncertain. Circles numbered 2, 3, 4, and 5 (*L-U*) represent the most anterior of the secondary, tertiary, etc. units. The *wavy lines* indicate the extent of the germ-cell mass. *Crosses* (in individuals *K-O*) show the position of the most posterior of the *functional* units. The position of the opening of the Wolffian duct into the cloaca is shown at the bottom of the diagram (somite 20).

	<i>B</i>	<i>C</i>	<i>D</i>	<i>E</i>	<i>F</i>	<i>G</i>	<i>H</i>	<i>I</i>	<i>J</i>	<i>K</i>	<i>L</i>	<i>M</i>	<i>N</i>	<i>O</i>	<i>P</i>	<i>Q</i>	<i>R</i>	<i>S</i>	<i>T</i>	<i>U</i>	<i>B-K</i>	<i>L-U</i>	<i>B-U</i>	Probable Number of Units.
9	2	2							1												.5	0		1
10	2	2	2		2	1	2	1	1	1	1		1						1		1.4	.3	Average of all.	1 to 2
11	2	2	2	2	2	2	2	2	3	3	2	1	2	1	1	3	1		2	2	2.2	1.5		2
12	2	2	2	3	2	3	3	2	2	2	3	4	3	1	2	3	2	1	3	4	2.3	2.6		2
13	3	2	3	2	2	3	2	2	3	3	2	2	3	4	3	4	3	3	3	4	2.4	3.1		2 to 3
14			4	3	3	3	4	3	4	4	2	3	3	4	4	4	3	4	3	4	3.5	3.4		3 to 4
15					3	4	3	3		3	3	3	4	4	2	3	4	5	5	5	Average of younger ten.	Average of older ten.	3.6	3 to 4
16											6	4	6	5	3	3	5	5	5	6			4.7	4 to 5
17											6	4	5	7	4	5	5	5	4	7			5.2	5
18													5	8	5	6	6	5	5	8			6.0	6
19													6	6	6		6	7	8				6.5	
20													4		7		7	5						

TABLE 1.

Showing the number of units to each somite. The individual larvae are designated by the letters *B* to *U*; the somites, by the numbers (9 to 20) in the first column.

(2) Are any primary units added in any somite after the first unit in that somite has appeared?

(3) What is the typical number of primary units for each somite?

It will be seen that in somites 9, 10, and 11 there are more units in the younger than in the older larvae. In attempting to account for this fact, two possibilities must be considered; either some of the units degenerate or they migrate caudad, thus shortening the mesonephros. In order to determine which of these alternatives is the true one, a line was drawn (Table 1) separating the ten larvae 17 mm. or less in length (*B-K*) from the ten which were over 17 mm. in length (*L-U*),¹ and the average number of units in each of the six anterior somites on one side of the line (*B-K*) compared with the average of the corresponding somites on the other side (*L-U*). The averages for somites 9, 10, and 11 of the younger ten (0.5, 1.4, 2.2) are *greater* than those of the older ten (0, 0.3, 1.5). The averages of somites 12, 13, and 14, on the contrary, are in general *less* for the younger than for the older ten (2.3, 2.4, 3.5, as compared with 2.6, 3.1, 3.4). The decrease in the number of units in the anterior somites as the larva grows older is thus probably due entirely to a shortening of the mesonephros. The preponderance of the units in the older ten, in somites 12, 13, and 14, over those in the younger ten, does not, however, quite make up for the paucity in somites 9, 10, and 11 of the older ten, and the conclusion is natural that the shortening of the mesonephros has also affected the region of somites 12, 13, and 14, and that on investigation it would be found that there had been a backward movement of units from this region into the somites immediately behind. Pursuing the method employed above, I divided the ten older larvae into two lots. On counting the units in somites 15, 16, and 17 of each lot, I found the sum of the units in the younger five to be sixty-six, that in the older five, seventy-two; that is, there is a preponderance of 0.4 of a unit per somite, for somites 15, 16, and 17 in the *older* five over those in the *younger*. As this preponderance is not large enough to suggest an actual addition of new units in each somite, it is confirmatory proof of a shortening of the mesonephros.

In answering question 1, question 2 has also been answered in the negative, at least for all but the one or two most posterior somites. There remains the question: What is the typical number of units for each somite? The simplest way to determine this would seem to be to find the average for each somite in the twenty larvae. As the arrangement of the units has been much modified in the more anterior

¹ Larva *A* of the diagram is not included in the table.

somites of the older larvae, I think a more significant series of averages is found by using for the six anterior somites only the ten younger larvae (columns *B-K*).

I should not include the average for somite 19 (6.5), as I do not think it trustworthy, from the fact that the mesonephros curves ventrad in that somite and hence is cut more or less frontally, which renders the determination of the number of units difficult. It is this curving which sometimes causes the units to appear as if they extended posterior to the opening of the duct into the cloaca, as in larva *P*. of the diagram.

In discussing the significance of these averages, I will first call attention to the diagram of larva *A*, which shows a single fundament for each somite, from the ninth to the eighteenth at least. It will be remembered that, while in posterior somites these fundaments could not be identified in the continuous blastema formed from the fused mesomers, in anterior somites they remained distinct and became the "blastulae of the first order," between which there soon appeared the smaller "blastulae of the second order." In the anterior four or five somites, usually not more than one of these smaller blastulae appeared between each two of the first order. Caudad, they appeared in increasing numbers. From the last column of the table (p. 57) it seems that the blastula of the second order is generally absent from somite 9, sometimes present in somite 10, and typically present in somites 11-13. In somite 13 a second one is sometimes added, making the total number of blastulae two to three. This process continues, an extra blastula being generally added in every second somite, as represented in the last column of the table (p. 57).

Primary and Secondary Units in Amblystoma and Ichthyophis.

It will be instructive to compare the condition in *Amblystoma* with that found in *Ichthyophis* by Semon ('92). In *Ichthyophis* the tubules of the first set are strictly segmental in position and resemble in structure the primary units in *Amblystoma*. Soon there appears a second set; these are first seen as small intersegmental balls of cells (blastulae), resting on short outgrowths from the duct. Then appear in succession a third, a fourth, and a fifth set, all in line (horizontally) with those of the first set, and *all opening into the duct*. Semon suggests that we have here a hint as to the origin of the dysmetamerism found in the higher Amphibia and in the Amniota, where, he suggests, the multiplication of the fundaments may take place very early. He assumes that in *Ichthyophis* these second units arise by a budding from those of the first

set, for he finds them connected with the Malpighian capsule of the latter by a cord of cells which soon disappears. He further suggests that a similar division of a [theoretical] first set takes place in the higher Amphibia. From my description of the formation of the blastema (see Stage V) it would seem that Semon's surmise as to the origin of the dysmetameric arrangement of the units in the higher Amphibia contains the essence of the truth. A more exact comparison between the process in Ichthyophis and that in Amblystoma seems to me to be as follows: in Ichthyophis that portion of the mesomer of each somite which remains after the detachment of the sclerotome becomes *entirely* converted into a single, segmental, mesonephric blastula. Any later units must therefore be derived *from this first one* by splitting or budding. In Amblystoma, the division into several units per somite takes place so early that the *mesomer itself* is directly differentiated into the full complement of primary blastulae belonging to its somite. Of these primary units, one (that of the "first order") in each somite appears earlier than the rest and is probably homologous with the "primary" units of Ichthyophis. The later primary units (those of the "second order") in Amblystoma, which soon appear between the earlier ones, are probably homologous with the second, third, etc., sets of Ichthyophis.

In Ichthyophis, the development of the second, third, etc., sets of units is followed, after a long period, by the appearance of two *dorsal sets*, whose origin is unknown. There is some evidence that these open into the tubules of the earlier units, but that point was left by Semon unsettled. It seems probable that these "dorsal sets" of units in Ichthyophis are alone strictly homologous with the secondary, tertiary, etc., sets of Amblystoma.

There is little doubt in my mind that the second, third, etc., sets of units in Ichthyophis represent a stage in phylogenetic development between the typical secondary (dorsal) units and the extra primary ones (those of the second order) of Amblystoma. During this evolution, the buds from which they arise have shifted their point of origin from the *dorsal* side of the primary blastula to its anterior (or posterior) side. This fact explains their connection with the duct instead of with the collecting trunks of the primary units. The new mode of opening has the great advantage of making them wholly independent of the primary units, so that they are free to mature as early as the primary. The theory set forth above offers an explanation of the fact that these second, third, etc., sets in Ichthyophis occupy a curious intermediate position between the primary and the true secondary (dorsal) units of Ichthyophis.

and Amblystoma. They resemble the primary in their position and in the fact that they open into the duct; they resemble the true secondary units in the fact that their outer tubules are formed after the unit has become quite complex, and in the fact that they do not form connections with the testis. Semon himself suggests that in Urodela the connecting of *all* of the primary units with the testis is a secondary acquirement.

Relations between Sexual and Secretory Portions of the Mesonephros.

As is well known, the mesonephros in Urodela is divided into a sexual and a secretory portion. The former is connected with the sexual glands by outgrowths from Bowman's capsules, permanently in the male, temporarily in the female. In the male the outer funnels of this portion of the kidney close and disappear. The secretory part, which lies posterior to the sexual gland and does not form connections with it, is characterized by the presence of dorsal sets of units. I will next consider the extent of these two parts in Amblystoma. From Diagram 1 it will be seen that scattered germ-cell masses may extend as far back as somite 19 (larva *G*). In the older larvae (from 23 mm. in length), however, the germ cells become restricted without exception to somites anterior to the sixteenth. Thus the sexual part of the mesonephros cannot extend back of the anterior end of somite 16. The rest of the kidney is to be considered as belonging to the secretory part. It will be noticed that a criterion which is generally used in defining the secretory part, namely, the presence of dorsal units, does not apply to the whole of the part, for those units do not extend farther cephalad than the posterior end of somite 17. Although they *may* be added to somites 17 and 16 at a later date, it seems very improbable that they are, from the fact that the formation and development of those already present progressed from in front backward. The posterior portion of the secretory part is thus distinguished from the anterior portion by an anatomical character, — the presence of dorsal units. Significance is given to this difference in anatomical character by a peculiarity in the development of this region of the mesonephros which, although not conspicuous, is to be considered as of some importance from a phylogenetic standpoint. The peculiarity consists in a *retardation in the appearance and development of the blastulae*. When the blastulae first become distinct, they extend back to the region of somite 16 (see Diagram 1, larvae *C*, *D*, etc.). From that stage to one represented by larva *J*, — a period of rapid development during which the animals have added six millimetres

to their length, — there is no further caudad extension of blastulae, the developmental processes being restricted to a maturation of the units already formed. In larvae about 16 mm. in length, this maturation process has resulted in the conversion of the three or four most anterior blastulae into functional units. As soon as this occurs, the addition of blastulae is resumed and progresses steadily through somites 17, 18, etc., so that in a larva of 24 mm. (*N*) all or nearly all of the primary units have appeared. During this process, this delayed set of primary tubules seems to remain quiescent until all have appeared. This fact explains the *sudden* transition, in the region of the sixteenth or seventeenth somite (larvae *K*, *L*, *M*), from complex units to simple blastulae as one follows the organ caudad.

Since Semper ('75) first suggested it, various authors have seen in the secretory portion of the Amphibian mesonephros a forerunner of the metanephros of the Amniota. Felix ('97) believes that it contains both mesonephric and metanephric elements, and Nussbaum ('97) takes a similar view. It seems to me that the phenomenon just recorded — the *retarded development* of a part of the mesonephros — is important evidence in favor of the view that a portion of the secretory part (that posterior to somite 16) is comparable with the metanephros of higher forms, for one of the chief peculiarities of an excretory system which is divisible into meso- and meta-nephros is a chronological break in its development.

B. RANA.

The earlier processes in the development of the somites in *Rana* are very similar to those in *Amblystoma*. The chief difference lies in the fact that development is more hurried and the cavity of the epicoelom becomes sooner filled by the ingrowth of the muscular tissue developed from the splanchnic wall. The sclerotome seems to arise essentially as in *Amblystoma*, from the splanchnoderm of the ventral wall of the somite. I apply to *Rana* the same conception as to the extent of the mesomer as in the case of *Amblystoma*.

The first figure (Fig. 6, Plate 1) is of a section through the middle of the sixth somite¹ of a larva 3.25 mm. in length, which corresponds to the stage of *Amblystoma* illustrated by Figure 13, Plate 2. Although the three pronephric nephrostomes are open, the Wolffian duct has not yet

¹ In numbering the somites, the three pronephric nephrostomes are considered as opening in the second, third, and fourth somites.

reached the cloaca. About fifteen somites are recognizable. No blood-cells have as yet appeared.

As shown in the figure, splanchnoderm (*spl'drm. l.*) and somatoderm (*so'drm. l.*) are pressed together, so that the arrangement of the cells and the presence of deeper pigmentation alone indicate the line of demarcation. Both layers are seen to be continuous throughout the three regions of the mesoderm, — epimer, mesomer, and lateral plates. Toward the posterior end of each mesomer the coelom is represented by an actual lumen.

Figure 14 (Plate 2) represents a section through the sixth somite of a larva 4.5 mm. in length and corresponding approximately to the stage in *Amblystoma* illustrated by Figure 2. The Wolffian ducts are just opening into the cloaca, and blood-cells are numerous in the ventral and lateral lacunae of the entoderm. Occasionally one is seen to have migrated dorsad into the fundament of the blood-vessels (*va. sng.*). In the figure, the sclerotome is seen as a proliferation of the mesomeric splanchnoderm. In sections posterior to the one figured, it extends to the dorsal angle of the epimer. In the outer angle of the epimer is seen a small lumen, caused by the separation of the somatic and splanchnic layers. Later, this lumen is obliterated, as in *Amblystoma*, by a disintegration of its lateral wall (compare Fig. 4, Plate 1). The mesomer (*ms'mer.*), leaving out of account the sclerotomic portion, is less clearly marked than in *Amblystoma*, but careful study shows that it contains tissue belonging to both somatic and splanchnic layers.

In the larva represented by Figure 4, the obliquity of the somites has increased to such an extent that a section through the centre of one cuts the next anterior one as well. The lower somite in this figure is the ninth, the upper one the tenth. The larva measures seven millimetres and shows a well-developed glomus and ciliated nephrostome.

That Figures 6 and 14 represent sections anterior to the position of the future mesonephros is immaterial, as there is no essential difference *at those stages* between the mesonephric region and that immediately in front of it. However, in the larva now under discussion and in older ones, sections through the mesonephric region and those through the region anterior to it present very different aspects, for, while anteriorly the mesomer remains inconspicuous, in the mesonephric region it becomes more and more massive, as may be seen from Figures 4, 16, and 15, *fnl. ms'nph.* The statement that the *mesomer* becomes massive is not quite accurate. What really happens is that the mesomers of successive somites fuse to form a flattened band of tissue, the *mesonephric blastema*,

in which local swellings appear. The section represented by Figure 4 passes through such a swelling. It will be seen (even more clearly in Figure 16) that, on the one hand, the mesomer is now entirely severed from the sclerotome, and on the other retains only an indefinite connection with the somatic layer of the epimer.

In the particular larva from which Figure 4 is taken there is one swelling in the blastema for each of the somites 8, 9, 10, and 11 (see larva *B*, Diag. 2, p. 65). This would lead one to suppose that each swelling corresponds to one of the original mesomers. Such a supposition, if true in this particular case, cannot be so generally, as there are usually more swellings than somites. On plotting the swellings in thirteen larvae (*A-M*. in Diagram 2) varying from 6.5 mm. to 9.5 mm. in length, it was found that

somite 7 contains an average of 0.08 swellings

8	"	"	1.08	"
9	"	"	1.23	"
10	"	"	1.6	"
11	"	"	1.8	"
12	"	"	0.4	"

In other words, the seventh somite occasionally develops a swelling; somite 8 has generally one, rarely two; somite 9 often has two; somites 10 and 11 have more often two than one, and somite 12 shows an occasional one. As these numbers agree fairly well with the number of primary units in the fully developed mesonephros, the conclusion suggests itself that the swellings are the fundamentals of the blastulae. On that assumption, it is true, there are not enough swellings in the posterior somites, especially somites 11 and 12; but it is clear that in some cases they have not all appeared, and it is also possible that some of the swellings contain the fundamentals of more than one blastula. As development proceeds, their appearance confirms the idea that they are young blastulae. They increase in diameter, and the deeply staining nuclei show a radial arrangement (see Fig. 15, Plate 2). These blastulae are spindle-shaped and more elongated antero-posteriorly than in *Amblystoma*, and are usually, although not always, continuous with each other by their tapering ends. There are thus formed cord-like connections, which are retained in many cases to a late period; these connecting parts may even become massive, and seem to contribute a portion of the tissue from which the secondary units are formed.

It will be recalled that in *Amblystoma* the fundamentals of the "units

DIAGRAM 2.

Mesonephric units of Rana. For explanation of signs see Explanation of Diagram 1 (p. 57). In larvae T and U, primary, secondary, and tertiary units are plotted in separate vertical columns, and the openings of the collecting trunks are indicated by a short horizontal line.

of the first order," one for each somite, appeared in the posterior part of the mesomers before these were cut off from the epimers to form the mesonephric blastema. The question naturally arises as to whether there is in *Rana* any such sign of the primitive metameric arrangement of the mesonephric units. I find no such condition as that described in *Amblystoma*. The only hint at a segmental arrangement is found in a few cases (Diagram 2, larvae *B*, *G*, *K*, *P*), where there is but one "swelling" per somite. As suggested above, some of these swellings may really contain the fundamentals of more than one blastula. This is difficult to believe, however, in such cases as larvae *K* and *P*, for there the swellings are in the shape of distinct blastulae (Figure 15 shows the one in the twelfth somite of larva *K*), and it seems probable that, were any of them going to divide, some signs of the fact would already be observable. It seems possible, then, that such cases show an atavistic condition, and that if a large number of *adults* were examined, cases might be found showing the primitive condition of a strictly segmental arrangement of the *primary* units of the mesonephros.

Development of Primary, and Origin of Secondary, Blastulae.

As development proceeds, the blastulae grow more massive and resemble those of *Amblystoma*, with the exception already mentioned that their anterior and posterior ends are prolonged to form a connecting cord. In later stages, this cord is often clearly interrupted, generally nearer the posterior than the anterior blastula. Even when the cord seems to be continuous, it is possible that there is really only close *contact* between successive blastulae. Figure 102 (Plate 8) shows the relative size of two blastulae and connecting cord in the posterior portion of the mesonephros, — where the blastulae, being more numerous, are naturally more closely approximated than farther forward. This figure was made by superposing drawings of six consecutive frontal sections.¹ One of the sections used in the reconstruction is shown in Figure 18, Plate 2. As the blastula was cut obliquely, only its posterior prolongation shows.

For the sake of clearness and brevity I have illustrated the differentiation in a mesonephric unit by a series of six diagrammatic cross-sections (Figs. 94–100, Plate 8). Figure 94 represents a cross-section at the stage when the blastula has the form of a simple, longitudinally elongated spindle. The next step in the process, represented in Figure 95, is the partial division of the blastula into a smaller dorsal and a larger ventral

¹ This method gives only a silhouette and hence affords no proof of the continuity of the connecting rod.

chamber. In this partial division, the anterior and posterior prolongations become associated exclusively with the dorsal chamber, which thus takes on the form of a longitudinal tube whose ends are, at least generally, in close contact with the similar tubes (that is, upper chambers) of the adjacent units. This condition will be made clear by a glance at Figure 30 (Plate 3), which is a dorso-median view of a reconstruction in wax of four blastulae and the Wolffian duct from the right side of a larva. The two anterior blastulae are approximately at the stage represented in Figure 94, the third in that represented in Figure 95. The ventral chamber is destined to form the *primary mesonephric unit*. The dorsal chamber remains without change for a considerable period and gives rise successively to the *dorsal sets* (secondary, tertiary, etc.)

The primary blastula (lower chamber) enlarges, its median and lateral walls showing a decided difference in thickness. The lateral wall, which is the thicker, buds out an evagination, which abuts on the duct. This stage is represented in Figure 96 (Plate 3), and in the most posterior unit of the wax model (Fig. 30, Plate 3). A section corresponding in position to the dotted line of Figure 30 is shown in Figure 28.

At the next stage (Fig. 97, Plate 3) we recognize that the evagination in Figure 28 is the fundament of the inner tubule. It has grown in length, its free end (*tbl. ms'nph.*) has been crowded upward, and there it becomes attached to the duct. Ventro-median to the fundament of the inner tubule, the wall of the blastula again evaginates and proliferates cells to form a cone extending toward the peritoneum (Fig. 97, *tbl. nph'stm.*). This is, of course, the young outer tubule. At a stage as early as that of Figure 97 the fundaments of all the parts of the complete mesonephric unit can be recognized; the inner tubule, the outer tubule, and the glomerulus (exclusive of the vascular part), the last consisting of the glomerular covering (*cps. Bow. i.*) and Bowman's capsule (*cps. Bow. ex.*). Having determined the positions of the various fundaments in the present stage, we can now identify their positions in the preceding stage (Fig. 28), if we bear in mind that between these two stages the unit has rotated some forty degrees about its longitudinal axis (compare Figs. 96 and 97). In Figure 28 the fundament of the outer tubule (*tbl. nph'stm.*) composes the ventral wall of the blastula median to the evagination which forms the inner tubule (*tbl. ms'nph.*). The fundament of Bowman's capsule is contained in the tissue of the thin median wall (*cps. Bow. ex.*), and the glomerular covering is derived from the dorso-lateral portion of the thick lateral wall (*cps. Bow. i.*).

The succeeding diagrammatic figures (98, 99, and 100) scarcely need explanation. The only differences between the condition shown in Figure 99 and that seen in actual sections are: (1) the outer tubule is not encountered in the same section as the inner tubule, because it enters the Malpighian neck from a slightly anterior direction; and (2) the fundament of the dorsal sets of tubules (*fund. ms'nph. 2*) is also displaced, being generally posterior, though sometimes anterior, to the rest of the unit, and hence is not seen in a section through the centre of the blastula. Although on account of this displacement the relationship between the dorsal fundament and its parent cannot be shown in a single section in the case of the primary unit, it can be shown in the case of the secondary, where often there is no displacement. Thus Figure 29 (Plate 3) shows the secondary blastula and the fundament of the more dorsal sets (*fund. ms'nph. 3*), connected by an attenuated cord. A corresponding stage of the primary unit is represented in Figure 100.

To recapitulate briefly, the fundament of the dorsal sets of units is developed from a "dorsal chamber" constricted off from the primary blastula. This dorsal chamber, at first tubular, becomes a typical blastula, probably by a shrinking or shortening of the tube to form a spherical mass. With the growth of the mesonephric mass, the dorsal fundament is forced farther from the parent one and is finally severed from it. For some time, however, the two remain connected by a cord of cells, which indicates clearly the point of origin of the dorsal fundament, — the dorso-median region of Bowman's capsule.

In comparing the history of the fundaments of the dorsal sets of tubules in *Rana* with that in *Amblystoma*, we see that the only essential difference is that in *Rana* each fundament remains connected for a considerable period with the primary unit from which it took its origin, instead of being entirely cut off from it at an early period, as in *Amblystoma*.¹

The development of the tertiary from the secondary, the quaternary from the tertiary, etc., shows the same difference in the two animals.

In the later development of the dorsal units, the opening of each into the inner tubule of the next ventral (parent) one, is established in a manner similar to that traced in *Amblystoma*, and as far as could be determined, there is one secondary for each primary (throughout the

¹ The secondary units in the earliest stages seen by Semon ('92) in *Ichthyophis* consisted of spherical masses connected with Bowman's capsule by a cord of cells. From this he suggests that probably they had recently budded out from the Malpighian body.

range of the secondary), one tertiary for each secondary, etc. The development of additional dorsal units is continued to a surprisingly late period. Thus I found young, non-functioning units in a large, adult female of *Rana virescens*.

Outer Tubules and Nephrostomes.

As is well known, the outer tubules in Anura, after reaching the peritoneum, become cut off from the rest of the unit and open into venous spaces (see Fig. 100). This fact I confirmed in *Rana sylvatica*, *Rana virescens*, and *Hyla versicolor* in sections of the larvae, where the cilia at the inner end of the tubule can be very plainly seen extending into venous spaces. In *R. virescens* I also confirmed it in the adult by means of the method—first used by Nussbaum ('80), I believe—of injecting powdered carmine into the body cavity of the living animal, then fixing and sectioning.

It seems still undecided whether, in Anura, the outer tubule affords at any stage an actual communication between the coelom and the neck of the Malpighian body. At the time when it is still joined to this neck and to the peritoneum it possesses a lumen throughout a part of its length, but more I cannot affirm. Whether the lumen is continuous with the coelom and with the cavity of the Malpighian neck, I found it impossible to determine, as cross-sections of the animal cut it at an unfavorable angle. After all, the continuity or discontinuity of the lumen is a matter of small theoretical importance, as it is perfectly clear that the outer tubule arises exactly as in the Urodela, and that the adult peculiarity is ontogenetically acquired. A matter of more importance is the origin of the large number of nephrostomes which appear as the animal matures. Are they (1) the openings of outer tubules which grow down independently and become cut off from the dorsal sets of units; are they (2) evaginations of the peritoneum; or are they (3) developed from the original outer tubules by division? The second and third suppositions seem both to be true. The outer tubules (in an old larva of *R. virescens*) have every appearance of dividing, and occasionally there are also to be seen short, deeply staining, peritoneal evaginations at a considerable distance from any older ones. It is of course possible that these arise from cells derived from dorsal units, but I have looked in vain for cell-strands growing out from those units toward the peritoneum.

Order of Appearance and Number of Primary Units.

It is usually stated that in Anura the posterior mesonephric units are the first to appear, the more anterior ones following in order. This is not strictly true for *R. sylvatica*. As will be seen from Diagram 2 (*A-T*), from four to nine primary fundaments, in the shape of swellings in the blastema, appear *simultaneously*. Of these the more posterior *develop* most rapidly, so that in passing cephalad one finds the blastulae less and less mature.

In none of the larvae nineteen millimetres or less in length whose mesonephric units are plotted in Diagram 2 (*A-T*) are there more than nine primary units. In larva *T* there are twelve collecting trunks opening into the duct; in larva *U* there are eleven, and in one individual (32 mm. long), not represented in the diagram, there are *fifteen*. There are two possible explanations of the preponderance in the number of these collecting trunks over that of primary units in the younger specimens. Either new primary units have been added, or some belonging to the secondary set have sent their tubules directly to the Wolffian duct instead of to the collecting trunks of the primary units. That the number of tubules opening into the duct in larva *T* exceeds by three the number of units plotted as primary ones, seems to favor the latter view, but it must be borne in mind that the units were plotted as belonging to the primary or secondary set solely from the position of the Malpighian body, and that this may easily have been displaced by crowding. Whether or not secondary units have simulated primary ones by sending their tubules directly to the duct, there is no doubt that true primary units are added to the original series, for in both larvae *T* and *U*, young, deeply staining ones are seen at both the posterior and anterior ends of the kidney. Even in the older larva (32 mm. long) mentioned above, immature primary tubules are seen at the posterior end of the series. In this larva the most anterior tubule on either side of the body, although it is clearly functional, is not accompanied by any sign of a fundament of dorsal sets. From this it seems probable that at least one tubule may remain simple throughout life.

Diagram 2 (p. 65) shows that there is some shortening of the mesonephros. Much more striking is the shortening of the germ-cell mass (principally the posterior portion), which either shrinks by a rearrangement of cells or undergoes degeneration. The same phenomenon was noted in *Amblystoma*.

C. COMPARISON OF THE MESONEPHRIC FUNDAMENTS OF AMBLYSTOMA AND ICHTHYOPHIS.

As the most important of my conclusions relates to the derivation of the mesonephric fundamentals, I have endeavored to make clear, by Figures *E-H* (p. 72), the similarity between the mode of formation of the fundamentals in Ichthyophis and Amblystoma. The comparison of the two forms has importance not only from the fact that Ichthyophis is a primitive Amphibian, but mainly from the fact that it is comparatively easy to homologize the processes in the formation of the mesonephric fundamentals in that animal with those in elasmobranchs, a group which has (in my opinion) a very primitive or generalized mesonephros.

Figures *E* and *F* are based on Semon's ('92) Figures 9 and 10, the interpretation of the extent of the various portions of the mesodermic layers being, however, entirely my own. According to Semon's description, the development of a mesonephric fundament is briefly as follows. In the earliest stage shown by him the cavity of the somite is already separated from the body cavity by the fusion of somatoderm and splanchnoderm (see Fig. *E*). The cavity of the somite then becomes divided into a larger upper and a smaller lower chamber by the development of a cross-partition (Fig. *F*), which thus forms the ventral wall of the upper chamber and the dorsal wall of the lower. The partition then splits into two layers, of which the dorsal becomes a part of the now solid epimer (the lumen having become filled by proliferation from the median wall), and the ventral furnishes a part of the wall of the lower chamber. This chamber is the mesonephric blastula. Its region of contact (Fig. *F*, *nph'stm.*) with the lateral mesoderm becomes broader; then by the ingrowth of connective tissue the contact is interrupted except at two points, a lateral (Semon's "Contact *a*") and a median ("Contact *b*") region.¹ The lateral region is destined to form the outer tubule and nephrostome; the inner the sexual cord.

The direction and character of the shading will make clear what portions I consider homologous in Figures *E*, *F*, *G*, and *H*.

Figure *G* is based on the stage of Amblystoma represented by Figure 13 (Plate 2), Figure *H* on that represented by Figure 7 (Plate 1).

During the process which in Ichthyophis (Fig. *F*) separates the mesomer ("lower chamber") from the epimer and converts it into a mesonephric blastula, its cavity remains as an actual lumen. In

¹ For the sake of simplicity this later differentiation has been omitted in Figure *F*.

FIGURES E-H.

Four diagrammatic figures illustrating the similarity in origin of the fundus of a mesonephric blastula in *Ichthyophis* (E and F) and *Amblystoma* (G and H). The splanchnoderm of both epimer and lateral mesoderm is shaded with horizontal lines, that of the mesomer (exclusive of the sclerotome, which is indicated by double horizontal lines) with horizontal dashes. The somatoderm of both epimer and lateral mesoderm is shaded with oblique lines, that of the mesomer with oblique dots and dashes.

Amblystoma, on the contrary, the somatic and splanchnic layers of the mesomer are closely applied to each other during its severance from the epimer, and the lumen becomes apparent only in the well-formed blastula. I have consequently anticipated the conditions somewhat in giving the mesomer a lumen in Figure *H*. Aside from this the only important difference in the processes in the two animals is the formation of the nephrostome in Amblystoma by a secondary fusion of the outer tubule with the peritoneum. It seems probable, it is true, that some of the anterior nephrostomes in Amblystoma are formed as in Ichthyophis, from a persistent connection with the coelom, but posteriorly (and throughout the entire mesonephros in Rana) the connection is certainly a secondary one.

Although, as just stated, the final connection between mesomer and lateral plates (by means of the outer tubule) is a secondary one in Amblystoma and Rana, it seems probable that the two layers of the mesomer retain their relative positions and give rise to the same portions of the mesonephric unit as in Ichthyophis and elasmobranchs. What I believe these portions to be will be found illustrated in Figures 94-100, where the shading of the supposed somatoderm is made with continuous lines, that of the splanchnoderm with interrupted lines.

D. RECAPITULATION OF THE MESONEPHRIC DEVELOPMENT.

Amblystoma.

1. The mesonephric blastula is derived from a portion of the somite which is homologous with the mesomer of elasmobranchs, and it contains both splanchnoderm and somatoderm.

2. Contrary to the condition in elasmobranchs and Ichthyophis, the lumen of the mesomer at the time it is cut off from the epimer is only *potential*; it first appears as the cavity of the mesonephric blastula.

3. The more anterior blastulae probably never lose their connection with the two layers of the lateral mesoderm. The outer tubules (at least in the anterior primary units) therefore contain both somatoderm and splanchnoderm. In this connection it was noted that the morphologically dorsal angle of the body cavity is not at the upper limit of the mesentery, but lies just mesad to the Wolffian duct. Hence the germ cells (except in very early stages) all lie in the splanchnoderm.

4. The secondary character of the dysmetamerism of the urodele mesonephros shows itself in the fact that the primary blastulae can

be divided into two sets, in one of which the elements (those of the "first order") are metamerically arranged. It is suggested that the units of the "second order" represent the final product of a phylogenetic evolution in which a number of secondary units have been transformed into apparently primary ones. Their similarity to the true primary units (those of the first order) is due to the fact that they now arise almost simultaneously with these, and hence are developed under identical conditions. It is further suggested that the units of the second, third, etc., sets in *Ichthyophis* probably represent a stage in the evolutionary process intermediate between typical dorsal units and the extra primary ones (those of the second order) of *Urodela*, in that they connect with the duct, rather than with the tubules of the primary units, but have not as yet formed connections with the gonads.

5. One of the results of the early appearance of the extra primary units (those of the second order) in *Urodela* is that, instead of the entire mesomer of each somite being converted, as in *Ichthyophis*, into a single mesonephric blastula which gives rise to later generations by budding, the mesomer itself gives rise directly to more than one unit.

6. The appearance of the fundament of the dorsal sets of units takes place much earlier than has been hitherto supposed. They arise by a splitting or budding process from the primary blastulae shortly after the latter are formed, and while they are still small and simple. The tertiary sets arise in a similar manner from the secondary, the quaternary from the tertiary, etc.

7. At the period of the animal's metamorphosis only primary and secondary units have produced outer tubules, and in all probability the outer tubules are confined to these two sets of units throughout life.

8. By plotting the positions of the units at various ages it is learned that after the primary units are clearly differentiated in a somite no more are added, the apparent increase in number in certain somites being due to a concentration of the whole organ. There seems to be no degeneration of units in the ages examined.

9. The plotted diagram (p. 56) also brings out the fact that the appearance and development of units, caudad, is not uniform, there being a delay between their completion in the sexual and an anterior part of the secretory portion and their beginning in the remainder of the secretory portion. This fact is considered as important additional evidence in favor of the view, first suggested by Semper in 1875, that the secretory portion of the mesonephros in some of the *Anamnia* is the morphological representative of the amniote metanephros.

10. The extent of the germ-cell mass, caudad, becomes less as the animal grows older. This is due to a total disappearance of the germ cells, as such, they being transformed in all probability into ordinary peritoneal cells. A similar transformation is suggested to account for their disappearance from the somatoderm in the sexual portion of the mesonephros.

Rana.

1. As in *Amblystoma*, the mesomer contains tissue from both somatoderm and splanchnoderm. In the region of the mesonephros, the mesomers detach themselves from the rest of the somite and fuse to form a continuous mesonephric blastema, in which swellings are seen. These are the mesonephric blastulae, — the fundamentals of the mesonephric units. In a few cases they were found to correspond in number to the mesomers from which the blastema was derived (that is, are metameric in arrangement), but usually there is more than one to each somite. The distinction into swellings of the "first order" and those of the "second order," as observed in *Amblystoma*, cannot be made in *Rana*. The blastulae differ from those of *Amblystoma* in that they are (or seem to be) usually joined to each other by their tapering ends.

2. The dorsal sets of units develop from a fundament derived from the blastula of the primary unit, essentially as in *Amblystoma*. This fundament, however, instead of being early cut off from the primary blastula, retains its connection. When the development of the primary blastula is completed, this connection is found to be with its Bowman's capsule. As in *Amblystoma*, there seems to be one secondary unit for each primary, one tertiary for each secondary, etc. The number of dorsal units communicating with the collecting trunk of each primary decreases cephalad at such a rate that the most anterior primary may not possess even a secondary unit. There is not, however, as in *Urodela*, an extended region in which primary units are alone present.

3. The most striking peculiarity in the development of a mesonephric unit in *Anura* is found in the behavior of the outer tubule, — a peculiarity already observed by several authors. Each of the earlier outer tubules arising from the primary units grows out from the blastula in the manner described for *Amblystoma*. Shortly after its distal end reaches and coalesces with the peritoneum, its proximal end severs its connection with the rest of the unit and opens into a vein. Later in life many additional outer tubules appear. In *structure*, these are similar to the first ones, but their *origin* is quite different, and difficult to determine.

They seem to arise either (1) from a splitting of the first set, or (2) from independent evaginations of the peritoneum, or from both.

4. In regard to the *order of appearance* of the primary units, the usual statement that it progresses from behind forward, is incorrect (at least for *Rana sylvatica*). The majority of the primary units, those occupying all except the extreme ends of the kidney, *appear* simultaneously, but they *develop* from *behind forward*. Later, a few are added at both posterior and anterior ends of the series.

5. As in *Amblystoma*, the antero-posterior extent of the germ cells becomes much reduced as development proceeds.

III. Development of the Müllerian Duct.

The point of greatest phylogenetic interest in the development of the Müllerian duct, its relation to the Wolffian duct, is still in dispute. There seems no doubt that in elasmobranchs the greater part of it is derived from the Wolffian duct, and a similar origin has been claimed by the latest investigators for a portion of it in birds and mammals. In regard to the Amphibia, statements have been very contradictory, the Müllerian duct being described sometimes as developing independently of, sometimes in connection with, the Wolffian duct. Consequently my attention has been especially directed to this point.

Another problem, the solution of which may help in deciphering the phylogenetic history of the Müllerian duct, is the mode of formation of the *ostium abdominale*. In elasmobranchs, the ostium is said to be formed by a fusion of several of the pronephric nephrostomes. In birds and mammals, on the contrary, it would seem that it is formed by the coalescence of several evaginations of the coelomic epithelium, independently of the nephrostomes. In the Amphibia it has not been claimed, to my knowledge, that more than one coelomic evagination precedes the formation of the ostium. I, therefore, have given this question special attention in my investigations, in order, if possible, to throw some light on the suggested homology between the ostial evaginations of the higher vertebrates and the nephrostomes of the elasmobranch pronephros.

A. AMBLYSTOMA.

The Müllerian ducts of adult *Amblystoma* are rather simple structures, consisting of a pair of tubes, each having a single ostium abdominale opening into the body cavity, and a posterior outlet opening into

the cloaca. The development of the Müllerian duct shows that the organ was originally more complex, for a portion of its fundment degenerates completely. In accordance with this fact, it is not surprising that the earlier stages are quite variable. This variability has made it seem best to describe individual larvae, — a rather cumbersome way, but one which obviates the necessity of constantly mentioning exceptions. To a certain extent, the larvae successively described represent successive stages; that is, they are so arranged that each one shows, *on the whole*, an advance in oviducal development over the preceding one, although in some particulars it may be less advanced.

Larva I, 23 mm.

In order to understand the early development of the Müllerian duct, it is necessary to follow the successive changes in the body cavity.

In a larva in which no sign of the duct is yet present, a cross-section cutting the anterior portion of the pronephros shows no body cavity, the entire region being filled with loose mesenchymatous tissue. A section a little farther back, passing through the first nephrostome (Fig. 31, Plate 3), shows three divisions of the body cavity on each side of the body: (1) A ventral division (*coel. v.*) at the side of the pericardium (*pi'cr.*); (2) a dorsal division, the glomerular cavity (*cav. glm.*), into which the nephrostomes open and the glomus protrudes; and (3) a cavity between these two, which I shall call the sub-glomerular cavity (*cav. sb'glm.*). At the stage represented by the larva under consideration, the sub-glomerular cavity is recognizable for only two or three sections. It is really but a shallow anterior outpocketing of the glomerular cavity, or, from another point of view, it may be said that there is a narrow shelf of tissue (*tab.*) which juts out from the anterior wall of the glomerular cavity, extending from the alimentary tract on the median side to a region just ventral to the pronephros on the lateral side. For convenience, I shall refer to this tissue simply as the "*shelf*." Following the sections caudad, one finds that the glomerular and sub-glomerular cavities soon become confluent. The single cavity thus formed remains distinct from the ventral body cavity as far back as a point posterior to the pronephros. Figure 37 (Plate 3) taken from a section passing through the posterior part of the glomus on one side of the body (the right, in the figure left) and through the second nephrostome on the other, shows the dorsal (*coel. d.*) and ventral portions of the body cavity (*coel. v.*) separated by tissue joining the lung to the body wall (*pn. + par.*).

Larva II, 24 mm.

The condition of the body cavity in this larva is essentially as in Larva I, with the exception that the "shelf" has become more pronounced, now separating the glomerular cavity (Fig. 32, Plate 3, *cav. glm.*) from the sub-glomerular cavity (*cav. sb'glm.*) as far back as half-way between the two nephrostomes, instead of for a distance of only two or three sections.

In Larva I the epithelium of the nephrostomes was thickened.¹ In Larva II the thickening of the lower lip of the anterior nephrostome is continued as a band ventrad over the face of the pronephros on to the shelf, where it turns caudad. This is shown in Figure 32 (*tae. e'th. a*), which is from a section passing immediately posterior to the first nephrostome, whose cilia (omitted by the lithographer) occur in the dorso-lateral angle of the glomerular cavity. When this band reaches the posterior limit of the shelf it passes below it for a very short distance on the lateral wall of the body cavity, turning slightly forward (Fig. 33, *tae. e'th. γ'*). It is as if the band had at first grown directly ventrad from the first nephrostome and had then been pushed backward by the caudad growth of the shelf (compare Fig. I, p. 88).

Larva III, 21.5 mm.

There is in this larva a slight but important advance over Larva II. The thickening of the ventral lip of the first nephrostome is distinctly accentuated to form a small thick disk (Fig. 36, *evg. 1*). From this the band runs ventrad, inclining somewhat caudad, then caudad until free of the shelf, then cephalad, precisely as in larva II. A slight thickening below the ventral lip of the second nephrostome is observable on one side of the body.

Larva IV, 44 mm.

This larva shows the beginning of a process which seems to be preparatory to the degeneration of the pronephros; that is, a compression of the pronephros and glomerular cavity in a dorso-ventral direction (Figs. 38, 39, Plate 4). The glomus is also affected, becoming more and more attenuated. In Larva III it was confined to the space between the two nephrostomes, while in this larva it extends anterior to the first and posterior to the second. With the compression of the

¹ The term "thickening" is somewhat of a misnomer. The most conspicuous feature is often not so much a thickening of the epithelium as a crowding together of the nuclei, which stain more darkly than those of the surrounding tissue.

glomerular cavity, that portion of it which lies at the mouth of the first nephrostome becomes partially cut off to form what I shall call the "*nephrostomal cavity*" (Fig. 39, *cav. neph'stm.*). Whether this small cavity has any ontogenetic or phylogenetic significance, I do not know. It becomes more and more completely cut off in later stages, only to disappear entirely at a still later stage. The first nephrostome opens into the nephrostomal cavity four sections anterior to the point marked *cav. neph'stm.* in Figure 39. In the ventro-lateral angle of the nephrostomal cavity may be seen the thickened band already described for previous stages. It runs caudad and, just behind the point where the nephrostomal and glomerular cavities become confluent, passes out on to the shelf (Fig. 38, *tae. e'th. a*). Here it is joined by a similar band from the second nephrostome (*tae. e'th. β*). The section figured cuts this band just anterior to the point where it passes out to join the anterior band. The shelf extends much farther back than formerly (16 sections posterior to the 2nd. nephrostome). The thickened band runs downward around its posterior edge and then forward along its ventral surface, — that is, along the dorsal wall of the sub-glomerular cavity. The extent and position of the band are represented in Figure J, p. 88.

In another larva, otherwise like the one last described, there is a slight accentuation of the thickening of the lower lip of the *second nephrostome*, similar to, but smaller than that of the next stage, which is shown in Figure 40 (Plate 4). In neither of the larvae just described, however, has the thickened disk of the first nephrostome appeared, although it was present in Larva III.

Larva V, 41 mm.

In this larva the local thickenings near the first and second nephrostomes have both become quite pronounced (Fig. 41, *evg. 1*, and Fig. 40, *evg. 2*). The anterior one (Fig. 41) is not directly ventral to the first nephrostome, but lies behind it, for the nephrostome opens into the dorso-lateral angle of the nephrostomal cavity (*cav. neph'stm.*) eight sections anterior to the one figured. The nephrostomal cavity extends farther caudad than in previous larvae and its anterior end has become so narrow that it forms a postero-ventral continuation of the nephrostome, so that it is difficult to discern where the one ends and the other begins. At *tae. e'th. a* (Fig. 40) the band from the first nephrostome is shown.

Larva VI A, 40 mm.

The nephrostomal cavity is now still more completely cut off from the glomerular cavity than in Larva V. Figure 42 shows the section in which it becomes confluent with the glomerular cavity. The thickened disk which was seen in its ventro-lateral angle in the preceding larva (Fig. 41, *evg. 1*) is now seen to have evaginated to form a thick-walled pit (*evg. 1*, Fig. 42). In the evagination figured (from the right side of the body) there is a tendency toward a spiral coiling, a common but not universal feature in these anterior evaginations. The open lumen does not extend very far into the cell-mass, but the direction of its continuation is indicated by the arrangement of the nuclei. At the deep end of the spiral arises a duct (Fig. 43, *dt. 1*), which runs caudad for some sections, dwindles to a cord, and disappears (Fig. *K*, *dt. 1*). At the point of origin of "duct 1" a cord starts *cephalad* and continues for several sections. For the sake of convenience I shall call this the *pre-coelomic duct* (*dt. pr'coel.*, Fig. *K*). Its position at a later stage is shown in Figure 48, *dt. pr'coel.*

On the left side of the body, the first evagination is similar to that on the right side, with the exception that it arises more dorsally, from the middle of the lateral wall of the nephrostomal cavity (in a position corresponding to that of the thickening shown in Figure 41), and is a deep, *straight* pit with a wide lumen, much like the one shown in Figure 49.

From the mouth of the evagination the thickened band runs back (Fig. 43, *tae. e'th. a*) and out on the shelf, just as in previous stages, there to be joined by the band from the second or posterior nephrostome. The local thickening of the band from the second nephrostome is very conspicuous, but has not as yet evaginated. Figure *K* (p. 88) represents diagrammatically the condition of the evagination, etc., at this stage.

Larva VI B, 42 mm.

The anterior evagination on one side of this larva is similar to those in Larva VI A. On the other side it is very small, whether just arising or already degenerating, it is impossible to decide. An important advance over the preceding larva has been gained in that the thickened disk ventral to the *second nephrostome* has also evaginated both on the right and on the left sides of the body. These posterior evaginations, which, as will appear later, are the permanent ones, are not so deep as the anterior ones. Figure 44, *evg. 2*, shows that of the left side of the body and is drawn to the same scale of magnification as the anterior evagination

(*evg. 1*, Fig. 42). It is a simple outpocketing, which is continued caudad, first as a duct, then as a cord which soon dwindles and disappears. Figure 53 shows this cord (*dt. 2*), more highly magnified, eight sections behind the evagination shown in Figure 44, and three sections anterior to its distal end. As the figure shows, it is entirely free from the Wolffian duct (*dt. Wf.*).

Along the course of this posterior duct the peritoneal epithelium is slightly thickened (Fig. 53, *crs. o'dt.*). Posterior to the distal¹ end of the cord, this thickening accompanies the Wolffian duct mediad and then caudad, and is continued as that enigmatical welt which lies near the Wolffian duct throughout its entire length and has been called the "Tubenleiste" by German authors (see Fig. 54, Plate 5, *crs. o'dt.*). Its appearance always precedes the formation of the Müllerian duct, and Wilson ('94), Semon ('92), and others have seen in it the fundament of that structure. I cannot find that it has anything to do with the development of the essential part of the Müllerian duct, — the epithelial lining. It often seems, however, at least in the anterior region of the body, to be proliferating cells to form the outer layers of the duct. The "Tubenleiste," or oviducal welt, as I have termed it, later disappears entirely.

Larva VII, 35 mm.

The pronephros of this larva shows undoubted signs of degeneration. The first and second nephrostomes have drawn quite near to each other, a very common condition during degeneration. Both pairs of nephrostomes have migrated slightly caudad: the first on one side, and the second on the other have become closed, and remain connected with the peritoneum merely by cords. With the closure of the first nephrostome, the associated nephrostomal cavity is obliterated.² This obliteration of the nephrostomal cavity does not affect the anterior evagination, however, as it has already moved out of the cavity by a migration caudad. (Compare Fig. *L*, p. 88.)

The conditions of the evaginations on the two sides of the body are as follows: On the right side the first nephrostome and nephrostomal cavity are still present. The anterior evagination is behind them; it is still

¹ I use the term "distal" to designate the portion *farthest from the origin*.

² It would seem that the obliteration of the nephrostomal cavity takes place not by a flattening out of its walls to merge with the general epithelium of the glomerular cavity, but rather by the closure of its mouth, followed by an actual dissolution of the walls, similar to that which takes place in the nephrostomal canals and pronephric tubules. If this is true, it forms a suggestive parallel to the process in *Rana* (see page 90).

massive and sends a cord cephalad (the pre-coelomic duct) a distance of some fourteen sections.¹ Just anterior to the evagination, this cord shows, by the perfectly radial arrangement of its nuclei, that it is really a potential duct. In passing forward this radial arrangement is soon lost, but the cord remains very conspicuous and runs directly cephalad, deeply buried in the pronephros. Figure 48 (Plate 4, *dt. pr'coel.*) shows a cross-section of the cord five sections posterior to its cephalic end. The arrangement of cells in the form of loose concentric layers is very characteristic of this pre-coelomic duct, as well as of the *posterior* duct of the anterior evagination and, to a less degree, of the duct from the second or posterior evagination.

The posterior duct of the anterior evagination extends back only a few sections. I am convinced that this is not due to its never having been formed, but to its early degeneration, for the duct from the second evagination is in many places accompanied by a second duct, and finally sends off a free cord, which runs parallel with it for some distance and then ends. It would seem, then, that the duct from the first evagination had reached back to, and fused more or less completely with, the duct from the second evagination, and that it had then almost wholly degenerated between the two evaginations. I lay special stress on the condition on this side of the body, because I think it explains a puzzling condition on the opposite side.

The first (anterior) evagination on the *left* side sends back a cord which reaches the level of the second evagination and is there lost sight of (compare Fig. *L*, p. 88). The second evagination sends back its cord for about a somite and a half. Then for a distance there is *no sign* of one, until suddenly it *reappears* again for a short distance. This condition made me think, at first, that Wilson and others were right in believing a part of the duct to be formed *in situ* from the cells of the oviducal welt. I am convinced, however, from the condition on the right side described above, that this isolated piece is simply a fragment of the cord from the *first* evagination which has escaped degeneration. This belief is supported by the fact that similar isolated fragments of the first duct may remain, even in much later stages, between the two evaginations, where there can be no doubt as to their origin (see *dt. 1*, Fig. 52, Plate 4; and, for description, p. 87).

To sum up the condition of the fundement of the Müllerian duct at this stage: The thickened disks ventral to the first and second nephrostomes have evaginated to form open pits, which have begun to migrate

¹ On the left side of the body it extends cephalad for 19 sections.

caudad, especially the posterior one. From the anterior one a thickened epithelial band runs caudad, then ventrad around the free end of the shelf (which now extends some distance back of the pronephros), and then forward on its ventral surface. Both on the ventral and on the dorsal side of the shelf the band shows a tendency to slip off, as it were, on to the lateral body-wall, so that in its backward course it now passes close to the second evagination, thus reducing the length of the band which connects it with the second evagination.

From both first and second evaginations ducts (or cords) run caudad. That from the first fuses more or less completely with that from the second, and shows a tendency to degenerate between the two evaginations. There is an additional cord extending *cephalad* from the first evagination, which has no known ontogenetic meaning, but *may* have an important phylogenetic significance. As this cord (which is sometimes met with in later stages) completely degenerates without participating in the formation of the Müllerian duct, I shall leave it out of the description of subsequent stages. Finally, the sub-glomerular cavity has begun to extend itself cephalad beyond the glomerular cavity.

Larva VIII, 55 mm.

In this and later stages the distortion suffered by the degenerating pronephros gives rise to much variation in the relative position of its parts. Sometimes, as in the present larva, the glomus, narrowly confined in its cavity, lies wholly anterior to the tubule-mass of the pronephros. It may, however, lie opposite, or almost wholly behind the pronephros. Some or all of the nephrostomes may remain open until a much later period. Generally, however, the anterior ones at least are closed, and may even be wholly severed from the peritoneal epithelium. A like variation is found in their position. In general there is a tendency toward a caudal migration. In one case the first nephrostomal tubule on one side of the body had in its migration passed the second nephrostome and ended posterior to it near the peritoneum. The nephrostomal cavities are usually absent.

The condition of the evaginations in this larva differs from that in Larva VII, only in that they have all migrated caudad (Fig. *M*, p. 88). An important result of this migration is that it has brought the posterior evagination into a position posterior to the free edge of the shelf.

With the dorso-ventral compression of the pronephros (probably due to the growth of the stomach), the anterior evagination no longer lies at

a lower level than the nephrostomes. Instead it lies at the same level, or even more dorsally than they. As in the preceding larva, the duct from the anterior evagination disappears in that part of its course which is anterior to the second evagination, but the duct from the latter is in places double, showing that it has been formed by a fusion of the two ducts. The posterior duct on both sides of the body becomes curiously attenuated a short distance behind its origin, so that it is reduced in cross-section to two or three cells, but is always clearly marked off from the surrounding tissue by its sheath.¹ Farther back it again becomes a well-defined tube, which extends for some distance alongside the Wolffian duct. Figure *M*, page 88, illustrates this and the next stage.

Larva IX, 50 mm. — Gills reduced to stumps.

This larva is interesting from the fact that, although older than any of the preceding, the duct from the anterior evagination (both right and left) has not suffered any degeneration. It (*dt. 1*, Fig. 51, Plate 4) passes the second evagination and, after running parallel to the duct from the second evagination for some distance, approaches and fuses with it. The beginning of this fusion is shown in Figure 50 (*dt. 1, dt. 2*). The single duct thus formed continues caudad for some distance along the Wolffian duct. On one side of the body it ends independent of the Wolffian duct and enclosed in its own sheath. On the other side it approaches the Wolffian duct until the two are enclosed in a common sheath and then, applying itself to the Wolffian duct, disappears apparently by fusing with it. Figure 51 shows the thickened band (*tae. e'th. α*), which passes back from the first evagination, around the posterior edge of the shelf (*marg. p. tab.*) and forward again in the sub-glomerular cavity (*tae. e'th. γ'*).² Two sections behind the one figured, the shelf separates along the line *marg. p. tab.* from the lateral body-wall. Where this occurs, the two portions of the thickenings *tae. e'th. α* and *tae. e'th. γ'* are seen to be continuous. In the same section the ridge containing the Wolffian duct and fundaments of the Müllerian duct becomes well separated from the lateral body-wall (as in Figure 50) by an infolding, whose position is indicated in Figure 51 by the groove *sul.*

¹ In poorly preserved specimens this attenuated part of the duct might easily be overlooked. This condition may account for the conception of some authors that the duct is not developed continuously with the ostium.

² By comparing Figure *J* with *M* it will be understood that the only part of the epithelial band now remaining on the upper side of the shelf is that designated by *α*, *γ* having merged with *γ'* by being brought beneath the shelf.

Larva X, 53 mm. — Gills reduced to stumps.

On the right side of this larva the anterior evagination has almost totally disappeared, as well as that part of its duct which was anterior to the second evagination (Fig. *N*, p. 88). The duct from the second evagination divides, however, almost immediately into an open tube and an irregular cord. These soon reunite to form one large duct with two lumina, which finally merge into a single lumen. The condition of the distal (caudal) end of this duct I shall describe presently. On the left side of the body both evaginations are still present with their ducts, which at first are widely separated, then approach and have a common sheath. They do not unite completely until they reach the region of the *fiftieth* section back of the second evagination. The resultant duct fuses with the Wolffian duct. The second evagination is so far back that it lies in the ridge whose formation was traced in Larva IX. This causes the thickened band and the duct from the second evagination to form an almost straight line, as shown in Figure *N*.

The distal end of the Müllerian duct on the right side of the body presents as strong evidence as any I possess, that a portion of the Müllerian duct may fuse intimately with, and possibly take cells from, the Wolffian duct. As the question of the participation of the Wolffian duct in the formation of the Müllerian duct has been so much discussed and is of such great theoretical interest, it seemed best to make drawings of a number of *consecutive sections* and thus give the reader a better opportunity to judge for himself as to the evidence.

As was previously stated, the single duct, formed by the fusion of those from the two evaginations, runs for a certain distance close to the Wolffian duct, but enclosed in its own sheath; that is, a layer of connective tissue separates it from the Wolffian duct. Back of this the duct approaches the Wolffian duct and this connective-tissue layer is interrupted, thus allowing the Müllerian duct to apply itself to the Wolffian. Figures 54 to 63 (Plate 5) show ten consecutive sections immediately posterior to the point where this juxtaposition takes place.

In Figure 54 is seen a mass of tissue extending from the Müllerian duct (which a few sections farther forward is quite free and in cross-section regularly rounded) to apply itself to the Wolffian duct. The two following sections (Figs. 55 and 56) show the Wolffian duct distorted in such a way that its median wall is continuous with this mass of cells. In Figure 57 the mass is quite distinct from both ducts, and the Wolffian duct has regained, to a large extent, its typical shape. In Figures 58

and 59 the mass is seen to have again attached itself to the Wolffian duct and partially (Fig. 59) to the Müllerian duct as well. The two following sections (Figs. 60, 61) are especially significant, in that they show a cell which has just divided into two daughter-cells, one of which (Fig. 60) seems to constitute a part of the wall of the Wolffian duct, the other (Fig. 61) a part of the cell-mass which in turn is quite intimately connected with the Müllerian duct. In the two following sections (Figs. 62 and 63) the cell-mass nearly disappears, a portion of it allying itself with the Wolffian duct, the remainder forming a separate strand closely applied to the Müllerian duct. This and the Müllerian duct now become separated from the Wolffian duct by a layer of connective tissue. The strand just described is more or less distinctly differentiated from the mass of the Müllerian duct for some ten additional sections. It then separates entirely from that duct and, passing again through a gap in the connective tissue layer which separates the two ducts, fuses with the Wolffian duct. The posterior end of this fusion is shown in Figure 64, where the lumen of the Wolffian duct is seen to present a slight outpocketing ventrally, which represents the posterior end of the lumen of the strand just described. Posterior to this point, the Müllerian duct extends free for some distance and then ends.

The pictures presented by these sections may be interpreted in two ways: Either the duct had fused with the Wolffian duct and is now drawing away from it, leaving strands of tissue still connected with both ducts, or the Wolffian duct is participating in the formation of the Müllerian duct by proliferating cells which form irregular masses and strands of tissue extending from the former to the latter. The second view is supported by the presence of the dividing cell shown in Figures 60 and 61.

My conviction that the Wolffian duct participates, to a small extent, in the formation of the Müllerian duct, rests not only on the fact that at certain stages there is always at least a juxtaposition of the two, but also on the additional fact that, where this occurs, cell-division is frequently taking place in the wall of the Wolffian duct. This formation of new cells at a time and place where the Wolffian duct is functionless and about to degenerate is surely very significant.

Larva XI, 49 mm. — No gills.

The most anterior sign of the fundament of the Müllerian duct in this larva is the thickened band, which begins anterior to the pronephros and extends caudad on the dorso-lateral wall of the sub-glomerular cavity

(Fig. 49, Pl. 4, *tae. e'th. γ'*) along the line where the body-wall and shelf join each other. As the second evagination — which I shall henceforth call the *ostium* — has migrated caudad until it is well out of the glomerular cavity, the thickened band no longer needs to make a bend cephalad to reach it. Instead it runs straight back, becomes a groove, then by further folding a tube, and finally continues caudad as the Müllerian duct, which is now simple and shows no signs of its double origin (see Figure *N*, where, however, it is represented as double). Figure 52, *tae. e'th. γ'* , represents the band after it has passed the posterior limit of the shelf and a short distance anterior to the ostium.¹ On the left side of the body the anterior evagination and a portion of its duct are retained in a remarkable degree of perfection. Figure 49, *evg. 1*, shows in section this first evagination, which has lost all connection with the thickened band, as shown in Figure *N*. Its duct is represented by a continuous cord, the nuclei of which are arranged radially, which disappears, however, before it reaches the ostium (or second evagination). On the right side both the first evagination and its duct have disappeared, with the exception of a portion of the latter, which, though only a few sections in length, is well formed (Fig. 52, *dt. 1*). The retention of this detached bit of the anterior duct is important, as it lends strength to the assumption made in the description of Larva VII (page 82), that the detached portion there seen was a survival from the degenerating duct of the first evagination.

The grooved condition of the thickened band anterior to the ostium is especially noteworthy. It signifies that the process whereby the ostium is transferred to a more and more anterior position has already begun. This process consists in a longitudinal folding of the thickened band, followed by a fusion of the edges of the groove thus formed, which, beginning at the ostium, advances cephalad.

Larva XII, 55 mm. — Neither gills nor gill-slits.

This is the latest stage which I shall describe. It is essentially like the preceding, with the exception that all traces of the anterior evagination and its duct have disappeared. The glomerular cavity is much reduced in diameter. It has the form of a long narrow *tube* (Fig. 45, Plate 4, *cav. glm.*) nearly filled at its anterior end with the now thread-like glomus. It still connects with the sub-glomerular cavity (now synonymous with the body cavity, the pneumo-parietal fusion having

¹ At earlier stages, this portion of the band was designated as β .

FIGURES I-N.

Six diagrammatic figures to show the relation, at various stages, of the Müllerian evaginations, epithelial bands, and nephrostomes to the divisions of the body cavity in *Amblystoma*. A parasagittal cut, to the right of the stomach, exposes the body-wall. The head is to the left.

In Figure I the epithelial band from the first nephrostome is being deflected caudad by the growth of the shelf (*tab.*), which is destined to divide the upper portion of the body cavity into a glomerular and sub-glomerular cavity.

(See opposite page.)

disappeared) by a narrow slit (Fig. 46, near *marg. p. tab.*), that is, the posterior margin of the shelf (Fig. 45, *tab.*) is still free. Degenerate pronephric tubules (Fig. 45, *tbl. pr'nph.*) are recognizable. The grooving or folding of the thickened band (which is supported by a fold of the peritoneum) now extends for a long distance cephalad from the ostium (Fig. 47, *evg. 2*), instead of for only a few sections, as in Larva XI. It reaches an entire somite anterior to the position of the adult ostium, which is opposite the posterior end of the fourth vertebra. I believe this seemingly superfluous anterior portion is utilized in forming the *downward* curve of the anterior end of the adult duct, which, instead of opening near the dorsal line of the body cavity, curves downward and outward around the base of the lung to its final position in the ventral portion of the body cavity. This downward curving seems to be brought about by the progressive restriction of the body cavity anteriorly.

Figure 47 shows the ostium (*evg. 2*) two sections anterior to the point where it becomes closed off from the body cavity. For thirteen sections behind that point, the duct shows two lumina. This may be regarded as evidence of its double origin.

There is a rather constant difference in the formation of the Müllerian duct on the two sides of the body. On the left side, the thickened band lies more laterally, and the grooved condition always extends farther forward than on the right side. I have been unable to detect any difference in the formation of the duct in the two sexes. If, however, a larger number of specimens were examined with this special point in view, minor differences might perhaps be found.

The formation of the "shelf," which is also described by Hoffmann ('86) and Gemmill ('97) as existing in Triton, seems to me interesting. It has generally been held that the glomerular cavity in the Urodela is of little significance, it being a sort of accidental consequence of the temporary fusion of the lung with the body-wall. We see that there exists in *Amblystoma* a glomerular cavity of an independent and more

In Figure *J* the first evagination (the black dot beneath the first nephrostome) has appeared.

The epithelial band may be divided into four regions: (1) a portion (*tae. e'th. a*) running back from the first evagination; (2) one (*tae. e'th. β*) from the second nephrostome, joining (1); (3) their combined prolongation (*tae. e'th. γ*) above the shelf; and (4) the same (*tae. e'th. γ'*) extending forward beneath the shelf.

In Figure *K* the second evagination has appeared and the first has sent the pre-coelomic duct (*dt. pr'coel.*) forward and a duct (*dt. 1*) backward.

Figures *L*, *M*, *N* scarcely need further explanation. The second evagination sends back a duct (*dt. 2*) which fuses with portions of the duct from the first, the remainder of this latter duct, as well as the epithelial band from the first evagination, degenerating. The extent of the fusion of the lung with the body-wall (Fig. *I*, *sep. pn. par.*) is gradually diminished in the successive stages.

permanent character. It is true that it becomes well established only during the degeneration of the pronephros, but this fact is of little significance, from a phylogenetic standpoint, to those who would homologize the pronephric glomerular cavity with those of the mesonephros.

B. RANA.

As is well known, the three nephrostomes in *Anura* open separately into a portion of the body cavity which is partially cut off from the general body cavity by a fusion of the lung with the lateral body-wall, that is, with the surface of the pronephros. This pocket contains the glomus and is called the glomerular cavity. In *Rana sylvatica*, immediately before the degeneration of the pronephros, the glomerular cavity is forced to a more nearly median position and much reduced in size by the growth of a shelf¹ (Plate 5, Fig. 65, *tab.*) comparable with that found in *Amblystoma*. As the pronephros retains its original position, the nephrostomal tubules are compelled to elongate in order to retain their connection with the glomerular cavity. The three nephrostomal tubules, which originally opened quite far apart, converge toward a common point, so that they finally acquire a common opening, which I shall term the nephrostomal vestibule, or *common nephrostome*. Figure 65 shows this common nephrostome (*vst. neph.*), and also the second nephrostomal tubule (*tub. pr'neph.*) one section anterior to its opening into the common nephrostome. This condition, which, to my knowledge, has never been mentioned in descriptions of the degeneration of the pronephros, may, of course, exist only in *R. sylvatica*. In that form it exists, almost without exception, in all the larvae over twenty-five millimetres in length which I have examined. The common nephrostome bears some resemblance to, and may be homologous with, the nephrostomal cavity in *Amblystoma*. Just as the first nephrostome in *Amblystoma* was finally cut off by the closure of the nephrostomal cavity, so here the three nephrostomes become cut off from the coelom by the closure of the common nephrostome.

To anticipate a little, the later history of this common nephrostome is illustrated by Figures 68-77 (Plates 6, 7). It gradually becomes deeper and narrower until it resembles the ordinary nephrostomes. Like them it is ciliated, and may have been mistaken for the third nephrostome,

¹ The shelf in *Rana sylvatica* extends caudad but a short distance and is a temporary structure. Very often the lung, which early loses its connection with the lateral body-wall, is fused with the ventral side of the shelf.

which is generally described as persisting to a late stage. In Figure 68 is seen the end of the first nephrostomal tubule, in Figure 69 its opening into the common nephrostome. The connection of the latter with the coelom is shown in Figures 70, 71, and 72. The second nephrostomal tubule is shown in the same three figures, and the third in Figures 75-77. The first nephrostomal tubule comes into the common nephrostome from an anterior direction; the second from a point directly laterad, and the third curves dorsad and then cephalad.

The first sign of the fundament of the Müllerian duct appears in the form of a thickening of the peritoneal epithelium of the pronephros at a little later stage than the one from which Figure 65 was taken. It will be remembered that the peritoneal evaginations in *Amblystoma* which formed such an important part of the fundament of the Müllerian duct, arose just ventral to the two nephrostomes. The conclusion is obvious that the nephrostomes may in some way determine the position and number of these evaginations. If that is true, we should expect to find three evaginations in *Rana*, one beneath each nephrostome. But the fundament of the Müllerian duct does not arise until after the migration of the three nephrostomes to a common region, so that the tissue immediately ventral to them is now probably represented by tissue just ventral to the common nephrostome. Bearing this in mind, as well as the fact that the embryological processes in the highly specialized *Anura* are often hurried and obscure, as compared with those in the *Urodela*, I was not surprised to find that the theoretical three evaginations are generally represented by a single irregular mass of cells proliferated from the peritoneal epithelium. This mass is always *elongated antero-posteriorly*, and lies ventral to the common nephrostome. It usually shows more than one obscure evagination from the coelom extending into it. Only once did I find it represented by one large, well-formed evagination. I searched carefully for evidence that the three evaginations are not purely theoretical, and was fortunate enough to find one case in which the complete fusion of the three nephrostomes had been retarded until after the appearance of the fundament of the Müllerian duct. In this larva, on one side, the two anterior nephrostomes are fused, but the third still opens separately at some distance behind the common opening of the anterior ones. Ventral to the opening common to the first and second nephrostomes, there is a distinct evagination of the peritoneum (Plate 5, Fig. 66). From this a thickened band runs ventrad and cephalad over the face of the pronephros along its line of junction with the shelf. *Ventral to the third nephrostome is a thickened disk*

(Fig. 67), similar to those which formed the evaginations in *Amblystoma*. From this disk a thickened band runs ventrad and cephalad to join that from the first evagination. The opposite side of the body presents the normal condition of a single irregular evagination ventral to the common opening of the three nephrostomes.

It was stated above that even where the three nephrostomes have fused, the fundament of the Müllerian duct may show signs of being formed of separate proliferations or evaginations. I have represented ten successive sections through such a fundament in Figures 68-77 (Plates 6, 7).

In Figure 68 the proliferation (*evg. 1*) may represent the first evagination, although it is also possible that it is the posterior end of the fold of the thickened band which is described below. If it is really the first evagination, the mass of cells marked *dt. 1*, in Figures 69 and 70, would seem to represent the duct which in *Amblystoma* extends caudad from the first evagination. In Figure 70 the epithelial thickening shows no evagination or special proliferation. In Figures 71 and 72 the cell proliferation immediately beneath the common nephrostome is well marked and takes the form of a distinct evagination, whose lumen is shown in Figures 73 and 74 (*evg. 2*). These sections also show a group of cells (*dt. 2*) which may represent the duct from this second evagination. Owing to the thickness of the sections, this group of cells is longer than one would at first imagine. Figure 75 passes through the posterior margin of the second evagination. Directly ventral to it is the thickest point in the peritoneal epithelium, which marks the level at which the third evagination takes place. The opening of the third evagination is shown in one section only (Fig. 76, *evg. 3*). The next section (Fig. 77, Plate 7) passes through its posterior prolongation, and in the two following sections (not figured) is seen its duct, which is free from the peritoneum. This duct dwindles to a cord, which is short and ends in contact with, but independent of, the peritoneal epithelium. This cord forms the Müllerian duct, but whether alone or with the addition of anterior ducts (by fusion, as in *Amblystoma*), I was unable to determine. I must also leave undecided the important question whether the developing Müllerian duct comes into relationship with the Wolffian duct or not. Two factors render the determination of these points very difficult: the fold which contains the ducts turns mediad behind the pronephros, so that it is cut very obliquely in cross-sections of the body; this fold, like the degenerating pronephros, is filled with densely packed lymph cells. That the Müllerian duct takes cells from the Wolffian

duct in this region seems very improbable for the reason that by the time the former reaches this region the degeneration of the Wolffian duct has rendered it difficult of recognition if, indeed, it can be seen at all. Posterior to the point where the fold containing the ducts reaches its most nearly median position and turns again caudad, so that it is cut transversely, the Müllerian and Wolffian ducts are seen, in later stages, imbedded in the lymphoid tissue *at some little distance from each other*. The growth caudad of the Müllerian duct must be rather slow, for in a young female frog which had completed its metamorphosis and left the water, and in which the eggs were quite large and surrounded each by a distinct follicular layer, the Müllerian duct had not reached the mesonephros. On the other hand, the oviducal welt, in which it lies when developed, reaches as a well-defined ridge nearly to the cloaca, and is generally *widely separated from the Wolffian duct*.

To return to the history of the anterior end of the duct; as in *Amblystoma*, the adult ostium is not formed directly from any of the evaginations. Instead, the larval ostium is carried cephalad and ventrad, utilizing the thickened band which, from its first appearance, takes that course. The anterior extension of the Müllerian duct takes place at a much earlier stage in *Rana* than in *Amblystoma*, but is accomplished by fundamentally the same method, as follows: the thickened band which extends from the evaginations cephalad and ventrad becomes broader, and the dorsal edge folds downward as shown in Figure 79 (Plate 7).¹ The edge of the fold, which projects into the body cavity, becomes continuous caudad with the dorsal lip of an evagination which is probably the third, though it may be a composite of two or three evaginations. Beginning at this point, the free edge of the fold then fuses with the portion of the band which forms a part of the peritoneum, as shown in Figure 80, which is two sections posterior to the one represented in Figure 79. This bending down and fusion of the dorsal edge of the band with its ventral margin which begins in the region of Figures 79 and 80, continues cephalad and ventrad until the opening reaches the position of the adult ostium at the base of the lung. This process of the forward and ventrad shifting of the ostium begins about the time of the appearance of the fore legs.

¹ Anteriorly, where the band takes a ventral direction, this dorsal edge naturally becomes anterior in position and hence folds over in a caudad direction. The section figured cuts the band where it has turned ventrad, and hence quite obliquely. The free edge of the fold, therefore, appears much broader than it would if it were cut perpendicularly.

C. HYLÆ.

After writing the above description of the development of the Müllerian duct in *Rana sylvatica*, I chanced upon a form, *Hyla versicolor*, which seemed to show conditions worthy of careful study. As the results tend to confirm the conception of the multiple origin of the Müllerian evagination in *Rana sylvatica*, which was expressed in the above description, I have allowed that to stand as it was written.

The peculiarity in the development of *Hyla* which makes the development of the ostium more easily intelligible than that of *Rana* lies in the fact that only the two posterior pronephric nephrostomes, instead of all three, fuse to form a "common nephrostome." At what age the fusion of the two nephrostomes takes place could not be determined, as it had already taken place in my youngest specimen, in which the hind legs were still quite inconspicuous. In this specimen the second and third primary nephrostomes empty at some little distance from the peritoneal surface into a ciliated common nephrostome.

The development of the Müllerian duct takes place at about the same stage, relative to the external signs of metamorphosis, as in *Rana sylvatica*. In the youngest stage which I shall describe it is evident that the pronephros has but recently ceased functioning, as degeneration of the tubules and Wolffian duct has not proceeded far. Already, however, those thickenings of the peritoneal epithelium which participate in the formation of the Müllerian duct are conspicuous. Their condition is as follows: near the anterior end of the body cavity a thickening of the epithelium is visible ventrally. This curves dorsad and caudad, growing thicker as it proceeds. When it reaches the first nephrostome it is continuous with a much more marked thickening surrounding that opening. Contrary to the condition in *Amblystoma* and *Rana*, it is the *dorsal* lip which is especially thickened, and, as will be seen later, it is this thickening (*evg. 1*, Fig. 81, Plate 7) immediately dorsal to the nephrostome, which forms the anterior Müllerian evagination.

The first nephrostome opens anterior to the root of the glomus. The second — the *common nephrostome* — opens posterior to it. Along a line joining the first with the common nephrostome the general thickening of the surface of the pronephros is accentuated to such an extent that there is formed a conspicuous band of large cells. This band is almost invariably folded so as to form a groove or trough (Fig. 83, *tae. eth.*), whose concavity is directed toward the coelom. A thickened disk dorsal to the common nephrostome is also visible (Fig. 82, *evg. 2, 3*). Pos-

terior to the common nephrostome all traces of the peritoneal thickening disappear.

The further history of the various portions of this peritoneal thickening is as follows: the thickened disk dorsal to the first nephrostome evaginates to form a pit, which generally is slightly anterior to the nephrostome. Figures 87 to 93 (Plate 8) represent seven sections through such an anterior evagination. Figures 87-92 represent successive sections; Figure 93 is three sections posterior to 92.

This evagination is evidently comparable with the anterior evagination of *Amblystoma*, and there are sometimes distinct signs of a proliferation of cells from its distal end extending in a posterior direction, which may be considered homologous with the "posterior cord of the anterior evagination" of *Amblystoma*. In fact, it seems probable that these cell-proliferations sometimes take on the form of more definite cords, for there is occasionally seen in later stages a distinct cord — or even duct — which begins back of the degenerating evagination and extends caudad, close beneath the peritoneum. It is possible that such cords are really portions of the degenerating pronephric tubules, but I think not, as my attention was called to them by the fact that, instead of being indefinite tubules with large, pale cells, like those seen in the rest of the degenerating pronephros, they are clear-cut, with cells staining very darkly and possessing little cytoplasm.

Whether or not these cords form a part of the Müllerian fundament, it is clear that, as in *Amblystoma*, the anterior evagination and its cord play no *essential* rôle in the formation of the Müllerian duct and are but relics of a past history — for both evagination and cord disappear entirely.

While the anterior evagination is disappearing, the thickening dorsal to the common nephrostome grows more pronounced and in turn evaginates. From its distal end cells are proliferated to form a cord, then a duct, running straight caudad. This is of course the Müllerian duct. Figure 84 (Plate 7) shows such a posterior evagination (*evg. 2, 3*), the section being three sections posterior to the point where the second and third nephrostomal tubules (shown in the figure) are joined to the peritoneum by a cord of cells representing the degenerating common nephrostome. Figure 78 (Plate 7) shows the posterior evagination at a later stage. Sections posterior to the one figured show that it is continued caudad as a duct which soon dwindles to a cord and then ceases.

In *Hyla versicolor* the question as to whether the more anterior portion of the Müllerian duct during its growth caudad takes cells from the Wolffian duct, is easily answered in the negative, for the Wolffian

duct has generally degenerated nearly back to the region of the mesonephros before the Müllerian duct arises. In one case only was a small bit of the anterior portion of the Wolffian duct retained, and in that case the posterior end of the Müllerian duct, although near by, was clearly independent of it. What the relation of the two ducts is when the Müllerian reaches the undegenerated part of the Wolffian which extends along the mesonephros, I have not observed.

The processes which precede the establishment of the adult ostium show a close similarity to those described for *Amblystoma*. During the changes described above, the posterior evagination and its associated (degenerating) nephrostome have migrated caudad. The anterior evagination where traces of it remain, is seen to have retained its position near the root of the glomus. The posterior one, however, instead of lying a short distance behind that point, as formerly, has migrated sometimes as much as twenty sections, or about seventy-four micra, caudad. The thickened band, which was mentioned as connecting the two nephrostomes, being still present, has become greatly elongated. It is also much more conspicuous than during the earlier stages, partly because its cells have become higher, partly because the cells of the adjacent peritoneal epithelium have taken on a squamous form. The trough-like form of the band becomes more pronounced near the second evagination. Since the band is continuous with that structure, a progressive fusion of its edges, beginning at the second evagination, results in a displacement cephalad of the opening of the Müllerian duct, as described for *Amblystoma*. The approximation of the edges of the trough preparatory to their fusion is shown in Figure 101 (Plate 8). In the next section posterior to the one figured the trough is closed to form the Müllerian duct, which extends thence caudad. In this case the anterior migration of the opening has been but slight. The degenerating common nephrostome is only three or four sections posterior to the one figured and is *dorsal* to the opening of the duct. This is the only case I have seen in which the evagination is ventral to the nephrostome, and is important as an indication that the position of the evagination, dorsal or ventral to the nephrostome, is not important. On the other side of the body the evagination is dorsal, as usual.

This is as far as my material allowed me to follow the ostial development, but as the trough is continuous anteriorly with the thickening which curves ventrad, and as the adult ostium lies ventrally near the base of the lung, there can be no doubt that the rest of the development is essentially as in *Amblystoma*.

It will be remembered that I have claimed, on grounds of analogy, that the Müllerian evagination in *Rana sylvatica* represents three evaginations, and that evidence of at least two was not lacking. That evidence was twofold: (1) The cell-mass which proliferates to form the Müllerian duct sometimes evaginates at two (and possibly three) points. (2) In a case where the third nephrostome had not fused with the other two, there was present an evagination near the fused, anterior two, and a disk (representing an evagination) near the posterior, free one. It has been shown that in *Hyla versicolor* the anterior nephrostome is independent of the fused posterior ones, and that there is an evagination associated with the former as well as one with the latter. With two evaginations patent, I hoped to find evidences of a third by a careful study of the posterior one, which, theoretically, should consist of a combination of two. I have looked in vain for such evidence as was found in *Rana*. The posterior evagination, although often much elongated antero-posteriorly, never showed distinct signs of a separation into two pits. Fortunately, however, I found one case in which all three nephrostomes had remained distinct; that is, the two posterior had not undergone the normal fusion. As a parallel variation in *Rana* gave rise to a separation of the Müllerian evagination into two, it seemed probable that in this case three fundaments might be distinguished. In effect, the condition was as follows. Dorsal to the first nephrostome was a very conspicuous evagination. The second and third nephrostomes were far back of the first and quite near each other, the second being ventral and somewhat anterior to the third. Figure 85 (Plate 7) represents a section passing through the posterior edge of the second nephrostome and just anterior to the third (some cilia of the latter are cut). There will be noticed a rather marked thickening (*evg. 2*) dorsal to the second nephrostome. While not very conspicuous, it is so restricted, — so clearly marked off from the surrounding epithelium, — and resembles so closely in staining properties, etc., the disk which always precedes the formation of a Müllerian evagination, that there is no doubt in my own mind that it really represents a second evagination. The evagination, associated with the third nephrostome is typical. It is shown in Figure 86 (*evg. 3*), which is from the second section behind the nephrostome.

It will be seen that in the development of the Müllerian duct, *Hyla versicolor* occupies a place midway between *Amblystoma* and *Rana sylvatica*. In the presence of well-defined evaginations in connection with *more than one* nephrostome, the oviducal development approaches

that of *Amblystoma*. Furthermore, the caudad migration of the posterior evagination and the method of carrying the opening of the Müllerian duct forward again along a trough of columnar cells by a progressive fusion of the edges of the trough, is exactly similar to what was seen in *Amblystoma*. On the other hand, the fusion of nephrostomes allies the development with that of *Rana*. As in *Rana* the fusion of all three nephrostomes caused either a suppression or a combination of the Müllerian evaginations into one, so in *Hyla* the fusion of two nephrostomes reduces the number of evaginations to two.

D. COMPARISON WITH THE RESULTS OF OTHER AUTHORS.

Perhaps the most satisfactory way to give an idea of the various views which have been held in regard to the development of the Müllerian duct in Amphibia is to give a brief résumé of those accounts which are most important, either from their completeness or the recentness of their appearance.

Urodela.

Fürbringer ('78) states that during the early stages in the degeneration of the pronephros of *Salamandra maculosa* — at the time when the gills are disappearing — its glomerular cavity becomes more extensively separated from the body cavity. Along the lateral margin of the glomerular cavity the peritoneal epithelium becomes thickened. This thickening spreads out laterally and "distally" (that is, caudad) from the pronephros and forms a part of the fundament of the Müllerian duct. At the same time, from the ventral side of that portion of the Wolffian duct which is immediately posterior to the pronephros, a solid cord of cells is cut off, which then gains a lumen and is transformed into a duct. The hollowing-out process begins proximally (cephalad) and progresses caudad. Its cephalic end then fuses with the thickening above described, and through it opens into the body cavity to form the ostium abdominale. Caudad the duct continues to be cut off from the Wolffian duct and to become hollowed out. Its caudal end dwindles to a cord and is lost in the ventral or lateral wall of the Wolffian duct. It may, however, *end free*, with a blunt point, this condition being observed but once.

If the development in *Salamandra* is like that in *Amblystoma*, it would seem that in the earlier stages Fürbringer mistook for the Müllerian duct the degenerating duct which passes backward from the first evagination. If he observed that the duct from the first evagination ended

blindly in front, as it sometimes does in *Amblystoma*, and if he later found the Müllerian duct connected anteriorly with the second evagination, the impression would be natural that the ostium was formed secondarily. That he found no evagination at that early stage may be due to the fact that the first evagination degenerated before the second was formed — although I have never observed such a condition in *Amblystoma*. Or, it would be very easy to mistake the first evagination for a nephrostome. It must not be thought, however, that I criticise the observations of Fürbringer, or other authors, as necessarily incorrect. Since a certain controversy in regard to the development of the vasa efferentia in *Rana*, which had its origin in the fact that the observers were working on different species, we have been taught that it is not safe to take for granted that the details of embryonic development are alike even in the *same genus*.

In general Hoffmann ('86) confirms for *Triton cristatus* the observations of Fürbringer on *Salamandra*. After reaching the height of its development, the pronephros migrates to a more median and dorsal position and the two nephrostomes draw nearer together. The glomus, which originally occupied a position between the two nephrostomes, is brought to lie opposite the first. About the time when the gills begin to degenerate, the segmental duct splits longitudinally to form the Wolffian duct (dorso-median) and the Müllerian duct (ventro-lateral). The splitting begins anteriorly and progresses gradually caudad. Shortly after the first appearance of the Müllerian duct its anterior end forms the ostium abdominale by fusing with the thickened peritoneal epithelium, — generally lateral to, and on a level with, or just posterior to, the second nephrostome, sometimes between the two. This thickening, which is formed by the cells of the peritoneum taking on the columnar shape, existed "lateralwärts neben und zwischen den beiden Trichtern" before the appearance of the Müllerian duct. The backward growth of the duct is different in the two sexes. In the female its whole length is formed by evagination from the segmental duct. In the male it very early separates from the segmental duct to grow back free. Hoffmann was unable to determine whether or not the Wolffian duct remained connected for a short time with the pronephros after the formation of the Müllerian duct. Shortly after that event, the pronephros is certainly completely isolated. The ostium is at first quite shallow. The surrounding thickened peritoneal epithelium shares in its enlargement.

With the formation of the ostium, the degeneration of the pronephros begins. The first steps are the closure of the first nephrostome and the

complete cutting off of the glomus from the body cavity by an outgrowth¹ from the radix mesenterii, which passes ventral to the glomus and fuses with the pronephric wall.

The second nephrostome remains after the complete disappearance of the rest of the pronephros. The Wolffian duct degenerates back almost to the mesonephros, even while the first nephrostome is still present. The glomus remains, in a modified condition, in half-grown animals, where it is entirely enclosed in the radix mesenterii.

In a short paper, which has not, so far as I know, been followed by any more extended account, Wilson ('94) gives the following description of the formation of the Müllerian duct in the Axolotl (*Siredon pisciformis*): "In a 25 mm. long larva one finds the coelomic epithelium of the portion of the body cavity that surrounds the glomerulus of the pronephros partially modified to form a *band of cylindric cells*, that runs close to the outer boundary of the space, in contact with the limit formed by the fusion of the lung and pronephros. *This band is a direct continuation backwards of the ciliated epithelium that forms the first pronephric nephrostome*, and where the lung frees itself from the pronephros the band spreads out laterally to form a plate of cylindric epithelium that extends far beyond the lateral boundary of the pronephros, but only to narrow again in the region of the second nephrostome, with the epithelium of which it fuses. Posterior to the second nephrostome the cylindric epithelium rapidly narrows to a thread of cells that lie outside the segmental duct. There can be no doubt as to the origin of these cells, for (1) the coelomic epithelium is markedly thickened and proliferating, and (2) the segmental duct is rounded and well defined, and shows no sign of budding off new cells or splitting. Sometimes the thickening is only one cell deep and three or four in breadth; sometimes it is several cells deep. It extends back at least as far as the mesonephros."

It will be seen that the condition here described is very similar to an early stage in *Amblystoma*. The thickening of the epithelium between the nephrostomes corresponds to what I have called the "thickened band," and that which "extends back at least as far as the mesonephros" is what I have termed the oviducal welt.

The author then goes on to say that in a larva twenty-seven millimetres in length the thickening in the pronephric region is very similar to that in the younger animal, although not so marked. Just behind the second nephrostome, however, there is a more marked proliferation

¹ Evidently this corresponds to the structure which I have designated as "shelf."

of cells to form a mass [evidently corresponding to the "first evagination" after its caudal migration has begun] in the middle of which a rod appears. This rod is continued back for some distance, but is occasionally interrupted by merging with the cell mass,—or it may be represented by only a few heightened cells of the peritoneal epithelium. The cord is entirely distinct here, *as always* from the Wolffian duct.

In still older specimens the rod becomes more marked, but shows the same irregularity as before; that is, the cord merges at times with the cells of the oviducal welt, or, if development has gone so far that a distinct tube is present, there are places where it is just appearing. In all cases the posterior end is continued as a simple epithelial thickening. During this caudad growth the anterior end of the thickening loses its connection with the degenerating nephrostomes. The thickening now extends from the region of the pronephros caudad and mediad almost to the mid-dorsal line. At this point, in a larva forty-five millimetres in length, the thickening begins to be raised into a ridge, and still farther back, grooved. Forty-eight sections behind the beginning of the fundament, the edges of the groove close over [probably the "second evagination" is here described] to form a rod, or, on one side of the body, a distinct tube for one or two sections, followed by the interrupted rod above described.

It is worthy of note that in the forty-five millimetre larva, the thickening begins to be raised to form a ridge at the point where it approaches the mid-dorsal line, the grooving beginning farther back, while in a specimen of fifty-one millimetres in length (which shows an advance in the differentiation of the Müllerian duct and hence really is older and not simply longer) the *grooving* begins at this point. Although the author does not call attention to the fact, there has evidently been a *progression cephalad* in the raising and infolding of the epithelium to form the duct.

The fact just alluded to makes me suspect that Wilson saw the ostium only after it had begun its forward migration, that is, some time after its first appearance. The free portion of the duct, unconnected with the ostium and present before that structure had appeared, and the isolated bits of duct might be explained as in my criticism of Fürbringer's description. It is needless to say that I consider Wilson in error in describing the posterior end of the developing duct as continuous with the peritoneal epithelium of the oviducal welt.

In *Triton punctatus* Gemmill ('97) describes the fundament of the Müllerian duct as first appearing while the pronephros is still com-

pletely functional and before its glomus has become enclosed in a glomerular cavity. At this stage the fundament appears as a thickening of the peritoneal epithelium lateral (morphologically ventral) to the second nephrostome. This thickening is reinforced by connective tissue, so that there is formed a pad which becomes a groove, probably by an evagination of the epithelium. The floor of the groove is continued as a solid cord extending caudad a short distance between the Wolffian duct and the peritoneum and *independent of both*. In slightly older larvae the peritoneal thickening also stretches caudad as a narrow welt (the oviducal welt) which indicates the path along which the Müllerian duct develops, but which *does not contribute cells to the growing duct*. The Müllerian duct develops from the cord described above. The groove is the fundament of the ostium. Immediately anterior to the mesonephros the cord fuses indistinguishably with the Wolffian duct, and in its further growth the posterior end is always represented by a thickening of the ventral side of that duct. As this growth proceeds, the proximal portion separates from the Wolffian duct, and receives a connective sheath of its own. The lumen of the duct appears as a prolongation of the lumen of the groove and progresses regularly caudad. Gemmill believes that the growth of the duct is brought about by a multiplication of its own cells with the addition of cells from the Wolffian duct. The ostium he considers as absolutely independent of the pronephric nephrostomes, and holds that the Müllerian duct cannot therefore be considered as representing in any way a duct of the pronephros. Aside from the lack of any mention of an anterior evagination and a cephalic displacement of the ostium, Gemmill's description is in close agreement with my own. The fact that I had not seen his paper until after my description of the oviducal development in *Amblystoma*, *Rana*, and *Hyla* was completed makes this agreement the more satisfactory to me.

Gymnophiona.

The fundament of the Müllerian duct is, according to Semon ('92), very simple in *Ichthyophis*, and entirely different from that of the higher *Amphibia*. It arises entirely independent of pronephros or its duct, from a thickening of the peritoneum. This thickening extends two or three segments anterior to the pronephros, and from it the ostium is formed — sometimes on a level with the pronephros, generally somewhat anterior to it — by the fusion of the edges of a groove which exists in the thickening. The lumen of the ostium is continued back for a short distance in the form of a tube which loses itself in the

irregular mass of cells constituting the oviducal welt. The caudad prolongation of the duct, which is at first a solid cord, is formed by a rearrangement of the cells of the oviducal welt.

It will be seen that, contrary to what might have been expected in an animal which shows so many primitive characters in the urino-genital system, *Ichthyophis* has as yet thrown no light on the origin or development of the Müllerian duct in other forms.

Anura.

The conditions in *Anura* have been carefully studied by Hoffmann ('86) in the cases of *Rana temporaria*, *R. esculenta*, *Bufo cinereus*, by MacBride ('91, '92) in *Rana*, and by Gemmill ('97) in *Rana temporaria* and *Pelobates fuscus*.

According to the statement of Hoffmann, his was the first description of the development of the Müllerian duct in *Anura*. The first change preparatory to its development is a histological alteration of the pronephric duct between the pronephros and the mesonephros. This change consists in the transformation of its flat epithelial cells into those of a columnar shape and a reduction in the size of its lumen. The anterior end of the duct then separates from the degenerating pronephros and fuses with its peritoneal covering, — which is now also composed of cylindrical cells. A little anterior to the mesonephros, the segmental duct divides obliquely. Of the two portions thus formed, the posterior one, which ends blindly in front, retains its connection with the mesonephros and is the Wolffian duct. The anterior portion, connecting with the pronephric epithelium in front and ending blindly just lateral to the anterior end of the Wolffian duct, is the fundament of the Müllerian duct. The caudad growth of the Müllerian duct is independent of the Wolffian duct and is probably accomplished by the proliferation of a solid cord of cells from the neighboring thickened peritoneal epithelium, although of this Hoffmann is not certain.

Turning to the behavior of the anterior end of the Müllerian duct, its fusion with the peritoneal epithelium is converted into an opening. This is not, however, the ostium abdominale. From this opening a thickened band passes laterad and ventrad around the base of the lung and then turns caudad for some distance. By a folding of this band and a fusion of the lips thus formed the anterior opening is carried outward and downward, and then caudad. With the degeneration of the glomus, the duct moves mediad, and at the same time the edges of its cephalic opening begin to flatten out again to form a part of the

coelomic epithelium. This retrogressive process is continued until the ventral, caudally directed portion of the duct has been obliterated, and the opening — now the ostium abdominale — occupies its adult position.

In the degeneration of the pronephros, the anterior nephrostome is the first to disappear, the second next, and, after some time, the third. It is in the vicinity of the surviving third nephrostome that the fusion of the pronephric duct with the peritoneum takes place.

I think there is no doubt that Hoffmann mistook the developing Müllerian duct for the anterior end of the pronephric duct. His description of the mode of formation of the duct anterior to the point where it first opens into the body cavity is in accord with what I found in *Rana sylvatica*, with the exception of the obliteration of a temporary, cephalic portion. The description of the degeneration of the pronephros is, of course, entirely different from my own results.

According to MacBride ('91, '92) there is no trace of the Müllerian duct in "the frog" until the tadpole has lost all its larval organs except the tail. The first trace of the duct is ventral to the only remaining nephrostome which, from its position, is probably the first. The fundament consists of a groove lined with columnar cells and open below. "This columnar epithelium is continued out over the surface of the pronephros and beyond it, as described by Hoffmann." The groove changes, posteriorly, into a canal which ends in a thickening of the peritoneum. Anteriorly, in later stages, the groove extends ventrad and becomes closed to form a canal "opening somewhat ventrally." Posteriorly, the thickening of the peritoneum, which constitutes the duct, runs back along a line of columnar epithelium which extends along the outer border of the mesonephros. MacBride calls the cord of cells which forms the duct a "thickening of the peritoneum" because it appears to be derived from the peritoneum, although he cannot be certain of the origin of its cells on account of the lymphoid tissue with which the outer boundary of the mesonephros is filled. In describing the cord he says "it appears [in cross-sections] as a nodule of deeply staining tissue, the outermost cells of which pass at the side into the ordinary epithelium." The duct is formed from this cord by the rearrangement of some of its cells in a stellate manner. Anterior to the mesonephros the cord "grows back with some regularity," but it appears posterior to the mesonephros long before it does along the side of that organ.¹ The lumen appears first anterior, then posterior, to the mesonephros. Posteriorly it appears

¹ One cannot help suspecting that MacBride confused the Müllerian duct and oviducal welt.

in patches. MacBride saw no sign of a splitting of the pronephric duct as described by Hoffmann. He thinks it highly improbable that the portion just back of the pronephros takes any cells from the pronephric duct on account of the degenerate condition of the latter. Posteriorly, the growing cord comes nowhere in contact with the Wolffian duct.

Gemmill ('97) describes the development of the Müllerian duct in *Rana temporaria* and *Pelobates fuscus*. The evagination or groove appears lateral [ventral] to the third nephrostome, and development proceeds much as in *Triton punctatus* (as described by him), with this important difference, — the growing duct comes nowhere in contact with the Wolffian duct. While its tip is too close to the oviducal welt to affirm that it takes no cells from that structure in *Rana temporaria*, in *Pelobates* cases were seen on both sides where the tip was undoubtedly free. The author's description of the cephalic displacement of the ostium agrees with my own for *Rana sylvatica*.

Amniota: Mammalia.

It is not my intention to discuss the many contradictory accounts which have been given of the origin and development of the Müllerian duct in Amniota. For a résumé of this subject the reader is referred to Burger ('94, '94^a). According to the researches of Kip ('94, '94^a), mammals seem to present the nearest approach in the development of the Müllerian duct to that found in *Amblystoma*, although from the account of its development in the chick given by Balfour and Sedgwick ('79), birds also show a close similarity. The parallel between Kip's ('94, '94^a) description and mine is so close that I shall recapitulate briefly his observations on *Insectivora* (*Tupaia*, *Talpa*, *Erinaceus*) and *Rodentia* (rabbit, mouse).

Tupaia: On the ventral surface of the anterior end of the mesonephros there is a thickening of the epithelium about 200 micra in length, which forms a plate of uniform thickness. At three successive points of this plate, cell proliferation takes place to form three massive cones, which then become pits opening into the coelom.¹ The inner ends of these (or rather of the first two, as the third generally degenerates) fuse, and the resulting cord grows back and applies itself to the blind anterior end of the Wolffian duct. The evaginations grow wider and fuse at their

¹ The number of evaginations is variable. In one case but one was found; in another, four.

mouths to form a single large funnel. This union continuing inward, a single large duct is formed, which then grows in length cephalad by a fusion of the lips of the opening. In this manner the ostium is carried forward about 100 micra. In early stages, when the duct is represented by a cord which reaches back only about halfway along the mesonephros, the Wolffian duct contributes cells towards its formation. In older stages, when the cord has nearly reached the urino-genital sinus, it takes far fewer cells from the Wolffian duct and finally grows backward independent of that duct. Hence in *Tupaia* the Müllerian duct is derived from two entirely different sources :

(1) The anterior end — that is, the ostium and the adjoining portion of the duct — is formed from the peritoneal epithelium.

(2) The remainder of the duct is formed largely from the Wolffian duct. Anteriorly, however, it takes a larger percentage of cells from the Wolffian duct than posteriorly.

Erinaceus: There are two evaginations. As the Wolffian duct reaches much farther cephalad than in *Tupaia*, the two cords from the evaginations reach it *before they have fused*. As a consequence the Wolffian duct must form two cords which fuse comparatively late. The anterior evagination often *loses its connection with the peritoneum*, so that the Müllerian duct appears branched anteriorly. The posterior portion of the duct takes *no* cells from the Wolffian duct.

Mouse: The "vertical" portion of the duct arises entirely independent of the ostium, for stages are found in which a considerable extent of the vertical portion is present unconnected with the ostium by the horizontal portion, which develops later. Kip suggests an explanation of this condition which consists in the assumption that a rudimentary evagination, homologous with one of those found in *Erinaceus*, gives rise to the vertical portion of the duct and then atrophies, leaving the anterior end of the duct to end free, — just as one branch occasionally does in *Erinaceus*. This free end, he suggests, then becomes connected with an ostium which arises later, this ostium not being homologous with any found in the Insectivora.¹

In rodents the connection between Müllerian and Wolffian ducts is far less intimate than in Insectivora.

Kip states his belief that the development of the Müllerian duct has

¹ Kip found a rudimentary ostium in the rabbit posterior to the final ostium. The latter appears only after the degeneration of the rudimentary posterior one.

become independent of the Wolffian duct in reptiles, many birds, and possibly some mammals, by the extension cephalad of the method of formation seen in the posterior portion in insectivores. The ostia in mammals are homologous with the pronephric nephrostomes of elasmobranchs, but the ostia of insectivores cannot be homologous with the *same* nephrostomes as the ostia of rodents.

From the above abstract, it appears that a remarkable agreement exists between the development of the Müllerian duct in Insectivora and Amblystoma. In the rodents there would seem to be an additional process consisting in the formation of a second ostium, anterior to, and later than, the first. This condition might easily be derived from that in Amphibia by supposing that the lengthening of the duct, cephalad, was brought about not by a progressive infolding and fusion of the thickened band, *beginning at the ostium*, but in the following manner: The infolding and fusion begins at the *anterior* end of the band and progresses back to the ostium. The final result would be the same in both cases.

That the position of the evaginations in the Insectivora is as far back as the mesonephros could be explained by assuming that that portion of the tissue of the thickened band which gives rise to the evaginations migrates caudad *before* instead of after the proliferations have taken place.

For comparison I have briefly summarized below the observations of the various authors and my own.

Urodela.

Fürbringer: The Müllerian duct is formed from the Wolffian by a longitudinal splitting. The anterior end fuses *secondarily* with the thickened peritoneum to form the ostium. No cephalic migration of the ostial opening noted.

Hoffmann: The Müllerian duct is formed as described by Fürbringer, except that in the male only the more anterior portion of the duct arises from the Wolffian duct.

Wilson: The ostium and anterior end of the duct are formed by an evagination of the peritoneal epithelium. The rest of the duct arises from the peritoneal cells of the oviducal welt. He seems to have seen, without realizing the fact, two separate evaginations and a cephalic migration of the ostial opening.

Gemmill: The ostium and the anterior portions of the duct are from a peritoneal evagination. The remainder of the duct is developed partly from the Wolffian duct. No mention is made of a cephalic displacement of the ostial opening.

Hall: The ostium and the anterior end of the duct are formed from the peritoneal epithelium. This fundament had originally the shape of two separate evaginations. Only a small portion of the growing duct takes cells from the Wolffian duct. The remaining portion grows back independent of Wolffian duct and peritoneum. A cephalic migration of the ostial opening is brought about by the closure, from behind forward, of a thickened groove of peritoneal epithelium.

Gymnophiona.

Semon: The ostium and anterior end of the duct are formed from a peritoneal evagination, the remainder of the duct from cells of the oviducal welt.

Anura.

Hoffmann: The anterior portion of the Wolffian duct is converted bodily into the Müllerian duct. It separates from the pronephros and fuses with the thickened peritoneal epithelium to form the ostium. After dividing obliquely at the anterior end of the mesonephros, the anterior section grows back, probably with the aid of cells of the oviducal welt, to form the remainder of the Müllerian duct, the posterior section remaining as the Wolffian duct. A cephalic migration of the ostial opening takes place along a thickened groove of the peritoneal epithelium.

MacBride: The ostium and anterior end of the duct are formed from a peritoneal evagination, the remainder of the duct, at first in the form of discontinuous pieces, from cells of the oviducal welt. There exists a cephalic migration of the ostial opening similar to that described by Hoffmann.

Gemmill: The ostium is from a peritoneal evagination, and the entire duct is formed by a prolongation of the free end of this evagination. There is a cephalic displacement of the ostial opening as described by Hoffmann and MacBride.

Hall: My description is in agreement with that of Gemmill with the exception that evidences were seen of three original evaginations to form the ostial fundament.

Mammalia.

Kip: The ostium and the anterior end of the duct are from two or three separate peritoneal evaginations. A portion of the duct takes cells from the Wolffian duct. There is a cephalic displacement of the ostial opening similar to that described by me in *Amblystoma* and by various authors in *Anura*.

E. THEORETICAL CONSIDERATIONS.

Since Balfour and Sedgwick ('79) first suggested a homology between the evaginations in the chick which form the anterior end of the Müllerian duct, and the pronephros, there has been a tendency to derive the ostium in some way from the pronephric nephrostomes. Semon ('92) suggested that the eggs were originally emptied into the pronephric duct through canals homologous with the vasa efferentia of the testis, but that, on increasing in size, they fell directly into the body cavity and a pronephric tubule was specialized to transmit them to the pronephric duct, or to a duct derived from the pronephric by a splitting process.

In trying to trace the probable origin of the ostium and Müllerian duct, we are confronted by two very different conditions: In elasmobranchs the ostium is derived directly from the pronephric nephrostomes; in *Amphibia* the ostium *coexists* with the pronephric nephrostomes and is independent of them. It seems to me that these two conditions can be reconciled by supposing a diverging differentiation, somewhat after the following manner:

In the elasmobranchs, the large amount of yolk which serves for the nourishment of the young is, of course, a secondary acquirement. The ancestral form we may picture as having lived as a free larva, and as having possessed a pronephros which, in addition to functioning as an excretory organ, had to prepare itself for the function of carrying off, in the adult, the eggs set free in the body cavity. This was accomplished by the pronephric duct dividing¹ to form two potentially separate ducts, much as the hermaphroditic duct of the pulmonate gastropods is divided by a longitudinal infolding. The halves of the duct diverged from each other posteriorly and opened separately. Phylogenetically, this splitting and separation was carried cephalad until a stage of nearly complete

¹ That this division would separate the excretions of the pronephros from those of the mesonephros is of no consequence. The best explanation seems to me to be that of Van Wijhe ('89), who sees in it a means of preventing self-fertilization, — the early vertebrates having been, probably, hermaphroditic.

independence was reached ; then more or less of the posterior ends grew back independently of each other. With the acquisition of more and more yolk, the period at which the young fish began its independent existence (and more active metabolism) was retarded until finally the secretory function of the pronephros was superfluous, especially as the mesonephros arises early in elasmobranchs and reaches forward to the pronephric region. The same process — the accumulation of food material in the egg — necessitated an increased development of the duct which carried off the now enormous eggs, and the pronephros very early in ontogeny began its transformation into an ostium abdominale. This is accomplished in modern elasmobranchs, according to Rabl ('96), by a degeneration of some, and a fusion of the rest of the nephrostomes (Figs. *O*, *P*, p. 111). Thus we have in modern elasmobranchs a pronephros which consists of a number of serially arranged funnels whose tubules fuse to form the pronephric duct.¹ This duct divides longitudinally, one-half receiving the mesonephric excretions, the other remaining connected with the pronephric nephrostomes, or rather the single ostium derived from them.

The ancestors of the Amphibia we can imagine as parting from those of the elasmobranchs at the stage when the pronephros still had a secretory function as well as a sexual one, but after the pronephric duct had acquired the double structure. With increase in cephalization, the pronephric tubules increased in number. Gradually there arose a division of labor, one set of tubules retaining the secretory function, the other set taking on the task of carrying off the eggs (Fig. *Q*). The loss in the number of secreting units thus brought about was compensated for by an increase in length and accompanying coiling of the anterior end of the pronephric duct to form the main bulk of the pronephros.² As the secreting action of the pronephros was retained during ontogenetic development until after the sexual or oviducal set of tubules had begun their transformation into an organ for carrying off the eggs, the secreting tubules retained their connection with the anterior end of the pronephric duct, while that part of the latter which split off to form the Müllerian duct was associated exclusively with the set of sexual tubules (Fig. *Q*). In *Amblystoma* (see Fig. *R*) we thus have the original pronephros repre-

¹ Perhaps the tubules fuse *and join* the pronephric duct. The origin of the latter is still in dispute.

² According to Semon ('92), the anterior end of the pronephric duct in Ichthyophis, where the pronephric tubules number *twelve on each side*, does not form the massive coil characteristic of the higher Amphibia.

FIGURES O-T.

Six diagrammatic figures representing the relation of the Müllerian evaginations to the nephrostomes, the Müllerian duct to the Wolffian, etc. The Müllerian evaginations are somewhat below the nephrostomes in each case and the Müllerian duct is below the Wolffian.

Figures O and P represent two stages in elasmobranchs; Figure Q, a hypothetical, primitive condition in Amphibia; Figure R shows the condition in *Amblystoma*; Figure S, that in *Hyla*; and Figure T, that in *Rana*.

sented by (1) two dorsal tubules (the secretory portion), whose fused ends are continued backward as the pronephric duct, and (2), ventral to these, two tubules (the sexual portion) arising from Müllerian evaginations, whose caudal ends join the pronephric duct some distance behind its coiled, anterior end. It would seem that in the ancestors of the Urodela and Anura there was originally one pronephric tubule for each of several segments and that the number was increased by the addition of a tubule in each of the segments already containing one (Figs. *R*, *S*, and *T*). These additional tubules lost their secretory function and took on a sexual one. The exact position of the sexual tubules in the somite is not significant. It seems probable that they arose ventral to the secreting set, for that is their position in *Amblystoma* and *Rana sylvatica*. In *Hyla versicolor*, it is true, they arise dorsally, but this position may have come about secondarily, as is suggested by the fact that in one case a Müllerian evagination was seen which was *ventral* to the nephrostome.

Such a duplication of tubules as postulated above seems to take place in *Amphiuma*, where, according to Field ('94), three somites on each side possess two tubules each, one dorsal and one ventral, making six in all. Whether one of these sets, the dorsal or the ventral, gives rise to the Müllerian duct or not, we do not know, as the development of the duct has not been studied. Such a result would not, however, be essential to a confirmation of the theory here set forth, as it is quite possible that in groups other than the Urodela and Anura the Müllerian evaginations have been derived from a third set of pronephric tubules, or from tubules of the posterior or anterior end of the single original series. In the latter case there would be no necessary correspondence in number between Müllerian evaginations and secretory tubules.

In *Amblystoma* (and probably all other forms above the elasmobranchs) the appearance of the sexual tubules is delayed, so that they arise much later than the secretory set. Their distal ends fuse with each other (to form the anterior end of the Müllerian duct) before they reach the Wolffian duct in all the cases that I have examined; but as the point of fusion is quite variable, they may sometimes reach the duct separately.¹ The original formation of the Müllerian duct in the remote ancestors of the Amphibia by a splitting of the Wolffian duct is indicated by the fact that the latter contributes cells to the growing Müllerian duct in the region where the two come in contact. Behind this point the Müllerian duct grows back independently. This inde-

¹ Kip ('94, '94a) notes such cases in mammals (see page 106).

pendent growth probably represents an extension cephalad of the process whereby the posterior end of the Müllerian duct reached a separate external opening. As suggested by Kip ('94, '94^a), one can imagine this process as phylogenetically advancing cephalad until the posterior prolongation of the ostial evagination reaches the cloaca without establishing any connection with the Wolffian duct. This stage seems, indeed, to have been reached in the Anura.¹ A connection between the two ducts has been claimed, however, for members of every group of the vertebrates which possess a Müllerian duct, with the exception of the Reptilia. It may be noted, also, that the reptiles are the only remaining group (since my observations on the Amphibia now exclude that group) in which we have not some evidence that there is more than one evagination as forerunner of the ostium abdominale.²

F. RECAPITULATION OF THE DEVELOPMENT OF THE MÜLLERIAN DUCT.

Amblystoma.

The first trace of the fundament of the Müllerian duct appears, some time before the degeneration of the gills and pronephros, in the shape of a thickening of the peritoneal epithelium beneath the first nephrostome. This thickening forms a band of crowded, cylindrical cells, which extends ventrad from the nephrostome, but is soon forced to turn caudad by the growth of a "shelf" of tissue which extends horizontally across that portion of the body cavity which is dorsal to the fusion of the lung with the lateral body-wall. This shelf thus divides the dorsal portion of the body cavity into an upper chamber, the glomerular cavity, and a lower chamber, the sub-glomerular cavity.

Soon the thickened band extends from the first nephrostome back along the dorsal surface of the shelf, then ventrad around its posterior edge and forward again on its ventral surface. As it passes back beneath the second nephrostome it is joined by a similar band from that organ.

Immediately ventral to the first nephrostome there appears a local accentuation of the thickening to form a small, thick disk. A similar one then appears beneath the second nephrostome. A depression in the surface of each of these disks results in the formation of an open pit, the wall of which extends into the substance of the pronephros.

¹ Figures *S* and *T* (page 111) represent the conditions in *Hyla* and *Rana*, — a total independence of Müllerian and Wolffian ducts. They also show, when compared with Figure *Q*, the modifications undergone by nephrostomes and Müllerian evaginations.

² Burger ('94, '94^a) describes the duck as having as many as fifteen.

The portion of the glomerular cavity surrounding the mouth of the anterior of the two pits and the neighboring nephrostome becomes partially closed off to form what I term the nephrostomal cavity.

From the distal (deep) end of the first pit, or Müllerian evagination, two ducts take their origin, one of which, the *precoelomic duct*, extends cephalad and later degenerates completely. The other, which I have called the first duct, ignoring the precoelomic duct, extends caudad past the second evagination and there fuses with a similar (second) duct from that evagination. That portion of the first duct which lies anterior to the union with the second duct degenerates.

In the mean time both evaginations have migrated caudad. This movement withdraws the first evagination from the nephrostomal cavity (which closes and with its associated nephrostome disappears) and brings the second to lie behind the posterior limit of the shelf, and hence out of the glomerular cavity. The thickened epithelial band is consequently no longer forced to make a detour to reach the second evagination; it extends from the anterior end of the sub-glomerular cavity, back along the ventral surface of the shelf (or along the adjoining lateral wall of the body), and is continuous through the second evagination, with the duct leading caudad from the latter.

The band from the first to the second evagination disappears. The first evagination also degenerates completely.

That part of the Müllerian duct which is immediately posterior to the second evagination is composed of the duct of that evagination *plus* a portion of the duct of the anterior evagination. After the fusion of these two components to form a single duct, the latter grows back near the Wolffian duct, fuses with it for a variable, but never great distance, and then grows backward free. Later, the fused portion again separates from the Wolffian duct. That the Wolffian duct contributes cells helping to form the Müllerian duct in this region, seems almost beyond question. The greater part of the duct, however, — that is, throughout the entire extent of the mesonephros, — grows back independent of the Wolffian duct.

The Müllerian duct increases in length cephalad by utilizing the thickened band which extends anterior to the second evagination, that being the only one which persists. This is accomplished by a folding of the band into a groove, beginning at the evagination and progressing cephalad. The fusion of the edges of the groove carries the opening of the duct cephalad and ventrad to its position in the adult.

Rana sylvatica.

Preceding the degeneration of the pronephros, the three nephrostomes move closer and closer together and finally open into a common out-pocketing of the coelom, which forms a narrow, ciliated canal closely resembling the primary nephrostomes. This "common nephrostome" is comparable to the "nephrostomal cavity" in *Amblystoma* in that, by its closure, it severs the connection of the nephrostomes with the coelom, just as the closure of the "nephrostomal cavity" shuts off the first nephrostome.

As a result of the migration of the nephrostomes to a common point, the tissue of the peritoneum which was immediately ventral to each is represented by tissue ventral to the common nephrostome. It is suggested that this tissue contains the fundamentals of the three Müllerian evaginations which should theoretically be present if there is a correlation between the number of evaginations and nephrostomes, as the condition in *Amblystoma* suggests. As a consequence of the condensation of the tissue of the three fundamentals, the latter are generally represented by an irregular mass of proliferated cells. This mass is, however, elongated in the direction of the long axis of the body and usually shows two or three distinct regions of heightened proliferation, or may even show more than one distinct evagination. A fundament is figured in which there are two distinct evaginations and a proliferated cone which may represent a third. An additional proof that there was originally a Müllerian evagination associated with each of the three nephrostomes is seen in the fact that in one larva, in which the fusion of the nephrostomes had been retarded, there is one distinct evagination beneath the common opening of the first and second nephrostomes and a thickened disk, probably representing another, beneath the third nephrostome, which opens at some distance behind the other two.

In the case just mentioned, there are two thickened bands which fuse and extend cephalad and ventrad. In normal cases there is a single band. As the shelf in *Rana sylvatica* is a very transitory structure of small extent, the curving of the thickened band in passing forward to the sub-glomerular cavity, which is such a prominent feature in *Amblystoma*, is barely represented. Soon after the appearance of the evaginations, the band forms a conspicuous groove or fold, open below, so that cross-sections of it have the form of an inverted V. The dorso-median wall of the groove later becomes continuous with the dorso-median lip of the single remaining opening of the Müllerian duct, and the latter is carried

cephalad and ventrad by the progressive fusion of the edges of the groove.

The portion behind the Müllerian evagination is formed from a prolongation of its distal end. It was found impossible to decide whether the evagination was a single one, remaining after the degeneration of others, or a compound one formed by fusion. That the Wolffian duct contributes cells to the growing Müllerian duct seems improbable from the fact that, in the only region where the relationship between the two ducts cannot be clearly distinguished, the Wolffian duct is very degenerate. Posterior to that point the two ducts seem to be wholly independent of each other.

Hyla versicolor.

The phenomena exhibited in the degeneration of the pronephros of *Hyla* differ from those in *Rana* in one important particular, — the fusion of only the two posterior nephrostomes, instead of all three, to form a "common nephrostome." In consequence of this peculiarity, the evagination associated with the first nephrostome is allowed as free a development as the anterior evagination in *Amblystoma*. The fusion of the two posterior nephrostomes, however, brings about a crowding of tissue similar to that in *Rana*, and as a consequence but one evagination appears. This posterior evagination, from which the Müllerian duct develops, may represent the third (supposing one originally associated with each nephrostome), or it may represent a fusion of the second and third. Efforts to resolve it into two were unsuccessful in normal cases. In the abnormal case in which the two posterior nephrostomes remained separate, there was strong evidence of an evagination associated with the second in addition to those unquestionable ones associated with the first and third.

In regard to the establishment of the adult ostium, *Hyla* resembles *Amblystoma* far more closely than it does *Rana*. The cephalic displacement of the opening of the young Müllerian duct takes place along a trough-like groove which extends from the posterior evagination to the anterior, and is there continuous with a thickened band which extends cephalad and ventrad toward the point where the adult ostium is situated. The process of displacement was observed only in its initial stages, but at those stages it is accomplished by a progressive fusion of the lips of the groove in a manner similar to that seen in *Amblystoma*, and there can be little doubt that the remainder of the process is essentially as in that form.

To account for the two very different modes of origin of the Müllerian ducts found in elasmobranchs on the one hand and in the Amphibia (and probably the Amniota) on the other, it is suggested that the Müllerian evaginations in the Amphibia studied by me represent a ventral set of pronephric tubules comparable if not homologous with the ventral set in Amphiuma. This ventral set, which originally possessed a secretory function, has become, like the pronephric tubules of elasmobranchs, specialized to subserve a sexual function. Instead of opening into the pronephric duct, they form a duct of their own which, by fusing with the pronephric duct for a short distance in *Amblystoma* and many Amniota, still betrays the fact that it had its origin in a splitting of that duct.

NEW HAVEN, May, 1902.

Addendum.

Too late to be incorporated in the body of the text, there came to hand an extremely important paper by Brauer (:02). I shall refer to such parts only as have a direct bearing on points treated in my own paper. His material consisted of specimens of *Hypogeophis rostratus*, belonging to the Gymnophiona.

The mesonephros is very long, extending throughout seventy-six segments, — from the 24th to the 100th. Two greater divisions may be distinguished, that comprising the region of segments 24 to 29, and that including segments 30 to 100. In the former division the mesonephric units remain rudimentary and finally degenerate; in the latter both primary and secondary are formed, the primary reaching a functional stage. This posterior division also shows a differentiation into two regions; in segments 50 to 100, the secondary tubules become fully developed; in segments 30 to 50 they degenerate. The degeneration of the secondary units brings about a strictly metameric arrangement of the tubules in this region of the adult kidney, for the entire organ has from the beginning a metameric structure to the extent that there is but one *primary* unit in each segment.

As the units of the last ten mesonephric segments (somites 90 to 100) are peculiarly modified, typical development is present in only forty segments (somites 50 to 90). The development of a mesonephric unit in this region is as follows: the somites are constructed essentially as in *Amblystoma*, their lumina being, however, larger. The ventral (lateral) portion of the somite, corresponding to what I have called the mesomer,

is in the form of a tube whose lumen sets the lumen of the rest of the somite (the epimer) in communication with the general body cavity. This ventral, tubular portion of the somite becomes *directly transformed into a mesonephric blastula*. In the more posterior segments it becomes cut off from the lateral mesoderm, a slight widening of its lumen takes place (a process designated by Brauer as the formation of the *nephrostome*), and it becomes constricted from the epimer. In the median portion of the typical region, the widening of the lumen of the mesomer takes place *before* that structure loses its connection with the lateral plates. In either case the result is the transformation of the lower portion of the somite (the mesomer) into a single rounded mesonephric blastula, which is independent of all other organs. Very significant is the fact that in the more anterior portion of the typical region, certain of the mesomers *never lose their connection with the lateral mesoderm*, so that their splanchnoderm and somatoderm remain continuous with the corresponding layers of the lateral mesoderm and their lumina continuous with the general body cavity. The outer tubule and nephrostome of a primary unit may thus be formed, in certain cases, by a simple transformation of structures present from the very beginning of somite differentiation. This, as has already been noted, is typically the case in elasmobranchs. It will be remembered that there was evidence of a similar retention of continuity between mesomer and lateral mesoderm in the more anterior portion of the mesonephros of *Amblystoma*. In that form, however, a continuous lumen was not recognizable.

The formation of a mesonephric blastula in *Hypogeophis* is thus similar to that in *Amblystoma* with the important exception that in the former genus the entire mesomer is transformed directly into a single primary unit, its lumen being not even temporarily obliterated.

The differentiation of the primary blastula is much as in *Amblystoma*. As in that form, the inner tubule arises as an *evagination of the lateral wall* of the blastula and is forced dorsad by the proximity of the Wolffian duct. If the peritoneal connection has not been retained, it is established by means of a nephrostomal evagination appearing at the ventrolateral angle of the blastula. The *secondary blastula* is then formed by an outbudding of the posterior, median portion of the blastula. It will be seen that the secondary blastula arises from the primary at a later period than in *Amblystoma*. The secondary blastula resembles that of *Rana sylvatica* in that it may retain its connection with the primary by means of a cord of cells. Where this occurs, it is seen to be attached to

the primary Malpighian body at a point similar to that of the attachment in the case of *Rana*.

Brauer lays stress on the fact, likewise emphasized in my introduction, that the inner tubule *grows out* from the *lateral* side of the blastula and is comparable with the pronephric tubule, while the Malpighian body (Bowman's capsule) is formed from the blastula by a direct transformation.

The history of the secondary unit differs somewhat from that in *Amblystoma*. After it is cut off from the primary, it lies close against the Wolffian duct, posterior to the opening of the main tubule of the primary unit. Where it touches the duct, a dark-staining evagination of that organ grows out, pushing the blastula before it. A long, tubular evagination of the Wolffian duct is thus formed into which the secondary tubule later opens. Differentiation of the secondary blastula is very similar to that of the primary. It develops in turn an evagination to form the inner tubule, one to form the outer tubule and one which becomes the tertiary unit. The tertiary blastula develops an inner tubule which meets and empties into a tubular outgrowth from the previous evagination of the Wolffian duct.

As many as eight units may be present in a single somite. Brauer is not certain that any beyond the quaternary form outer tubules and nephrostomes, but they may possibly connect with the body cavity in the manner in which the most posterior secondary units occasionally do, which is as follows. In Segments 90 to 100 the secondary outer tubule, instead of joining the peritoneum directly, sometimes joins the outer tubule of the primary unit, close to its nephrostome.

In the posterior segments a much more common condition than the one just described is the failure of both primary and secondary tubules to connect with the peritoneum. Instead, the outer tubule of the primary unit, avoiding the peritoneum, turns aside, meets and fuses with the outer tubule of the secondary unit, thus putting the two Malpighian bodies into connection with each other.

The most important, and, to me, satisfactory result of Brauer's work, the establishment of a close similarity between the mode of development of the pronephric and mesonephric units, I may not discuss, as it would carry us beyond the province of my paper. There remains, however, the *development of the Müllerian duct*. The first process in the formation of the Müllerian duct is a thickening of the lateral wall of the anterior half of the pronephros. On this thickened plate two longitudinal ridges arise. The free edge of the upper one folds ventrad, that of the lower, dorsad. On following the ridges caudad they are seen to form a tube by the

coalescence of the folded edges. This tube, the Müllerian duct, soon ends blindly in close proximity to the peritoneum. The latter does not, however, contribute cells to the growing duct. The ostium seems thus to be formed entirely from one Müllerian evagination, but from both the description and figures of Brauer (compare especially Fig. 145, Taf. 9) there is no doubt in my mind that several other evaginations in a degenerate condition are present posterior to the chief one. Such an interpretation of the structures in question occurred to Brauer himself, for he says in describing them (page 140): "Weiter caudalwärts" (referring to the permanent ostial evagination) "erkennt man zwar noch erhöhtes Epithel, auch, wenn auch unregelmässig, scheinbare Anfänge von einer Faltenbildung, so dass der Anschein erweckt wird, als ob das Peritonealepithel in ähnlicher Weise wie zur Bildung der Tube sich rinnenförmig einsenke." One other similarity to the development of the duct in *Amblystoma* consists in a caudad transference of the ostium from its original position on the anterior half of the pronephros to one at the anterior end of the mesonephros. In *Amblystoma* the caudad migration is not so great and is seen in the Müllerian evagination, not in the adult ostium.

June, 1902.

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EXPLANATION OF PLATES.

All of the figures of sections were drawn with an Abbé camera and represent their anterior faces, so that what appears at the left in the figures is really at the right in the animal.

ABBREVIATIONS.

<i>ao.</i>	Aorta.	<i>fund. ms'nph.</i>	Fundament of mesonephros.
<i>cav. glm.</i>	Glomerular cavity.	<i>glm.</i>	Glomus or glomerulus.
<i>cav. nph'stm.</i> . . .	Nephrostomal cavity.	<i>hp.</i>	Liver.
<i>cav. sb'glm.</i> . . .	Subglomerular cavity.	<i>marg. p. tab.</i>	Posterior margin of the "shelf."
<i>cl. g.</i>	Germ cell.	<i>ms'drm. l.</i>	Lateral mesoderm.
<i>coel.</i>	Coelome.	<i>ms'ent.</i>	Mesentery.
<i>coel. d.</i>	Dorsal division of body cavity.	<i>ms'mer.</i>	Mesomer.
<i>coel. so.</i>	Coelome of somite.	<i>my'cm.</i>	Myocomma.
<i>coel. v.</i>	Ventral division of body cavity.	<i>my'tm.</i>	Myotome.
<i>cps. Bow. ex.</i> . . .	Outer wall of Bowman's capsule.	<i>nph'stm.</i>	Nephrostome.
<i>cps. Bow. i.</i> . . .	Inner wall of Bowman's capsule, which forms the glomerular covering.	<i>nph'tm.</i>	Nephrotome.
<i>crs. g.</i>	Germinal ridge.	<i>nt'cd.</i>	Notochord.
<i>crs. o'dt.</i>	Oviducal welt.	<i>pi'cr.</i>	Pericardium.
<i>crv. cp. Mpg.</i> . . .	Neck of Malpighian body.	<i>pn.</i>	Lung.
<i>dt. 1; dt. 2</i> . . .	Ducts from the first and second Müllerian evaginations.	<i>pn. + par.</i>	Fusion of lung with the lateral body-wall.
<i>dt. Muel.</i>	Müllerian duct.	<i>scl'tm.</i>	Sclerotome.
<i>dt. precoel.</i> . . .	Precoelomic duct.	<i>so'drm. l.</i>	Somatoderm of the lateral mesoderm.
<i>dt. Wf.</i>	Wolffian duct.	<i>so'drm. t.</i>	Transverse part of the somatic wall of the somite.
<i>ec'drm.</i>	Ectoderm.	<i>so. v-l.</i>	Ventro-lateral angle of somite.
<i>e'coel.</i>	Epicoelome.	<i>spl'drm. l.</i>	Splanchnoderm of the lateral mesoderm.
<i>e'mer.</i>	Epimer.	<i>spl'drm. t.</i>	Transverse part of the splanchnic wall of somite.
<i>evg. 1, 2, 3</i> . . .	First, second, and third Müllerian evaginations.	<i>sul.</i>	Groove.
		<i>tab.</i>	"Shelf."

<i>tae. e'th. α</i>	. .	Thickened epithelial band from the anterior evagination.	<i>tbl. ms'nph.</i>	. .	Mesonephric (inner) tubule.
<i>tae. e'th. β</i>	. .	Thickened epithelial band from the posterior evagination.	<i>tbl. nph'stm.</i>	. .	Nephrostomal (outer) tubule.
<i>tae. e'th. γ</i>	.	The band posterior to the fusion of portions α and β. That which is dorsal to the shelf is designated by γ, that ventral by γ'.	<i>tbl. pr'nph. 1, 2, 3</i>		First, second, and third pronephric tubules.
<i>tae. e'th. γ'</i>			<i>trn. clg.</i>	. . .	Collecting trunk.
			<i>trt. in.</i>	. . .	Alimentary tract.
			<i>va. sng.</i>	. . .	Blood-vessel.
			<i>vst. nph.</i>	. . .	Nephrostomal vestibule or common nephrostome.

PLATE 1.

All figures are of cross-sections and are of *Amblystoma* unless otherwise indicated.

FIG. 1. Stage I. A section through the middle of the seventh somite of the right side of the body. $\times 100$.

FIG. 2. Stage IV. Through the middle of the seventh somite of the left side.

FIG. 3. Stage II. Through the middle of the sixth somite of the right side. $\times 100$.

FIG. 4. *Rana*. Through the ninth (lower) and tenth (upper) somites of the left side. $\times 280$.

FIG. 5. Stage II. Through the middle of a somite of the right side, showing the germ cells in both layers of the lateral mesoderm. $\times 250$.

FIG. 6. *Rana*. Through the anterior half of the sixth somite of the left side of a larva 3.25 mm. long. $\times 280$.

FIGS. 7, 8, 9. Stage V. Three sections through somites of the right side of the body. $\times 335$.

FIG. 7. Cuts somites 11 and 12.

FIG. 8. Passes through the middle of somite 13.

FIG. 9. Passes through the posterior end of somite 13.

FIGS. 10, 11, 12. Stage VI. $\times 335$.

Fig. 10 represents a section through the thirteenth somite of the right side.

Figs. 11, 12 represent sections through the twelfth somite of the left side.

PLATE 2.

All figures are of cross-sections and are of *Amblystoma* unless otherwise indicated.

- FIG. 13. Stage III. Through the middle of somite 13 of the right side. $\times 335$.
FIG. 14. *Rana*. Through the anterior half of the seventh somite of the right side of a larva 4.5 mm. long. $\times 280$.
FIG. 15. *Rana*. Through the last mesonephric blastula of the left side of a larva 8.5 mm. long. $\times 410$.
FIG. 16. *Rana*. Through the eighth somite of the right side. $\times 380$.
FIG. 17. Stage VII. Through the posterior part of somite 11 of the right side. $\times 560$.
FIG. 18. *Rana*. One of the sections from which Figure 102 was constructed. The larva measured 11.5 mm. in length. $\times 410$.
FIG. 19. Stage VIII. Through the eleventh somites of both sides of the body, showing two mesonephric blastulae. $\times 305$.
FIGS. 20-23. Sections of four mesonephric units. All are from the posterior half of the sixteenth somite. That of Figure 22 is from the right side, the others from the left side of the body. The blastula of Figure 20 is in reality smaller than that of Figure 21, Figure 20 being magnified 500 diameters, while Figures 21, 22, 23 are magnified only 340 diameters.

PLATE 3.

All figures, except 30, 34, and 35, are of cross-sections, and all are of *Amblystoma* unless otherwise indicated.

- FIG. 24. Through somite 18 of the right side of a young adult about 60 mm. long. $\times 75$.
- FIG. 25. Through a primary and a secondary mesonephric unit from the left side of a larva 25 mm. long. $\times 188$.
- FIG. 26. Through a primary and secondary mesonephric blastula from the eighteenth somite of the right side of a larva 24 mm. long. $\times 350$.
- FIG. 27. Section of a primary, a secondary, and a tertiary unit from somite 18 of the right side of a larva 25 mm. long. $\times 195$.
- FIG. 28. *Rana*. Section of a mesonephric unit from the right side of the body. The same unit is reconstructed in Figure 30, a dotted line in this figure indicating the level of the section shown in Figure 28. $\times 410$.
- FIG. 29. *Rana*. A section showing a tertiary blastula still connected with the Malpighian body of a secondary unit, from the right side of the body. $\times 410$.
- FIG. 30. *Rana*. A dorso-median view of a wax reconstruction of four mesonephric units and the Wolffian duct of the right side of the body. For a drawing of a cross-section of the most posterior of the four units, see Figure 28.
- FIG. 31. Larva I. A cross-section through the first pronephric nephrostome of the left side of a larva 23 mm. long. $\times 36$.
- FIG. 32. Larva II. Section passing immediately posterior to the first pronephric nephrostome of the right side of a larva 25 mm. long. $\times 48$.
- FIG. 33. The third section behind that shown in Figure 32. $\times 48$.
- FIGS. 34, 35. Two drawings of a wax reconstruction of a mesonephric tubule of left side of the body of a larva 16 mm. long. Figure 34 is the anterior aspect; Figure 35, the ventro-median. $\times 120$.
- FIG. 36. Larva III. Through the first pronephric nephrostome of the right side of a larva 21.5 mm. long, showing the fundament of the anterior Müllerian evagination. $\times 147$. NOTE. — By oversight of the lithographer the nuclei of the tubules are left unshaded.
- FIG. 37. Through the second nephrostome of the left side of the larva shown in Figure 31. $\times 16$.

PLATE 4.

All figures are from cross-sections of *Amblystoma*.

- FIG. 38. Larva IV. Through the second nephrostome of the left side of a larva 44 mm. long. $\times 118$.
- FIG. 39. The fourth section posterior to that shown in Figure 38. It passes through the nephrostomal cavity. $\times 118$.
- FIG. 40. Larva V. Through the second nephrostome and the second Müllerian evagination of the right side of a larva 41 mm. long. $\times 100$.
- FIG. 41. Through the nephrostomal cavity and the fundament of the first Müllerian evagination of the left side of the larva represented in Figure 40. $\times 118$.
- FIG. 42. Larva VI. Through the anterior evagination of the right side of a larva 40 mm. long. $\times 200$.
- FIG. 43. Third section posterior to that of Figure 42. $\times 200$.
- FIG. 44. Larva VI *b*. Through the second nephrostome and the second (posterior) evagination of the left side of a larva 42 mm. long. $\times 200$.
- FIG. 45. Larva XII. Through the degenerate pronephroi of a larva 55 mm. long, in which the gill-slits have closed. It shows, on each side, the glomerular cavity and the epithelial band some distance anterior to the ostium. $\times 88$.
- FIG. 46. A section posterior to that of Figure 45, showing the opening of the right glomerular cavity into the coelome. $\times 118$.
- FIG. 47. Through the ostium of the left side of the larva shown in Figures 45 and 46. $\times 118$.
- FIG. 48. Larva VII. Through the right pronephros of a larva 35 mm. long, showing the precoelomic duct. $\times 200$.
- FIG. 49. Larva XI. Through the first Müllerian evagination (retained to a very late stage) of the left side of a larva 49 mm. long. $\times 156$.
- FIG. 50. Larva IX. Section showing the process of fusion of "duct 1" and "duct 2" of the left side of a larva 50 mm. long. $\times 335$.
- FIG. 51. A section anterior to that of Figure 50, passing through the second Müllerian evagination of the left side. $\times 156$.
- FIG. 52. Through the opposite side of the same larva as that represented by Figure 49, showing a remnant of "duct 1" and the epithelial band. $\times 130$.
- FIG. 53. The sixth section behind that drawn in Figure 44, showing the dwindling end of "duct 2" and the oviducal welt. $\times 250$.

PLATE 5.

All figures are of cross-sections, 54-64 of *Amblystoma*; 65-67 of *Rana*.

- FIGS. 54-64. Larva X. Eleven figures showing the relation between the Müllerian and Wolffian ducts. Figures 54 to 63 represent consecutive sections, of which 54 is the most anterior; Figure 64 a section considerably posterior to that of Figure 63. $\times 420$.
- FIG. 65. Through the common nephrostome of the right side of a larva 25 mm. long. $\times 56$.
- FIG. 66. Through the common opening of the first and second nephrostomes of the right side of a larva 37 mm. long, showing the first (first + second?) Müllerian evaginations. $\times 195$. NOTE.—By an oversight the nuclei of the tubules in Figs. 66, 67, are left unshaded.
- FIG. 67. A section immediately anterior to the third nephrostome of the right side of the larva of Figure 66, showing the fundament of the second (third?) Müllerian evagination. $\times 195$.

PLATE 6.

Cross-sections of *Rana*.

FIGS. 68-77. Ten consecutive sections through the Müllerian evaginations of the right side of a larva 34 mm. long. The fundament is seen to be resolvable into an anterior, questionable evagination (Fig. 68) and two distinct ones (Figs. 74, 76). Figure 77 is on Plate 7. $\times 315$.

PLATE 7.

All figures are of cross-sections.

- FIG. 77. (See explanation of Plate 6.)
- FIG. 78. *Hyla*. A cross-section immediately posterior to the common nephrostome and cutting the third (second + third ?) Müllerian evagination. $\times 308$.
- FIG. 79. *Rana*. A cross-section through the folded portion of the epithelial band of the right side of the body of a larva 35 mm. long. $\times 188$.
- FIG. 80. *Rana*. A section behind that of Figure 79, showing the coalescence of the edges of the folded epithelial band. $\times 188$.
- FIGS. 81-83. *Hyla*. Three sections through the right pronephros of a young larva. The first (Fig. 81) passes through the first nephrostome, cutting the fundament of the first Müllerian evagination; the second (Fig. 82) passes through the common nephrostome, cutting the second (second + third ?) evagination; the third (Fig. 83) cuts the epithelial band midway between the first and the common nephrostome. $\times 150$.
- FIG. 84. *Hyla*. A section of the second (second + third ?) evagination at an earlier stage than that of Figure 78. $\times 308$.
- FIGS. 85, 86. *Hyla*. Two sections from the left side of an abnormal larva. That of Figure 85 passes between the second and third nephrostomes (which have not fused to form a common nephrostome) and cuts the fundament of the second Müllerian evagination. That of Figure 86 passes behind the third nephrostome and cuts the third evagination. $\times 308$.

PLATE 8.

- FIGS. 87-93. *Hyla*. Seven cross-sections through the first evagination of the left side of the body. Figures 87-92 are of consecutive sections; Figure 93 is of the third section posterior to that of Figure 92. $\times 410$.
- FIGS. 94-100. *Rana*. Seven diagrammatic figures of the anterior faces of cross-sections illustrating the development of a primary mesonephric unit of the right side of the body. The somatic portion is shaded by lines, the splanchnic by dots.
- FIG. 101. *Hyla*. A cross-section through the folded epithelial band of the right side of the body. In the next section posterior to this, the edges of the fold coalesce to form the Müllerian duct. In the third posterior, the common nephrostome joins the peritoneum. It is, in this exceptional case, *dorsal* (mesal) to the opening of the Müllerian duct. $\times 410$.
- FIG. 102. *Rana*. An outline drawing, ventral aspect, of two mesonephric blastulae and the Wolffian duct from the left side of the body, made by superposing drawings of six consecutive frontal sections.

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE.

E. L. MARK, *Director*.

*** Abbreviations used:—

B. M. C. Z. for Bull. Mus. Comp. Zoöl.
P. A. A. for Proceed. Amer. Acad. Arts and Sci.
P. B. S. N. H. for Proceed. Bost. Soc. Nat. Hist.

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