

XXIII.—*The Development of the Müllerian Ducts of Reptiles.* By GREGG WILSON, D.Sc.
Communicated by Professor J. C. EWART, F.R.S. (With Two Plates.)

(Read 5th July 1897.)

We have already accounts of the development of the Müllerian ducts of reptiles from BRAUN (1), MIHALKOVICS (2), HOFFMANN (3), and WIEDERSHEIM (4). All of these writers agree in saying that the Müllerian ducts arise quite independently of the segmental ducts; but in view of recent attempts to show that in the other groups of vertebrates there are forms in which the Müllerian ducts are derived from the segmental ducts, it seemed expedient to reconsider this conclusion,* and I have accordingly examined the development of the ducts in *Crocodylus biporcatus*, *Chelone viridis*, and *Lacerta agilis*.

As regards the derivation of the Müllerian ducts from coelomic epithelium, I can only confirm the above-mentioned authorities; but I am able to supplement what they say as to the first foundation and the formation of the anterior end. I find that the anterior end is formed in reptiles, very much as in amphibians, by a modification of the coelomic epithelium in the region of the pronephros. Backward growth proceeds independently alike of the segmental duct and of the epithelium of the body-cavity posterior to the *ostium abdominale*.

BRAUN examined all stages of the development of the ducts in *Lacerta agilis*, *Anguis fragilis*, and *Tropidonotus natrix*, and controlled his results by observations on *Coronella lævis*. He found essential uniformity in all.

In *Anguis fragilis* he described two anterior diverticula of the coelom, separated by a bridge of connective tissue. These are, of course, lined by peritoneal epithelium, and BRAUN remarked that this, at one place on the *pleura costalis*, near its transition to the *pleura visceralis*, shows an incomprehensible thickening—*eine mir völlig unverständliche Verdickung*. BRAUN made no suggestion as to the significance of this thickening, and did not attempt to connect it with the origination of the Müllerian duct. He described the first Anlage of this as further back, where the diverticula open into the coelom proper, and the mesonephros projects freely into the body-cavity. Here he described the peritoneal epithelium as being thickened and raised on a longitudinal ridge that has appeared on the excretory organ. Most anteriorly this ridge is almost quite ventral, but it passes gradually in a spiral till it comes to lie dorsal to the mesonephros. It then accompanies the Wolffian duct to the posterior end of the coelom. In the thickened epithelium at the anterior end of this ridge an invagination appears, and the funnel so formed grows back along the ridge. BRAUN is emphatic as to the independent

* BURGER (5) suggests that probably the Müllerian ducts of reptiles are derived from the segmental ducts. He even makes the statement that there is no evidence of independent origin.

backward growth of the foundation. He had apparently expected to find some such origin of the Müllerian ducts as SEMPER had described in the Elasmobranchs; for he says his results, though so simple, had cost him much trouble, inasmuch as he had expected them to be quite different. He also mentions that he carefully examined the tip of the foundation to determine if it showed any communication with the peritoneal epithelium such as WALDEYER had previously found in the chick; but he saw no evidence of this. The peritoneal epithelium and the growing duct appeared sharply marked off from one another, except in some specimens that had been cut obliquely, or that had suffered otherwise in the course of preparation.

MIHALKOVICS confirmed the observations of BRAUN. He examined the adder and lizard, and found that at the proximal end of the Wolffian body, and lateral to it, the coelomic epithelium becomes cylindric over a triangular area. The edges of the distal end of this area rise till they meet, and form a closed tube or funnel. This runs to a fine point, which grows back in a previously formed *Tubenfalte*. MIHALKOVICS compared the early foundation to a slipper set on end: the elongated oval opening representing the mouth, while the closed part of the shoe corresponds to the part of the duct formed by the union of the lateral edges of the foundation. MIHALKOVICS denied that the development of the Müllerian ducts of reptiles was at all dependent on the mesonephric duct. He believed that growth backwards was effected by increase of the cells at the tip of the foundation.

HOFFMANN's general concurrence in the views of BRAUN and MIHALKOVICS is the more remarkable because of his published work on the ducts of *Rana* and *Triton*, in both of which he described at least partial derivation of the Müllerian ducts from the segmental ducts. In the lizards he mentions a relatively high cylinder-epithelium, lying ventral to the coelom in the region of the pronephros. Further on he describes the epithelium ventral to the pronephros, as distinguished from that of the lateral and median parts by the high form of its cells; and he adds that it is this patch of epithelium that forms the foundation of the Müllerian duct. The heightened epithelium passes laterally till it comes into close proximity to the segmental duct, and can be followed back along this duct to the cloaca—at least, in female specimens. It is by invagination of the high cylindric epithelium of the pronephros that the *ostium abdominale* of the Müllerian duct is formed. HOFFMANN concludes that in the case of the lizards further development is independent of the segmental duct; but, at the same time, he says he is unable to determine whether the growth backwards of the Müllerian duct is also independent of the thickened band of epithelium that lies immediately external to it.

WIEDERSHEIM investigated the development of the Müllerian ducts in *Crocodylus* and *Chelone*. He agrees, in the main, with previous workers on the reptiles, but finds that in *Chelone* the backward growth of the Müllerian duct foundation is dependent on proliferation of the cells of the thickened epithelium outside the duct.

THE MÜLLERIAN DUCTS OF THE CROCODILE.

I shall now describe the various stages examined by me in *Crocodilus biporcatus*.

The first of these (A) is found in a specimen of 10 mm. in extreme length. In this the coelom is simple in the region of the pronephros.* There are, however, lateral ridges along the alimentary canal, indicating the line of the usual secondary connection with the somatopleure (fig. 1, *l.r.*). These ridges gradually become lower as we follow them towards the posterior end, and finally are lost in the mesentery.

The first section through the pronephros shows a nephrostome, one tubule, and the anterior end of the glomus. The nephrostome has already lost connection with the pronephros, so that the funnel is quite isolated; while, posterior to the nephrostome, the pronephros has degenerated so far that through several sections it ceases to appear. It is noteworthy, however, that the heightened epithelium of the nephrostome extends out on all sides, and passes back towards the posterior end as a distinct thickened band. This unites the anterior nephrostomes, and passes gradually into the ordinary epithelium of the coelom.

The next stage that I have is got in a specimen (B) 12 mm. long. Anterior to the excretory organ and the glomus, we see in transverse section three divisions of the coelom; and in the dorsal diverticula formed by secondary fusion of the alimentary canal with the body-wall, we find again distinct thickenings of the epithelium. These, at first, are ventral in position (fig. 2, *m.d.*); but, anterior to the beginning of the glomus, they lie on the lateral and dorsal walls of the diverticula (fig. 3). The lateral anterior part of the embryonic excretory organ found in A has disappeared, and with it its nephrostomes; but a few sections further back than the anterior of the glomus, the remainder of the embryonic excretory organ is met with, and just external to this the above-mentioned thickening runs along the lateral wall of the coelom. It is not, however, only on the lateral wall immediately external to the pronephros that the thickening is found passing back, for, opposite the anterior end of the mesonephros, the thickening, which is at first simple, passes back as two distinct bands, one of which lies close to the mesonephros, while the other is quite ventral to the diverticulum (fig. 4). The lateral wall shows an intermediate area of ordinary coelomic epithelium. A little further back, where the dorsal diverticulum opens into the coelom proper, the ventral thickening is altogether separated from the dorsal one (fig. 5). It gradually becomes less conspicuous, and passes into the ordinary epithelium of the coelom.

The occurrence of this band recalls the ventral extension of the Müllerian ducts in elasmobranchs, and the temporary ventral growth of the Müllerian duct foundation in *Rana*.

The more dorsal backward prolongation of the lateral plate narrows gradually as it passes back. It comes to lie on a bridge of tissue that is between the cardinal vein and the mesonephros; and at the same time it becomes grooved. External to the thickening,

* Identified by WIEDERSHEIM.

a second furrow appears, indenting the lateral wall of the coelom, and as it gets deeper, cutting off the Müllerian duct foundation from the lateral wall (fig. 6). Further back, the band of thickened epithelium passes on to the mesonephros. Some twenty-five sections—about $150\ \mu$ —posterior to the passing over of the Anlage to the excretory organ, the grooved thickening closes to form a tube. Through thirty sections more this remains open; then the Müllerian duct foundation abruptly ends, and its tip or growing-point appears, independent alike of the contiguous coelomic epithelium and of the segmental duct that lies just internal to the Müllerian duct. The segmental duct, it is true, shows an obliquity in a few of the sections near the termination of the Müllerian duct, and the obliquely cut side nearest to the Müllerian duct Anlage might, at first sight, be supposed to show a process of budding; but careful examination makes it clear that the Müllerian and segmental ducts are well marked off from one another, and the staining differences emphasise this distinction. The obliquity of the sections of the segmental duct in the neighbourhood of the growing point of the Müllerian duct is to be explained by the intrusion of the Müllerian duct causing the segmental duct to deviate from its first position close to the coelomic epithelium.

Outside the Müllerian duct there is a distinct thickening of the coelomic epithelium, and this is specially noticeable in the region immediately posterior to the growing tip of the duct; but the thickening does not appear to take part in the formation of the duct proper, though it may contribute to the formation of sheathing tissue.

It thus appears that the simple epithelial thickening found in the region of the pronephros in specimen A is represented in B by a similar lateral plate with two posterior continuations, the one ventral, and passing into the ordinary coelomic epithelium, the other dorsal, passing into the already tubular Müllerian duct. It is, of course, open to anyone to assert that there may be a missing intermediate stage between A and B, showing trace of the derivation of some of the cells of the Müllerian duct from the segmental duct. I can only say that the anterior of the Müllerian duct is clearly derived from the coelomic epithelium, and that at such an early stage as is represented in B there is no evidence of any other derivation; while growth backwards is distinctly not dependent on any budding from the segmental duct.

The two new facts that I am able to add from my examination of stages A and B to what WIEDERSHEIM has written on the subject are:—(1) That the anterior and first foundations of the Müllerian ducts are thickened areas of the coelomic epithelium in the region of the pronephros; and (2) that there is a distinct ventral development of this foundation, comparable to the temporary ventral development of the Müllerian duct in *Rana*.

Both of these facts are made clearer by the study of longitudinal horizontal sections. Fig. 7 represents such a section through an embryo that is somewhat further advanced than B. The open *ostium abdominale* is seen, and stretching away in front of it, and anterior to the mesonephros, is the thickened plate of epithelium that has already been described as the first foundation of the Müllerian duct. Fig. 8 shows a more ventral

section of the same series. In it the thickened plate is seen yet further forward in the lateral diverticulum of the coelom. Figs. 9 and 10, which represent still more ventral sections, show the ventral extension of the plate: in the former, the thickening appears still dorsal and internal, but projecting towards the lateral wall of the coelom; in the latter, the seventy-fourth section more ventral than fig. 9, the end of the ventral extension of the anterior plate is seen raised on a more prominent ridge, just anterior to the liver.

My third stage (C), found in a specimen of probably less than 20 mm. in length, shows a modification of the anterior thickened epithelial plate, that is interesting as being similar to what is found in amphibia (6). The plate is undermined by a diverticulum of the coelom; and by the splitting of the plate the foundation is partly divided into two areas, the one of which is connected with the ventral extension of the plate, while the other leads directly back to the Müllerian duct.

The pronephros of C has degenerated completely, but along the anterior coelomic diverticulum there is still a distinct band of thickened epithelium. This spreads out to form a broad plate in the region just in front of the mesonephros. Under this plate a slight diverticulum of the coelom is seen (*d.*, fig. 11), and examination of the posterior margin of the plate reveals the fact that the plate has been partially divided by the breaking down of the slight partition between the old diverticulum and the new one. The inner end of the plate remains projecting laterally between the united diverticula, while the outer end projects slightly from the lateral wall (*r.*, fig. 11). From the fact that the external remnant of the plate continues to extend into the body-cavity through a considerable number of sections, it is evident that the anterior plate formerly extended much further.

My next specimen (D) is 19 mm. in length, and illustrates even better than the last one the division of the anterior foundation.

The anterior diverticula expand posteriorly, and along the lateral epithelium, but nearly dorsal, there appears a distinct narrow band of thickened epithelium. Where the glomus first appears, projecting slightly forwards into the diverticula, the ridge spreads out to form a plate, and at the same time the diverticula open into the main division of the coelom. The anterior part of the plate has apparently been largely obliterated by the secondary attachment of the *radix mesenterii* to the lateral body-wall. The plate is at this stage divided at the anterior end of the mesonephros, and, as in C, the two posterior (ventral and dorsal) continuations of the thickened plate pass back, separated by a deep channel. The dorsal division hangs free into the coelom, which has undermined it from its ventral edge; and it only gradually passes into connection with the mesonephros. The ventral division is found to pass the base of the lung, and ends just anterior to the beginning of the liver.

I have examined specimens up to 75 mm. in length, and all of them show similar relations of parts. In all, there is the anterior lateral plate. It is usually slightly undermined, and is divided posteriorly to form two bands, one of which leads to the

Müllerian duct, while the other ends close to the anterior attachment of the liver. It is noteworthy that the ventral extension of the anterior plate passes posteriorly across the secondary bridge, connecting the alimentary tract and the lateral body-wall, and comes to project freely into the coelom from near the base of the lung.

THE MÜLLERIAN DUCTS OF CHELONE.

As I mentioned above, the development of the Müllerian ducts of *Chelone* has been investigated by Professor WIEDERSHEIM. He describes, in a 13 mm. embryo, a well-marked proliferation of the peritoneal epithelium on the side of the anterior region of the mesonephros. This extends to the parietal peritoneum. The formerly smooth surface has become rough and uneven, and in numerous places involution of the epithelium is visible, and proliferation inwards. In an embryo of 21 mm. the inequalities have, for the most part, disappeared, and in their place there is a rapidly increasing fold hanging into the body-cavity. This fold, according to WIEDERSHEIM, hangs down the side of the mesonephros, is applied to it, and fuses with it; and so the *ostium abdominale* is formed. Three sections further towards the posterior the duct stops, and is followed by a solid pointed rod, such as occurs at the growing tip of the foundation in the crocodile. As in the case of the crocodile, this solid rod lies in the immediate neighbourhood of the mesonephric duct and of the *Tubenfalte*. In the rod, a few sections posterior to the ostium, a slight lumen appears.

As to backward growth, WIEDERSHEIM asserts that there is not merely appositional growth, such as is generally described for Amniota. He figures two sections, showing proliferation inwards of the thickened epithelium of the *Tubenfalte*; and he believes that the coelomic epithelium thus contributes directly to the backward growth of the foundation.

By the kindness of Professor WIEDERSHEIM, in whose laboratory much of the work recorded in this paper was done, I have had an opportunity of examining a number of series of sections of embryos of *Chelone*; and I shall now state the facts that I have observed.

In an embryo (A) of 13 mm. in length, there is a lateral thickening of the coelomic epithelium lining the anterior diverticulum, and extending on to the excretory organ, along which it passes, as described by WIEDERSHEIM.

A specimen (B), 21 mm. long, shows the lateral thickening to be undermined anteriorly (fig. 12). Further back, the plate is divided, as in the case of the crocodile, by the breaking down of the partition between the two diverticula (fig. 13). One remnant of the thickening projects into the coelom from the ventral body-wall; another is intimately connected with the mesonephros (fig. 14). In the posterior extension of the plate that passes along the mesonephros there is a funnel-like pit (fig. 15). This conical funnel is the *ostium abdominale tubæ*. It is quite distinct from the mesonephric duct, and its inner pointed end, which extends a very short distance towards the posterior, is quite independent of the epithelial thickening that continues back external to the mesonephric duct.

The next stage is found in an embryo (C) of 25 mm. In this, as in B, the lateral thickened area of the coelomic epithelium is undermined; and ventral and dorsal extensions of it pass towards the posterior. Here, also, the ostium lies into the side of the mesonephros. The funnel turns towards the posterior, and its lumen may be followed back through several sections. Further back there is a solid rod of cells in direct continuation of the tube, but this extends only through a few sections. On the right side the tip of the rod is quite distinct from the segmental duct, beside which, however, it lies. On the other side I had, at first, difficulty in distinguishing the tip of the Müllerian duct from the obliquely cut segmental duct, which, from being somewhat remote from the coelomic epithelium, passes close up to it, just behind the Müllerian duct. Fig. 16 shows the blunt point of the latter lying close to the segmental duct. Fig. 17 shows the next section with no remainder of the Müllerian duct, but with the segmental duct filling the space immediately posterior to the end of the Müllerian duct. Here, as in other cases, we must assume that the growing tip of the Müllerian duct thrusts itself between the segmental duct and the coelomic epithelium, and causes a shifting of the position of the former. Fig. 18 bears out this view by showing the altered position of the segmental duct in the second section, posterior to the end of the Müllerian duct. It shows, at the same time, the inward proliferation of the epithelial cells in this neighbourhood, described by Professor WIEDERSHEIM; but I would point out that these are probably destined to take part in the formation of the sheath of the Müllerian duct, rather than the duct itself; for the posterior end of the duct is absolutely distinct from the thickened epithelial band (fig. 16).

A further stage is met with in an embryo (D) of 23 mm., in which the Müllerian ducts are considerably better developed. The relations of parts at the anterior end of the foundation are similar to those described in C. The *ostium abdominale* lies, as in other specimens, on the side of the mesonephros, at its anterior end; the open funnel passes inwards and back towards the posterior through five or six sections; then a rod-like continuation is met with in several sections, behind which a lumen is again met with; and after a few sections the foundation ends. In this specimen, again, the tip of the Müllerian duct lies on the mesonephric duct.

The last specimen (E) that I have to describe is of unknown length. It is considerably larger than D, and shows the relations of the various parts more distinctly than any other stage that I have.

A few sections after the beginning of the excretory organ, the lateral diverticulum is met with. Projecting into this from the side of the excretory organ is the thickened epithelial plate, in which, further back, the *ostium abdominale* appears. Just outside the excretory organ, on the lateral wall of the coelom, there is a remnant of the original anterior plate, and it projects towards the thickening on the excretory organ. In more posterior sections the ventral thickening may be traced passing back, and extending far round ventralwards.

The *ostium abdominale* leads to a solid foundation, which is found through many

sections before a part is reached in which a lumen occurs. The lumen is distinct till within a few sections of the end of the foundation. The solid rod that forms the tip of the foundation lies external to the segmental duct, touching it, but independent of it, and remote from the coelomic epithelium. In the section immediately posterior to that which contains the last cells of the rod-like apex there is no appearance of budding of the cells of the mesonephric duct, such as one would expect if growth backwards of the Müllerian duct were dependent on it; and there is no indication of any contribution of cells from the coelomic epithelium to add to the growing tip.

It thus appears clear that in this specimen growth backwards is by apical proliferation; and I conclude that, as in the formation of the anterior end, so in the manner of growth backwards there is essential agreement between *Chelone* and *Crocodylus*.

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DESCRIPTION OF FIGURES.

Fig. 1. Transverse section through the pronephric region of crocodile of 10 mm. in length. *l.r.* is the lateral ridge that in older stages forms the secondary connection between the alimentary canal and the body-wall.

Fig. 2. Section across crocodile 12 mm. in length, showing thickened epithelium (*m.d.*) on the ventral wall of the coelomic diverticulum, anterior to the glomus.

Fig. 3. Section through the same embryo further back, and showing an extensive lateral epithelial thickening on a level with the anterior end of the glomus.

Figs. 4 and 5. Sections through the same embryo further back, showing the two posterior extensions of the pronephric thickened plate.

Fig. 6. Section through the same embryo, showing the grooved Müllerian duct foundation in relation to the mesonephros.

Figs. 7, 8, 9, 10. Sections from a series through an embryo further advanced than stage B, and showing the lateral and ventral extension of the Müllerian duct foundation.

Fig. 11. Transverse section through a crocodile embryo of about 20 mm., showing undermining of the anterior lateral plate of thickened epithelium.

Figs. 12, 13, and 14. Sections through embryo of *Chelone* of 21 mm., showing undermining of anterior lateral plate.

Fig. 15. Section through the same embryo, showing the *ostium abdominale*.

Fig. 16. Section through *Chelone* embryo of 25 mm., showing the end of the Müllerian duct in close proximity to the segmental duct.

Fig. 17. Next section posterior to that shown in fig. 16, to show the segmental duct passing obliquely behind the Müllerian duct.

Fig. 18. Next section to that illustrated in fig. 17. The segmental duct is seen in the position occupied further forward by the Müllerian duct.

<i>al.c.</i> = alimentary canal.	<i>lu.</i> = lung.
<i>ao.</i> = aorta.	<i>m.d.</i> = Müllerian duct or its foundation.
<i>br.</i> = bronchus.	<i>mes.</i> = mesonephros.
<i>c.</i> = coelom.	<i>n.</i> = nephrostome.
<i>ch.</i> = notochord.	<i>o.</i> = <i>ostium abd. tub.</i>
<i>c.v.</i> = cardinal vein.	<i>pr.</i> = pronephros.
<i>d.</i> = diverticulum.	<i>r.</i> = remnant of lateral plate.
<i>gl.</i> = glomus.	<i>s.d.</i> = segmental duct.
<i>li.</i> = liver.	<i>tr.</i> = trachea.

DR GREGG WILSON: MÜLLERIAN DUCTS OF REPTILES—PLATE I



