

The following papers were read:—

1. The Development of the Subdivisions of the Pleuro-peritoneal Cavity in Birds. By MARGARET POOLE.*

[Received February 9, 1909.]

(Text-figures 24–37.)

The subject of this paper was suggested to me by Professor Bourne, and it was by his advice that I undertook a reinvestigation of the development of the subdivisions of the body-cavity in birds; my object being to confirm and enlarge the results put forward in a paper on the subject by Mr. G. W. Butler in these 'Proceedings.' At that time I knew of no other work on this part of the question; and it was only when I had almost completed my study of the development of these structures, that Mr. Beddard kindly referred me to the work of Dr. Bertelli. This I found was published in an Italian journal not—so far as I could discover—taken in by any of the scientific libraries either in Oxford or London; and it was only by the very great kindness of Dr. Bertelli, who sent me a copy, that I was at last able to see it. I then found that he had worked out and described in great detail and with admirable clearness, almost the whole of the development upon which I was engaged. But since this valuable paper is practically inaccessible to English students, Dr. Bourne advised me to publish the results of my own investigations, which I had arrived at independently. I may here state that my results entirely confirm those of Mr. Butler, and, except in two small points, those of Dr. Bertelli also.

The work was done in the Zoological Laboratory at Oxford by the kindness of Professor Bourne, and I wish to take this opportunity of expressing my warmest thanks to all in the Department—and especially to Mr. Goodrich—who have helped me by continual suggestions and advice.

I wish likewise to express my gratitude to Dr. Bertelli for his kindness, not only in sending me a copy of his work, but also for his permission to make any use of his observations in my own paper.

NOMENCLATURE.

The pulmonary aponeurosis of Huxley [12] and Butler [9]—diaphragme pulmonaire of Sappey [16]—Bertelli [6, 8] calls the diaframma ornitico.

The oblique septum of Huxley, employed by Butler, Beddard and others—the diaphragme thoraco-abdominal of Sappey—Bertelli does not consider to be a septum at all, but only the ventral walls of the intermediate air-sacs together with the posterior wall of

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the pericardium. Butler takes the pulmonary aponeurosis and the oblique septum as forming together a single septum, which he terms the avian diaphragm. The backward prolongation of this in connection with the development of the posterior air-sacs, he calls the oblique abdominal septum. Since, however, Bertelli's diaframma ornitico is but half of Butler's avian diaphragm, I shall use neither of these terms, but call the whole of Butler's avian diaphragm together with his oblique abdominal septum, the post-pulmonary septum; this, in the early stages of its development, corresponds to what Bertelli calls the "diaframma primario."

For the air-sacs I shall use the terms employed by Bertelli in his earlier paper [7]:—Anterior intermediate, posterior intermediate, and posterior; except for the latter, which he calls abdominal, Butler uses the same names.

The blind anterior diverticula of the peritoneal cavity I shall call, after Butler, the pulmo-hepatic recesses; these are the "recessi polmonali-enterici" of Bertelli. Butler's pulmo-hepatic ligaments correspond to Bertelli's ventral pulmonary ligaments, and I shall use these latter terms in describing the development.

Finally, I shall call, with Butler, the horizontal septum of Beddard [1] the post-hepatic septum; since this term, while indicating its essential position, does not depend upon its direction which is very variable.

I. EMBRYOLOGY.

The Post-pulmonary Septum.

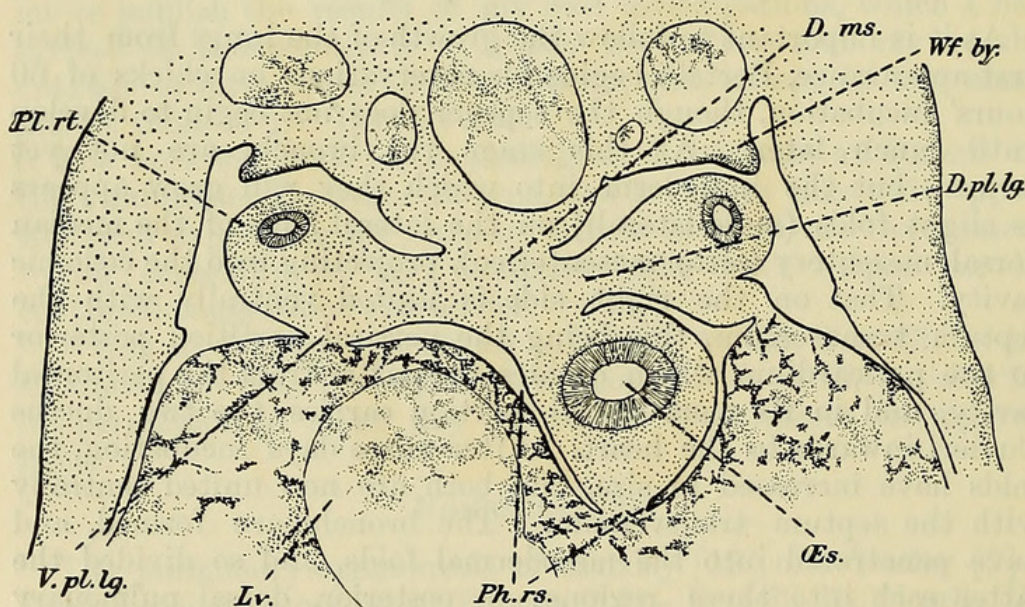
As it is important to follow the growth of the lungs from their first appearance, Bertelli begins his observations on chicks of 60 hours' incubation, though the septum does not begin to develop until much later. At this stage the bronchi are not yet formed, but the mesoderm into which they will grow appears as slight folds (meso-laterali) on the lateral faces of the median dorsal mesentery (setto mesenterico), projecting into the coelomic cavity. That on the right side is united ventrally with the septum transversum, this being the vertical partition posterior to the pericardium which divides the latter from the peritoneal cavity, and in its more dorsal portion carries the two ductus Cuvieri inwards to the heart. After three days' incubation, the folds have increased in size, and both are now united ventrally with the septum transversum. The bronchi are formed, and have penetrated into the mesodermal folds, and so divided the latter each into three regions: a posterior, dorsal pulmonary ligament, a median, pulmonary rudiment (abbozzo polmonale), and an anterior, ventral pulmonary ligament. Between the ventral pulmonary ligaments on each side, and the median dorsal mesentery, lie the narrowed anterior prolongations of the peritoneal cavity—the pulmo-hepatic recesses. On the fourth day, the relations between these parts remain the same, but in a chick of five days' incubation the pulmonary rudiments have greatly

increased in size, and the ventral pulmonary ligaments have united ventrally with the lower edge of the median dorsal mesentery, the dorsal surface of the liver, and the pericardio-pleuro-peritoneal membrane. The latter is what is called in younger stages the septum transversum; it now forms a mass of tissue separating the pericardium from the pleural and the peritoneal regions of the cœlom. Posteriorly, the ventral pulmonary ligaments spread out laterally to unite with the antero-lateral corners of the now well-developed liver; and at the same time the dorsal pulmonary ligaments and the lung rudiments themselves assume an almost transversely horizontal position; so that in this region there is now a septum across the cœlomic cavity, complete except at its extreme lateral margins where the pleural and peritoneal divisions communicate by a narrow aperture on either side. At a later stage these passages will be closed by the union of the ventral pulmonary ligaments and the lateral body-walls, and thus the post-pulmonary septum—Bertelli's "diaframma primario"—will be formed.

The pronephric folds appear at this stage as thickenings of the connective tissue on the external walls of the anterior part of the pleuro-peritoneal cavity; posteriorly they are seen in close connection with the developing Wolffian bodies on the dorsal wall of the cœlomic cavity.

Text-fig. 24 is of a transverse section of a chick of 5 days'

Text-fig. 24.



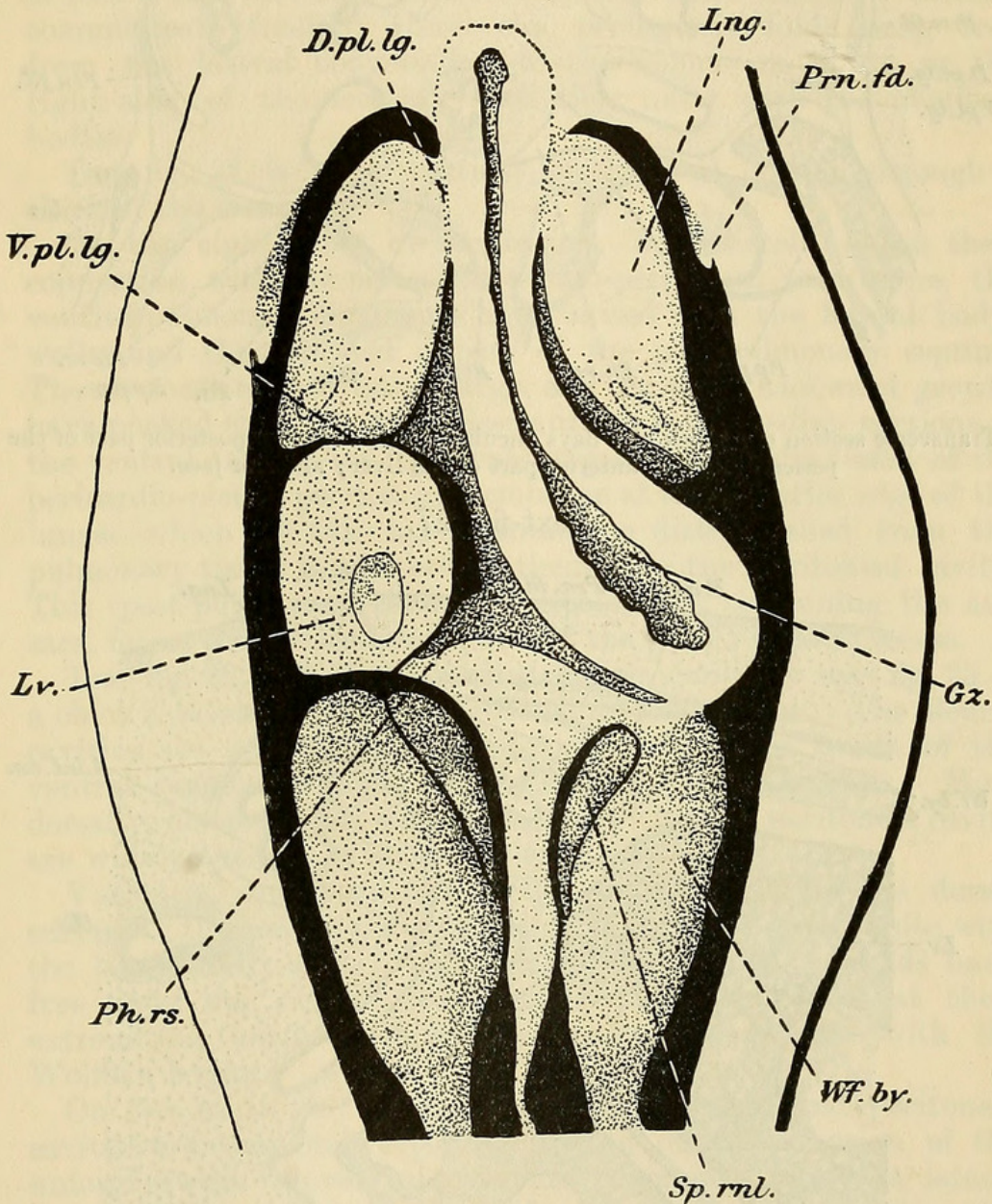
Transverse section of a chick of 5 days' incubation, through the anterior region of the liver; anterior face.

For explanation of abbreviations in text-figures see p. 235.

incubation, taken through the region where the septum will be formed, the anterior face being shown. The developing pronephros is seen on the dorsal wall of the pleuro-peritoneal cavity.

Text-fig. 25 is a slightly diagrammatic reconstruction from longitudinal horizontal sections of a chick of six days' incubation, seen from the ventral side. The pericardium and heart, the ventral part of the alimentary canal, and all the liver except the most dorsal corner of the right lobe have been removed.

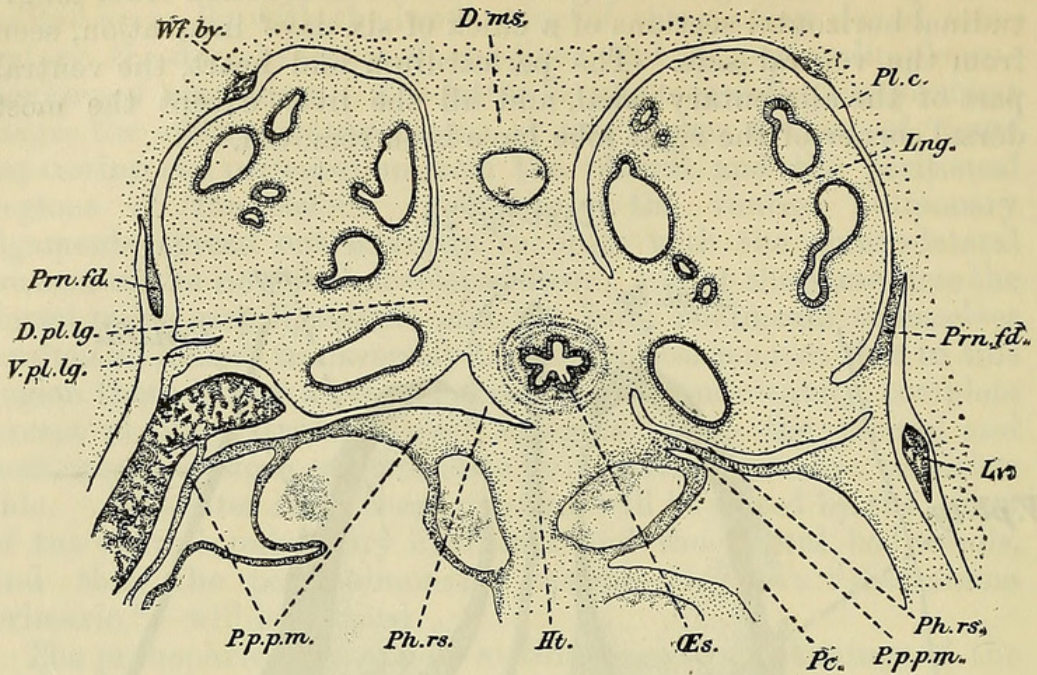
Text-fig. 25.



Slightly diagrammatic reconstruction from horizontal longitudinal sections of a chick of 6 days' incubation; seen from the ventral side. The pericardium and heart, the ventral part of the alimentary canal, and all the liver except the most dorsal corner of the right lobe have been removed.

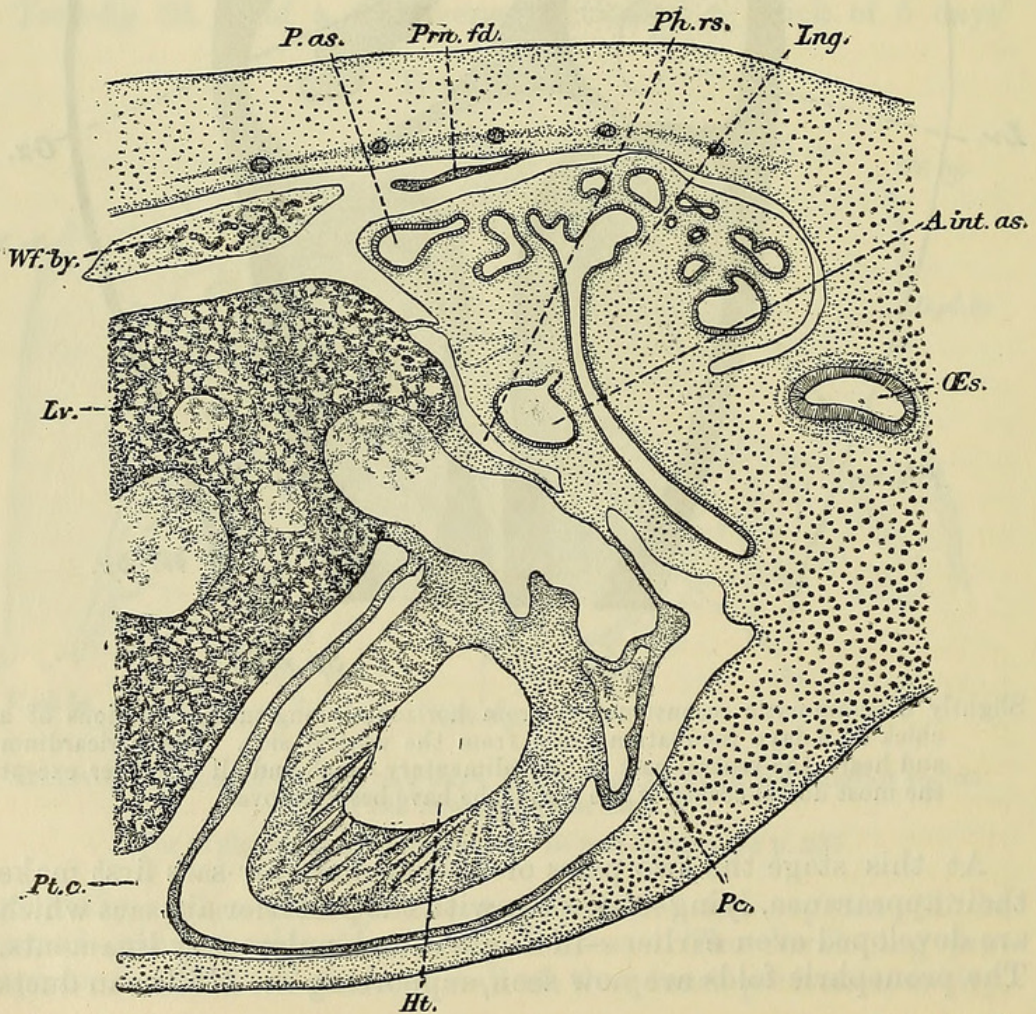
At this stage the two pairs of intermediate air-sacs first make their appearance, lying—together with the posterior air-sacs which are developed even earlier—in the ventral pulmonary ligaments. The pronephric folds are now seen, supporting the Müllerian ducts

Text-fig. 26.



Transverse section of a chick of 7 days' incubation, through the posterior part of the pericardium and anterior part of the liver; anterior face.

Text-fig. 27.



Longitudinal vertical section of a chick of 7 days' incubation, taken a little to the left of the middle line; seen from the right side.

at their extremities, projecting from the dorsal walls of the pleural parts of the coelomic cavity. Posteriorly they unite with the pericardio-pleuro-peritoneal membrane, and thus for a short space, the pleural and peritoneal cavities are separated from one another. This is shown in text-fig. 26, which is of a transverse section of a chick of 7 days' incubation. On the left side of the section this connection has disappeared; on the right side it is lost a few sections further back, and then the two cavities communicate freely. Here the pronephric folds hang free from the lateral body-walls into the coelom—as shown on the right side of the section—until they unite with the Wolffian bodies.

Text-fig. 27 is of a vertical longitudinal section through a chick of the same age.

On the eighth day of incubation, immediately above their connection with the pericardio-pleuro-peritoneal membrane, the ventral pulmonary ligaments have united with the lateral body-walls, and thus formed a part of the post-pulmonary septum. The air-sacs are now quite large, and by their backward growth have pushed the connective tissue of the more median portions of the ventral pulmonary ligaments, together with the tissue of the pericardio-pleuro-peritoneal membrane at the posterior edge of the lungs—which at this time cannot be distinguished from the pulmonary tissue itself—before them into the peritoneal cavity. This post-pulmonary tissue on either side, containing the air-sacs, forms the antero-lateral wall of the pulmo-hepatic recess.

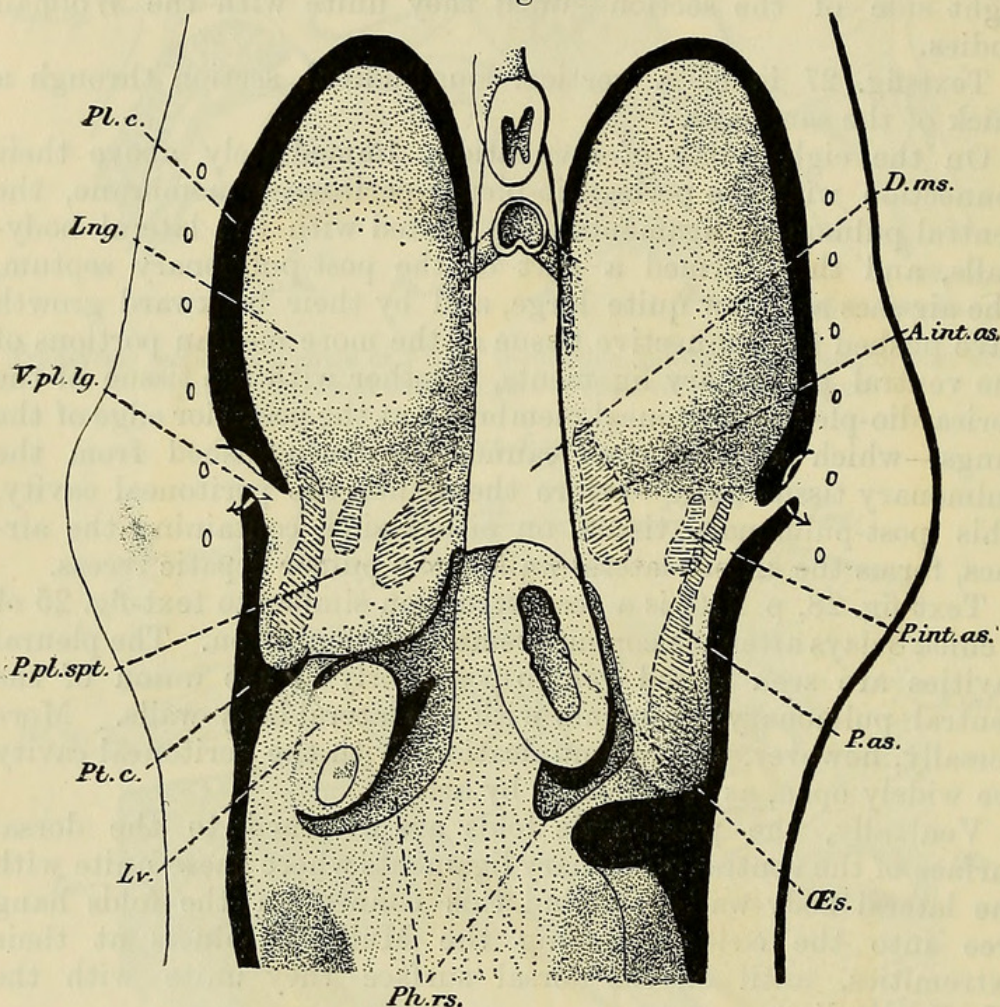
Text-fig. 28, p. 216, is a reconstruction similar to text-fig. 25 of a chick 8 days after the commencement of incubation. The pleural cavities are seen closed ventro-posteriorly by the union of the ventral pulmonary ligaments with the lateral body-walls. More dorsally, however, the communications with the peritoneal cavity are widely open, as is indicated by arrows.

Ventrally, the pronephric folds are attached to the dorsal surface of the ventral pulmonary ligaments where these unite with the lateral body-walls; behind this connection the folds hang free into the coelom, bearing the Müllerian ducts at their extremities, until on the dorsal surface they unite with the Wolffian bodies.

On the tenth day of incubation, the pleural and peritoneal cavities are completely separated by the dorsal extension of the union between the ventral pulmonary ligaments and the lateral body-walls on either side. Besides this, however, the backwardly growing post-pulmonary tissue containing the air-sacs, which appeared on the eighth day as projecting freely into the peritoneal cavity, has become united with the lateral body-walls behind the ventral pulmonary ligament connection. As this union takes place gradually during the ninth day, from before backwards, the anterior prolongations of the peritoneal cavity—previously forming the lateral boundaries of the post-pulmonary masses of tissue—become completely obliterated. Thus the post-pulmonary septum, Bertelli's "*diaframma primario*," is established.

The anterior intermediate air-sacs are at this stage large oval vesicles lying in the post-pulmonary septum near the middle line and close against the base of the lungs. The posterior intermediate air-sacs are much smaller, and enclosed in the extreme lateral portions of the same septum. The posterior air-sacs, arising from the postero-lateral corners of the lungs, are very large and project backwards for a considerable distance into the peritoneal cavity. Bertelli says that their posterior ends project

Text-fig. 28.



Reconstruction, similar to text-fig. 25, of a chick of 8 days' incubation.

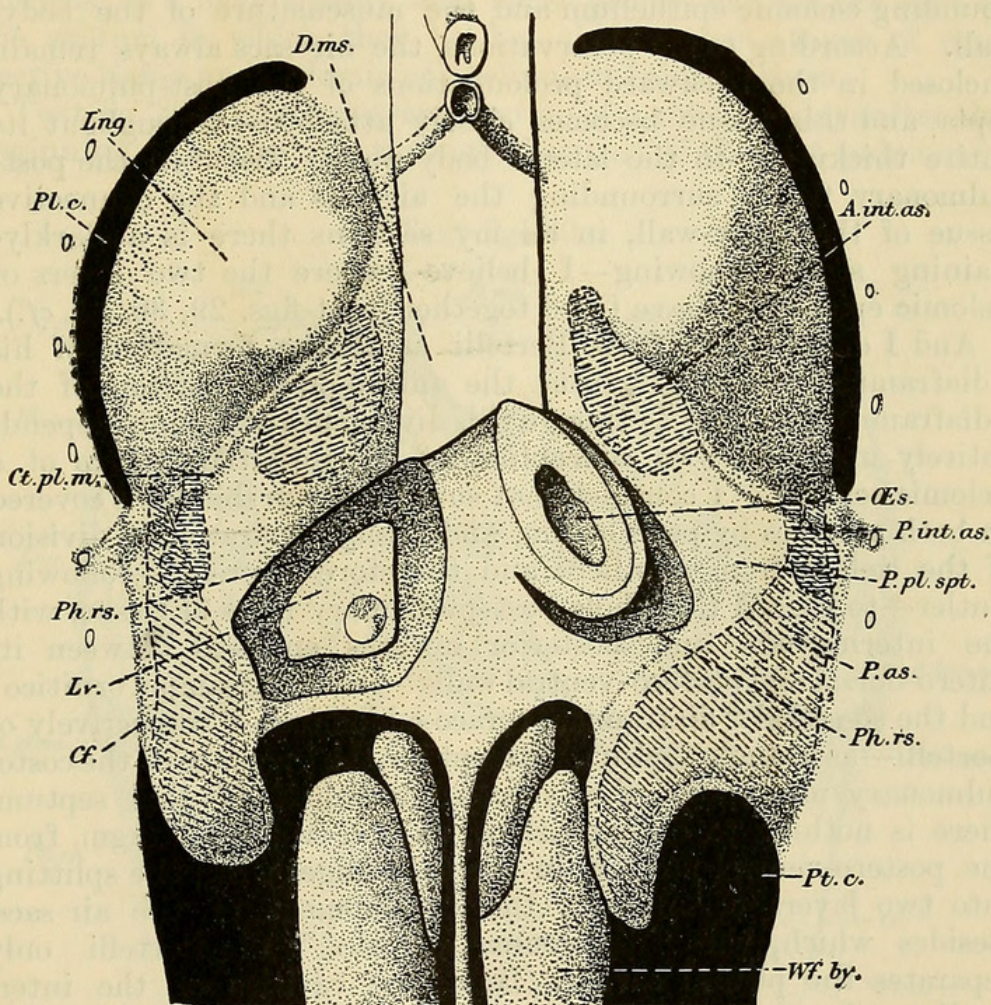
beyond the diaphragmatic tissue and thus “resta libero nella cavità addominale tra la parete laterale di questa, il corpo di Wolff e l'intestino a sinistra, tra la parete laterale dell'addome, il corpo di Wolff e il fegato a destra.” On this point my own observations differ slightly from his. I believe that the posterior ends of these air-sacs never extend beyond the hindmost edge of the post-pulmonary septum. However far these air-sacs extend among the abdominal viscera, they always push before them a layer of connective tissue covered with cœlomic epithelium.

Text-fig. 29 is of a reconstruction, similar to text-figs. 25 and 28,

of these structures in a chick of 10 days' incubation. In addition, this figure shows the origin of the first costo-pulmonary muscles from the fifth ribs, which run into the post-pulmonary septum following the ventral and posterior border of the lungs. These will be supplemented by others arising later from the third, fourth, and sixth ribs, and give rise to the aponeurotic membrane, which in the adult covers the postero-ventral face of the lungs and separates these organs from the intermediate air-sacs.

The pronephric folds are attached ventrally to the antero-lateral walls of the post-pulmonary septum, and dorsally are connected with the external margins of the Wolffian bodies.

Text-fig. 29.



Reconstruction, similar to text-figs. 25 and 28, of a chick of 10 days' incubation.

The post-pulmonary septum, now fully formed from the median dorsal mesentery in the middle line, the pericardio-pleuro-peritoneal membrane with the ventral pulmonary ligaments, and slightly also from the pronephric folds laterally, constitutes a complete partition dividing the coelomic cavity into a pleural and a peritoneal portion. Bertelli calls this septum the

“*diaframma primario*” because he says it is a temporary structure which will later give rise to the “*diaframma definitivo*” and also to the ventral walls of the intermediate air-sacs. At this stage—ten days after incubation—he says the anterior intermediate air-sacs lie enclosed in the primary diaphragm, and by splitting it into two layers, form with their dorsal walls the definitive diaphragm and with their ventral walls the so-called “*diaframma toraco-addominale*.” The posterior intermediate and the posterior air-sacs likewise split the primary diaphragm into two layers; and behind this he describes them as lying in the lateral abdominal walls, covered by their peritoneum, and bounded externally by the connective tissue which surrounds the muscles of the body-wall. Now I do not find any signs of these air-sacs actually penetrating into the walls of the peritoneal cavity so as to lie between its bounding cœlomic epithelium and the musculature of the body-wall. According to my observations, the air-sacs always remain enclosed in the backward prolongations of the post-pulmonary septa, and this tissue becomes closely attached—throughout its entire thickness—to the lateral body-walls. Between the post-pulmonary tissue surrounding the air-sacs and the connective tissue of the body-wall, in all my sections there is a darkly-staining streak, showing—I believe—where the two layers of cœlomic epithelium have fused together (text-figs. 29, 30, 31, *cf.*).

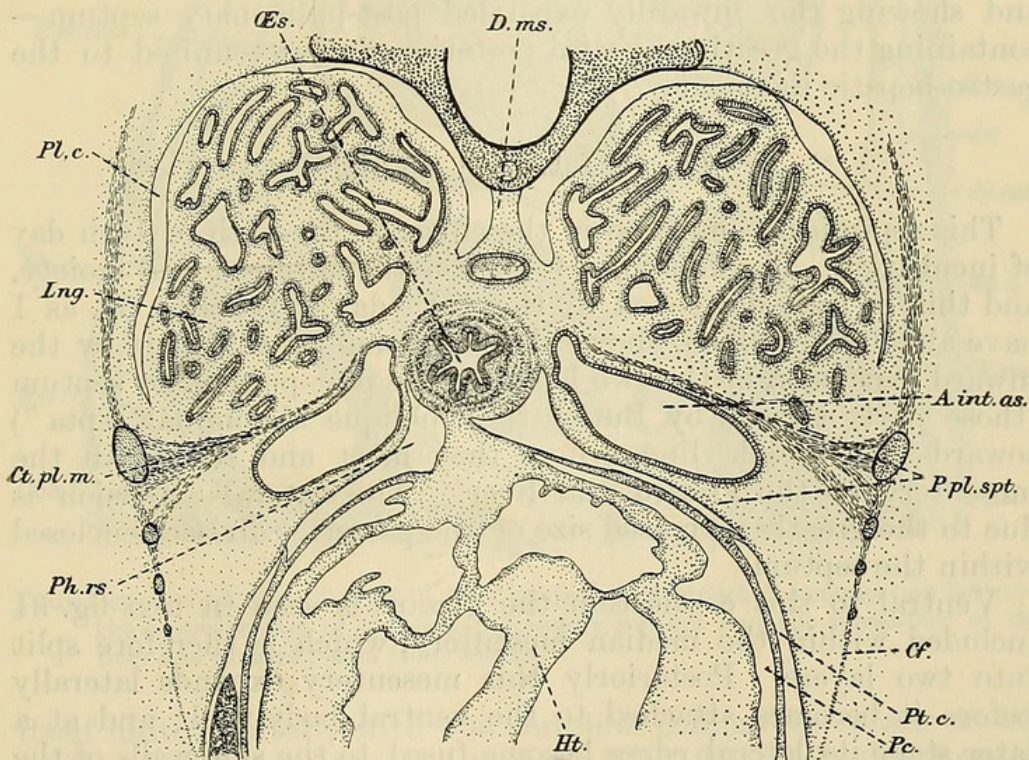
And I differ a little from Bertelli as to the formation of his “*diaframma definitivo*” from the antero-dorsal portion of the “*diaframma primario*”; though this divergence of opinion depends entirely upon my own conception of the essential nature of a cœlomic septum. I consider that such a septum should be covered on both surfaces by peritoneum, and really separate one division of the cœlom from another; and therefore I prefer—following Butler—to regard the whole post-pulmonary mass of tissue, with the intermediate and posterior air-sacs enclosed between its antero-dorsal and postero-ventral walls—the “*diaframma ornitico*” and the so-called “*diaframma toraco-addominale*” respectively of Bertelli—as a single septum. Except for the presence of the costopulmonary muscles in the antero-dorsal half of this septum, there is nothing to distinguish it, as the true diaphragm, from the postero-ventral portion, in the first stages when the splitting into two layers occurs with the development of the air-sacs. Besides which, the “*diaframma ornitico*” of Bertelli only separates the pleural cavities from the cavities of the intermediate air-sacs, and is consequently covered only on one face by peritoneal epithelium; the other surface being invested by the endoderm of the air-sacs. What I have described as the post-pulmonary septum, on the other hand, does really separate the pleural from the peritoneal cavity, and is covered ventrally, as well as dorsally—except where the septum is continuous with the tissue of the lungs—by cœlomic epithelium. The interposition of the air-sacs between its two surfaces, does not, I believe, essentially alter the nature of the whole. My observations

entirely confirm Butler's conclusion, that "the avian diaphragm is seen to be completed as a single structure, and its separation into its two laminae is a secondary detail arising in connection with the development of the two pairs of intermediate air-sacs, which first penetrate it at a time when no distinct line can be drawn between the tissue that goes to form it, and that of the developing lung itself."

The adult arrangement of these structures is shown in text-fig. 32, p. 222, which is of a section of a Rook through the region of the liver and gizzard, seen from the ventral side. The post-pulmonary tissue is seen united to the lateral body-walls for a very considerable distance on either side, and ventrally and towards the middle line is pushed out irregularly into the peritoneal cavity by the growth within it of the posterior air-sacs. The latter, however, as I have already said, never project beyond the edge of the septum in which they lie, but always carry a layer of connective tissue and coelomic epithelium in front of them.

Text-fig. 30 is of a transverse section of a chick, 13 days after the beginning of incubation, through that part of the post-pulmonary

Text-fig. 30.



Transverse section of a chick of 13 days' incubation, through the region of the pericardium and anterior intermediate air-sacs; seen from behind.

septum which encloses the anterior intermediate air-sacs. The lungs are seen now lying in completely closed pleural cavities, separated from each other in the middle line by the median dorsal mesentery.

The post-pulmonary septum stretches across the coelomic cavity from one side to the other, closely fused to the lateral body-walls throughout its entire thickness. In it, near the middle line, lie the anterior intermediate air-sacs. The costo-pulmonary muscles pass inwards from the ribs dorsal to the air-sacs following the ventral border of the lungs. They really form a continuous layer dorsal to the œsophagus, but in the section figured they are interrupted by the ostia of the anterior intermediate air-sacs. Forming the ventral boundaries of the post-pulmonary septum are, medianly, the pulmo-hepatic recesses, and laterally, the abdominal cavity. Behind the pericardium at this stage the posterior intermediate air-sacs, still comparatively small, lie in the periphery of the septum, and more posteriorly the posterior air-sacs occupy the same position. These however have extended both ventrally and also towards the middle line, always carrying some tissue of the post-pulmonary septum with them, and have united with the median mesentery of the gizzard and liver, dorsal to these organs and ventral to the Wolffian bodies. This union forms the beginning of the post-hepatic septum to be described below. Text-fig. 31 is of a transverse section of the same chick of 13 days' incubation, taken through the region of the spleen, and showing the inwardly expanded post-pulmonary septum—containing the greatly enlarged posterior air-sacs—united to the gastro-hepatic ligament.

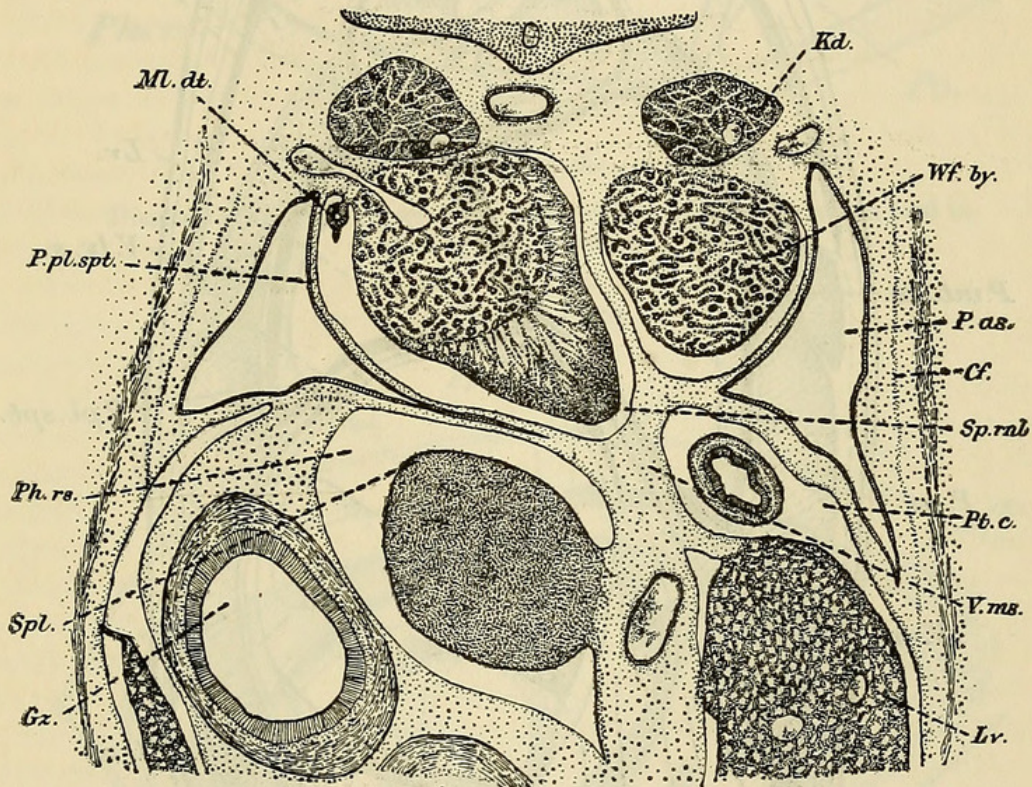
The Post-hepatic Septum.

This septum is completed in the chick on the 15th or 16th day of incubation. The first to be formed is the antero-dorsal moiety, and this is fully developed by the 13th day. Text-fig. 31, as I have already described, shows the formation of this part by the inward expansion of the two halves of the post-pulmonary septum (those parts termed by Butler the "oblique abdominal septa") towards the middle line, where they meet and fuse with the mesentery of the gizzard and liver. This lateral extension is due to the greatly increased size of the posterior air-sacs enclosed within the septum.

Ventral to this connection the gizzard is seen in text-fig. 31 included within the median mesentery, which is therefore split into two layers. Posteriorly this mesentery expands laterally before it becomes attached to the ventral body-wall; and at a later stage its lateral edges become fused to the side walls of the peritoneal cavity, thus constituting the postero-ventral portion of the post-hepatic septum. When fully formed, this is a membrane passing obliquely from the antero-dorsal to the postero-ventral walls of the peritoneal cavity and enclosing within its thickness the gizzard in the more posterior portion. It is a complete partition except on the left side where the dorsal and ventral components never quite meet, and so there remains always a narrow communication between the post-hepatic intestinal cavity and the

pulmo-hepatic recess of that side. Text-fig. 33, p. 223, shows very diagrammatically the divisions of the coelom in the adult bird in longitudinal vertical section. Text-fig. 34 is of a chick 17 days after the beginning of incubation, bisected longitudinally a little to the left of the middle line, and seen from the right side. The arrangement of the septa is the same as in the adult fowl but is shown more clearly, since in the latter the mesenteries are often loaded with fat. The gizzard is seen enclosed in the post-hepatic septum just dorsal to the attachment of the latter to the ventral body-wall, and in front of the umbilicus. Dorsally the septum is seen formed first by that part of the median mesentery which supports the spleen in the left pulmo-hepatic recess (see also text-fig. 31), and then by the post-pulmonary septum which is

Text-fig. 31.



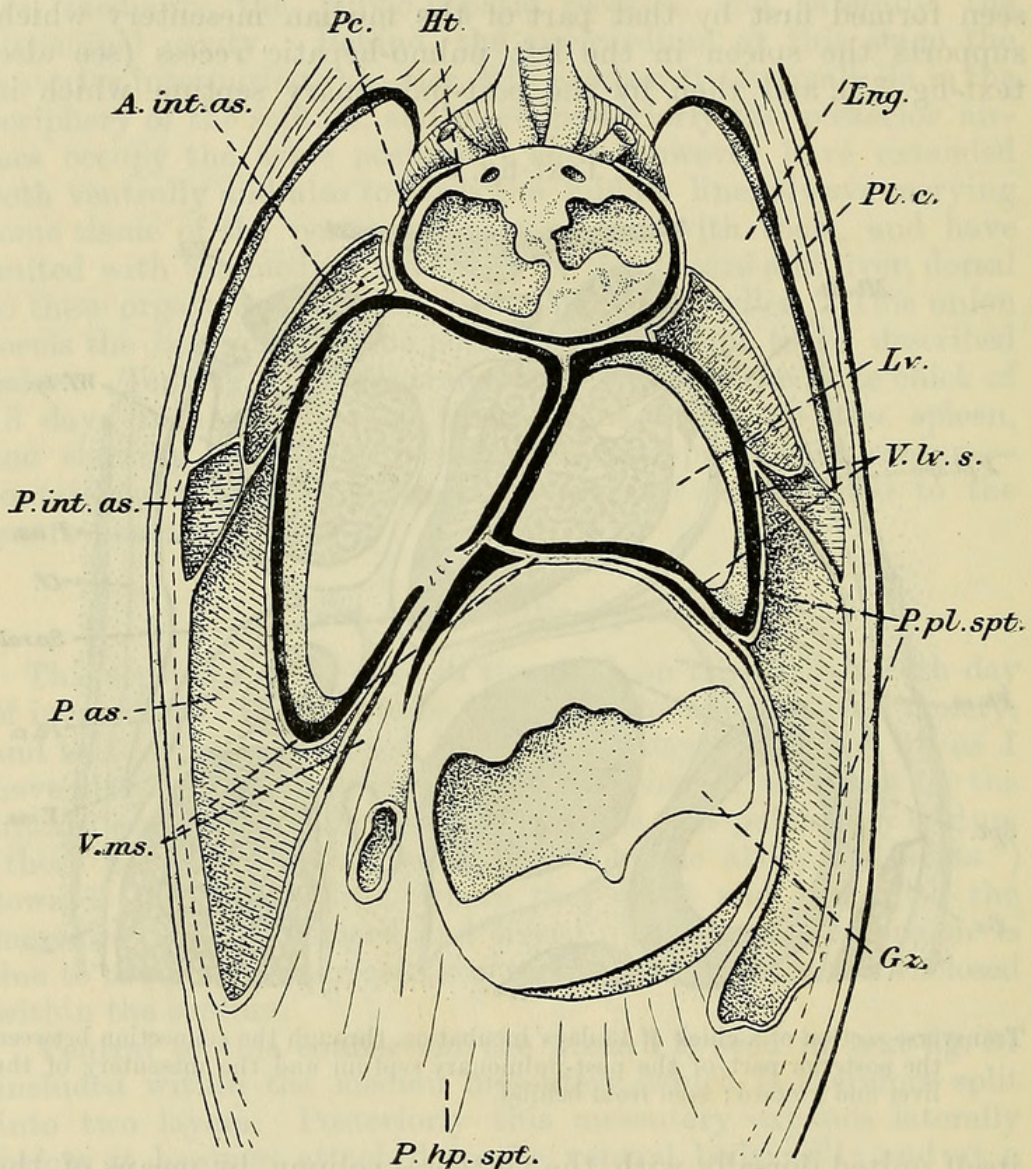
Transverse section of a chick of 13 days' incubation, through the connection between the posterior part of the post-pulmonary septum and the mesentery of the liver and gizzard; seen from behind.

itself united dorsally with the vertebral column by means of the median dorsal mesentery (see text-fig. 30, p. 219). By this time the air-sacs have increased so much in size, as completely to obliterate all the connective tissue of the post-pulmonary septum which at first surrounded and separated them from each other; and the walls of the adjacent air-sacs have become closely applied to each other. As a result of this, the post-hepatic septum appears in the figure to be completed dorsally by the posterior wall of the posterior intermediate air-sac together with the fused anterior

wall of the posterior air-sac. From an examination of the earlier stages, however, it is evident that the dorsal component of the post-hepatic septum is really formed by the whole of the more posterior portion of the post-pulmonary septum, with its contained air-sacs.

Text-figs. 32, 33, and 34 also show those peritoneal cavities, called by Butler the ventral liver-sacs, in which the two liver-

Text-fig. 32.

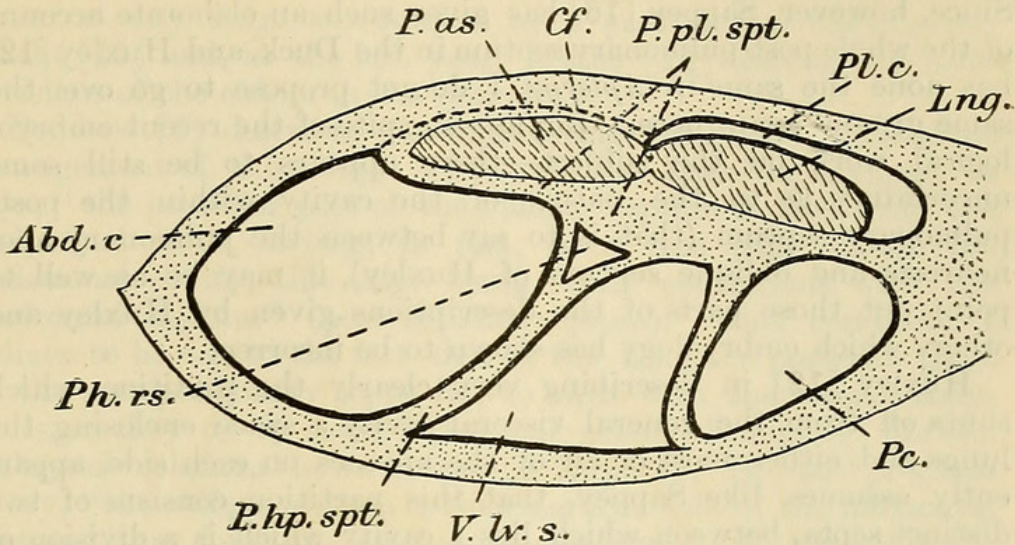


Adult Rook bisected horizontally through the region of the gizzard and liver-lobes, and slightly dissected anteriorly to expose the lungs; seen from the ventral side.

lobes are seen to lie upon opening a bird from the ventral side. These are clearly formed by no special development of septa, but are simply those parts of the peritoneal cavity which, by the ventral attachment to the body-wall of the post-hepatic septum, become shut off anteriorly between this septum and the posterior wall of

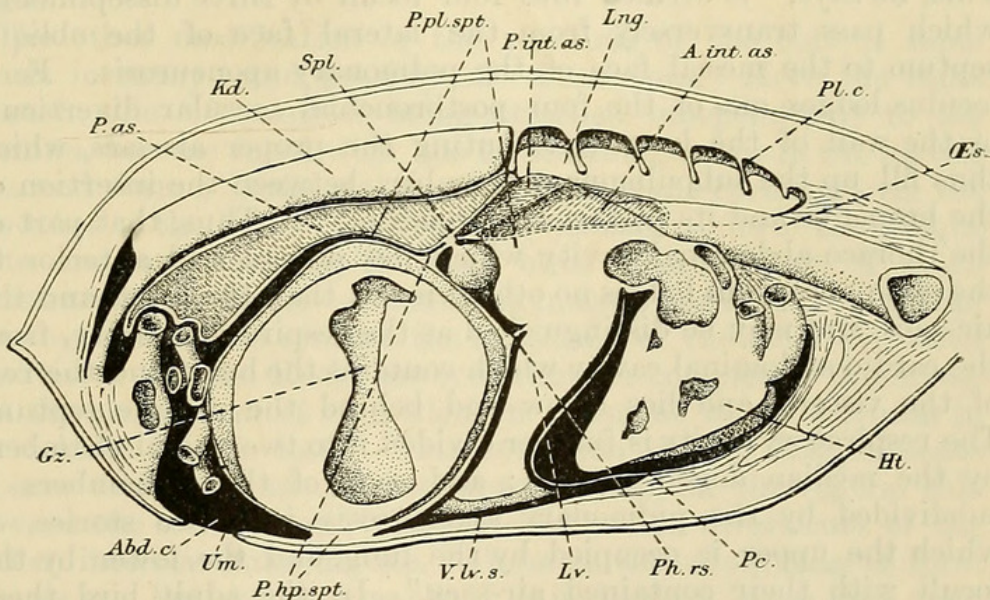
the pericardium. Their lateral walls are formed by the post-pulmonary septum, and the median partition between them is the ventral mesentery or falciform ligament.

Text-fig. 33.



Diagrammatic plan showing the subdivisions of the coelom in a bird in longitudinal section.

Text-fig. 34.



Chick of 17 days' incubation bisected longitudinally a little to the left of the middle line; seen from the right side.

These figures show likewise that the pleural cavities persist even in the adult; though they tend to get somewhat obscured by the fusion here and there of the adjacent layers of pleural epithelium, and the development of connective-tissue strands across the cavities.

II. ADULT ANATOMY.

The Post-pulmonary Septum.

Bertelli [8] gives an extremely clear description, accompanied by an excellent drawing, of his "diaframma ornitico" in the Fowl, with the attachments of all the costo-pulmonary muscles. Since, however, Sappey [16] has given such an elaborate account of the whole post-pulmonary septum in the Duck, and Huxley [12] has done the same in *Apteryx*, I do not propose to go over the same ground again here. But as—in spite of the recent embryological work on the subject—there appears to be still some uncertainty as to the nature of the cavity within the post-pulmonary septum (that is to say between the pulmonary aponeurosis and oblique septum of Huxley), it may be as well to point out those parts of the descriptions given by Huxley and others which embryology has shown to be incorrect.

Huxley [12] in describing very clearly the partition which shuts off from the general visceral cavity a space enclosing the lungs and either most or all of the air-sacs on each side, apparently assumes, like Sappey, that this partition consists of two distinct septa, between which lies a cavity which is a division of the coelom. For between the pulmonary aponeurosis dorsally and laterally, and the oblique septum ventrally and posteriorly, the lateral body-wall and the median dorsal septum, Huxley describes a space which he calls the subpulmonary chamber. This, he says, "is divided into four loculi by three dissepiments, which pass transversely from the lateral face of the oblique septum to the mesial face of the pulmonary aponeurosis. Each loculus lodges one of the four postbronchial saccular diverticula of the wall of the lung, constituting the proper air-sacs, which thus fill up the subpulmonary chamber, between the insertion of the bronchus and its posterior extremity. . . . Thus, that part of the thoraco-abdominal cavity which lies dorsad and anterior to the oblique septum lodges no other viscera than the lungs and the air-sacs, and may be distinguished as the respiratory cavity, from the cardio-abdominal cavity which contains the heart and the rest of the viscera, and lies below and behind the oblique septum. The respiratory cavity is further divided into two lateral chambers by the median dorsal septum; and each of these chambers is subdivided by the pulmonary aponeurosis into two stories, of which the upper is occupied by the lung, and the lower by the loculi with their contained air-sacs." In the adult bird these structures do appear as above described, but from working out the development, it is at once clear that the cavity lying between the pulmonary aponeurosis and the oblique septum on each side, is not a division of the coelom lined by peritoneum, but merely the cavities of the three posterior air-sacs, and therefore lined by endoderm. The dissepiments which are described as subdividing the subpulmonary chamber into loculi, are only the walls of the same air-sacs, which by the growth of the latter have become

closely applied to one another, and so have obliterated the connective tissue of the post-pulmonary septum which at first separated them. The pulmonary aponeurosis and the oblique septum, as already shown, together constitute a single partition across the coelomic cavity, into the thickness of which the intermediate and posterior air-sacs push their way as they develop; the latter are never at any stage surrounded by a part of the body-cavity. Roché [15] and, in the last year, Müller [14] describe the subdivisions of the coelom in the same way.

Beddard [5] describes two interesting variations in the adult arrangement of the oblique septa. In the Emu, for example, he says, "the posterior part of the oblique septum is free from the abdominal walls, ending, in fact, in a free edge within the abdominal cavity, this edge being really continuous with the horizontal septum" (post-hepatic septum). This condition I believe to be due to the fact that in the Emu the posterior parts of the post-pulmonary septa fail to unite with the lateral body-walls, as they do in most forms, but retain throughout life the embryonic relations shown in text-fig. 29, p. 217. Beddard proceeds to say, "the oblique septum is thus merely a fold of the horizontal septum; they form one continuous structure." In the adult the two septa are really continuous, but it must be borne in mind that from its development only the anterior dorsal moiety of the post-hepatic septum is of the same nature as the post-pulmonary septum, the posterior ventral portion having a quite separate origin.

The other modification of the relations of the oblique septa occurs in many—and possibly all—Passerines. Here the septa of each side, "instead of being attached independently to the sternum, become fused with the falciform ligament in the middle line, and form a horizontal sheet of membrane covering over the two lobes of the liver. The original (?) attachments of the oblique septa are not, however, in these birds entirely lost; a much fenestrated membrane—sometimes, indeed, reduced to a thread or two—remains to remind the anatomist of the more prevalent conditions. In the Rook, however, they are completely preserved. But the attachment of the falciform ligament to the sternum in the middle line is lost." This condition of the oblique septa appears to be due to the backward growth, on the ventral side between the sternum and the pericardium, of diverticula of the median interclavicular air-sac. These in the adult seem to form a single sac, but are presumably of paired origin, since they open into the interclavicular air-sac by distinctly paired orifices; and Bertelli [7] has shown that this air-sac itself arises in the embryo as a double structure. These diverticula would seem to push their way behind the peritoneum lining the ventral body-wall, and so carry it inwards until it comes to invest closely the pericardium and liver-lobes, as Beddard shows to be the case in the adult bird. The persistence or not of the sternal attachments of the oblique septa would in this case be of no especial significance, since it

would depend only on whether, as in the Rook, the diverticulum remains comparatively slightly expanded laterally, and so only detaches the peritoneum from the body-wall in the middle line; or whether, as may be the case in other birds, it extends far round against the lateral body-walls into the post-pulmonary septa.

As I have before mentioned, I cannot agree with Bertelli's contention that the oblique septum, the "diaframma toraco-addominale," is not a septum, or part of a septum, at all, but "non è altro che la parete ventrale dei sacchi aeriferi intermedi e la parete posteriore del pericardio." He shows how in the Fowl the ventral walls of the air-sacs are covered by muscular tissue, and how in the Duck this is more markedly the case; but holds that the muscular tissue has nothing to do with the subdivision of the body-cavity, but belongs to the walls of the air-sacs, together with the nerves which, according to Beddard, are of spinal origin. Since, as I have shown, the air-sacs never project beyond the edge of the post-pulmonary septum, the muscles would lie in the connective tissue between the peritoneum bounding the abdominal cavity and the endoderm of the air-sacs, and therefore in the tissue of the post-pulmonary septum. And I believe that the presence of muscular tissue justifies the description of this part of the abdominal wall as the postero-ventral portion of the post-pulmonary septum.

Huxley [12] also describes a layer of muscular fibres in the oblique septum of the Duck, and Beddard [2] finds a considerable sheet of muscle in part of the septum of the Puffin (*Fratercula arctica*). He says: "This layer of muscular fibres arises from the pubis—from the proximal and larger half of this bone; it is abundantly furnished with blood-vessels and nerves. The direction of the muscle is oblique; it covers the hinder region of the oblique septum, ending abruptly some little way in front of the posterior attachment of the latter; it is attached below to the upper surface of the sternum, and to the abdominal parietes along the last sternal rib." Beddard also finds similar muscles in two species of Penguins (*Eudyptula minor* and *Spheniscus demersus*) and also, though feebly developed, in the Toucan (*Rhamphastos ariel*).

The Post-hepatic Septum.

This septum in the adult fowl is a membrane extending, as I have shown, obliquely across the visceral cavity from its dorsal to its ventral wall. Dorsally and laterally in front it is continuous with the post-pulmonary septum, which in turn is united with the vertebral column by means of the median dorsal mesentery. Posteriorly and postero-laterally it is attached to the ventral body-wall. It thus forms a complete septum, except on the left side where the pulmo-hepatic recess remains in communication with the abdominal cavity by means of a narrow aperture. Except for this orifice, the two pulmo-hepatic recesses now form

entirely closed cavities, lying between the post-pulmonary and post-hepatic septa, the alimentary canal and the liver. The post-hepatic septum passes dorsal to and behind the liver-lobes, and ventral to and in front of the intestines, and carries on its ventral surface the right anterior abdominal vein. The gizzard is enclosed within its thickness, in the ventral portion of the septum, and is thus completely shut off from the ventral liver-sacs, the posterior walls of which are constituted by the anterior peritoneal layer of the sheath of the gizzard.

This septum has been described in the Stork (*Leptoptilus*) and the Flamingo (*Phoenicopterus antiquorum*) by Weldon [17], and in *Rhea*, *Struthio*, and *Dromæus* by Beddard [1]. In the Struthioness the liver-sacs are said to be closed off posteriorly from the space ventral to the post-hepatic septum, and this may possibly be compared with the condition found in the Crocodilia (see below). Beddard also describes the septum in Cranes and Horn-bills, in the Penguin (*Spheniscus demersus*), in the Spur-winged Goose (*Plectropterus gambensis*), and in *Bernicla brenta*, where the septum bears a second (left) anterior abdominal vein which apparently corresponds to that occurring in reptiles, in the Grue (*Cariamā*) and in many other birds; and I have myself observed it in the Golden Eagle. It probably therefore occurs throughout the entire group.

III. THE STRUCTURES POSSIBLY REPRESENTING THE AVIAN SEPTA IN REPTILES.

There are but few descriptions of the subdivision of the cœlom in the Reptilia, and these deal mostly with the adult anatomy; so that it is impossible to establish any homologies between these forms and Birds, in the almost complete absence of embryological evidence. I have therefore merely collected such facts regarding the subdivision of the cœlom in the various groups as may be of significance when more work on the development has been done.

In the Lacertilia generally there is no representative of either the post-pulmonary or the post-hepatic septum, but in many genera — *Lacerta*, *Iguana*, *Chamæleo*, and others—there is a well-developed pulmo-hepatic ligament, and consequently a pulmo-hepatic recess is formed on the right side [9]. This arrangement occurs again in *Sphenodon*, and is found of course also in Mammals [13]. In the Teiidae, however, Butler describes a well-developed post-hepatic septum in *Tupinambis teguexin*, and a slight approach to this condition in *Ameiva surinamensis* and *Callopiastes maculatus*, where the median ventral ligament is expanded laterally behind the liver, but does not become attached to the body-walls. In *Tupinambis*, however, the subdivision of the body-cavity into a pulmo-hepatic and an intestinal portion is almost complete except for a small aperture on either side. These are situated in the dorsal moiety of the septum, and hence Butler compares the latter with the ventral or omental part of the post-hepatic septum of birds; the absence of the dorsal portion in

consequence of the absence of air-sacs being indicated by the apertures in this region. That part of the septum which is present dorsally, he accounts for by the need of some such transverse membrane to carry the inferior vena cava to the liver, in the absence of the pulmo-hepatic ligament present in most other Lizards; and suggests that it may have been produced by the vena cava, instead of developing as in other Lacertilia and Birds in tissue continuous with the right pulmo-hepatic ligament, arising in a lateral expansion of the median dorsal mesentery.

In many species of *Monitor* and *Varanus*, Beddard [3] describes a horizontal (post-hepatic) membrane which covers the intestines when the body-wall is opened ventrally. He says it is attached anteriorly to the ventral body-wall in the middle line, and dorsally to the spinal column, while to the lateral parietes it is attached here and there by membranous bands. "It passes over the lobes of the liver and the stomach and shuts off the lungs from the abdominal cavity. The umbilical ligament dividing the two liver-lobes is present, and is attached to the dorsal side of the horizontal membrane. This horizontal membrane also separates the kidneys from the reproductive glands; the latter lie internally to it; the kidneys are placed outside it. . . . The fat-body when present lies below the membrane, and is therefore shut off from the abdominal cavity." Butler [11], however, describes how the fat-bodies in reptiles are typically placed outside the coelom and surrounded by distinct extra-peritoneal cavities—the circumadiposal spaces. He therefore considers it probable that the greater part of this horizontal membrane described by Beddard is the lining peritoneum which has become almost completely separated from the abdominal walls by the great extension of the circumadiposal cavities outside it. This view as to the nature of Beddard's horizontal septum seems to be further borne out by the position of the umbilical ligament, which he describes truly as being attached to the dorsal surface of the membrane; for in birds and crocodiles, where I believe a real post-hepatic septum exists, the ligament is attached to the ventral surface, and thence passes to the ventral body-wall. Butler also shows that the position of the kidneys and gonads in relation to the horizontal membrane, is no proof of the septal nature of the latter; for the kidneys are entirely excluded from the coelom in crocodiles, birds, chelonians, and sometimes in lizards, while they lie well within the body-cavity in the *Amphisbænidae*; and in *Monitor niloticus* the posterior part of these organs lies within, and the anterior portion without, the peritoneal cavity. That part of the septum which shuts off the lungs from the abdominal cavity is, however, quite a separate structure, and appears to resemble more closely the condition seen in some *Chelonia* than in any other reptiles. The lungs of *Varanus* seem also to be so intimately connected with the dorsal body-wall, that all trace of a pleural cavity is lost, and this again happens in *Testudo* (see below). Or Butler suggests that the exclusion of the lungs from the peritoneal cavity may

take place in the Varanidæ as in snakes, by the gradual growth of connective tissue from the ventral surface of the lung round to the dorsal side so as to fill up any cavity that originally surrounded it.

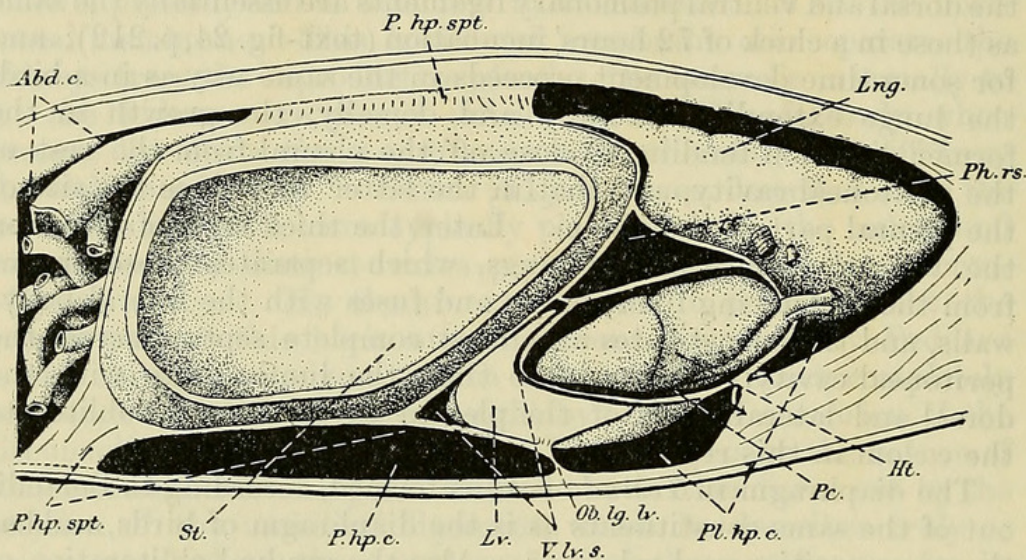
In the Chelonia, Bertelli describes the exclusion of the lungs from the general body-cavity by the development of a septum which he takes to be the homologue of the "diaframma ornitico." In the adult *Testudo græca*, this forms the ventral boundary of the lungs—round which it is fused with the lateral body-walls—as a layer of fibrous connective tissue covered by peritoneum. This condition is connected with that usually found among reptiles by intermediate stages, seen in *Thalassochelys caretta*, where this layer is very thin and does not completely shut off the lungs from the other viscera, and in *Emys lutaria*, where it is less developed, and the lungs for the greater part project free into the pleuro-peritoneal cavity. In an embryo of *Testudo*, 32 days after oviposition, the relations of the lung rudiments and the dorsal and ventral pulmonary ligaments are essentially the same as those in a chick of 72 hours' incubation (text-fig. 24, p. 212); and for some time development proceeds in the same way as in a bird, the lungs extending laterally and dorsally, the growth in the former direction tending to close off the pleural from the rest of the peritoneal cavity, and that in the latter to reduce the size of the pleural part of the cœlom. Later, the thick layer of tissue on the ventral surface of the lungs, which separates these organs from the underlying liver, meets and fuses with the lateral body-walls, and thus constitutes an almost complete septum across the peritoneal cavity. At the same time, the lungs unite with the dorsal and lateral walls of the pleural cavity so as to obliterate the cœlom in this region.

The diaphragm in *Testudo* is thus formed, according to Bertelli, out of the same constituents as is the diaphragm of birds, and has the same position and relations. Also the gradual obliteration of the pleural cavities takes place in the same way in the tortoise embryo as in the chick; although in the latter it is never complete, and there remains throughout life a narrow but distinct cavity bridged across here and there by strands of connective tissue. Since, however, the growth of the lungs in a dorsal and a lateral direction goes on at the same time, the obliteration of the cavity round the lungs, and the completion of the diaphragm, take place practically simultaneously; so that by the time the diaphragm is constituted in order to close off the pleural part from the rest of the peritoneal cavity, no pleural cavity remains. It appears, therefore, to be more likely that the condition seen in *Testudo* is to be compared with that occurring in the Varanidæ rather than with that found in Birds.

From the structure of several Crocodiles which I had the opportunity of examining, I believe that the arrangement of the cœlomic septa in this group of reptiles approaches most nearly to the avian condition, as Huxley and Beddard have already pointed

out [1, 2, 12]. Here the post-hepatic septum is well developed, and passes from its anterior dorsal attachment to the vertebral column, behind the liver-lobes and pericardium, to unite posteriorly with the ventral body-wall. As in birds, it encloses the stomach within its thickness, and carries on its ventral surface the anterior abdominal veins to the liver. It is attached to the lateral body-walls throughout its extent, so as to separate completely the pulmo-hepatic from the abdominal portion of the cœlom. Butler describes in a very young specimen a small passage between the abdominal cavity and the right pulmo-hepatic recess; but this presumably becomes closed at a later stage, for there was no such communication in the other animals which I dissected. The post-hepatic septum is apparently split secondarily in its ventral portion, and the flap thus formed on each side is closely applied to the liver-lobe so as to form a posterior wall to the liver-sac, and—together

Text-fig. 35.

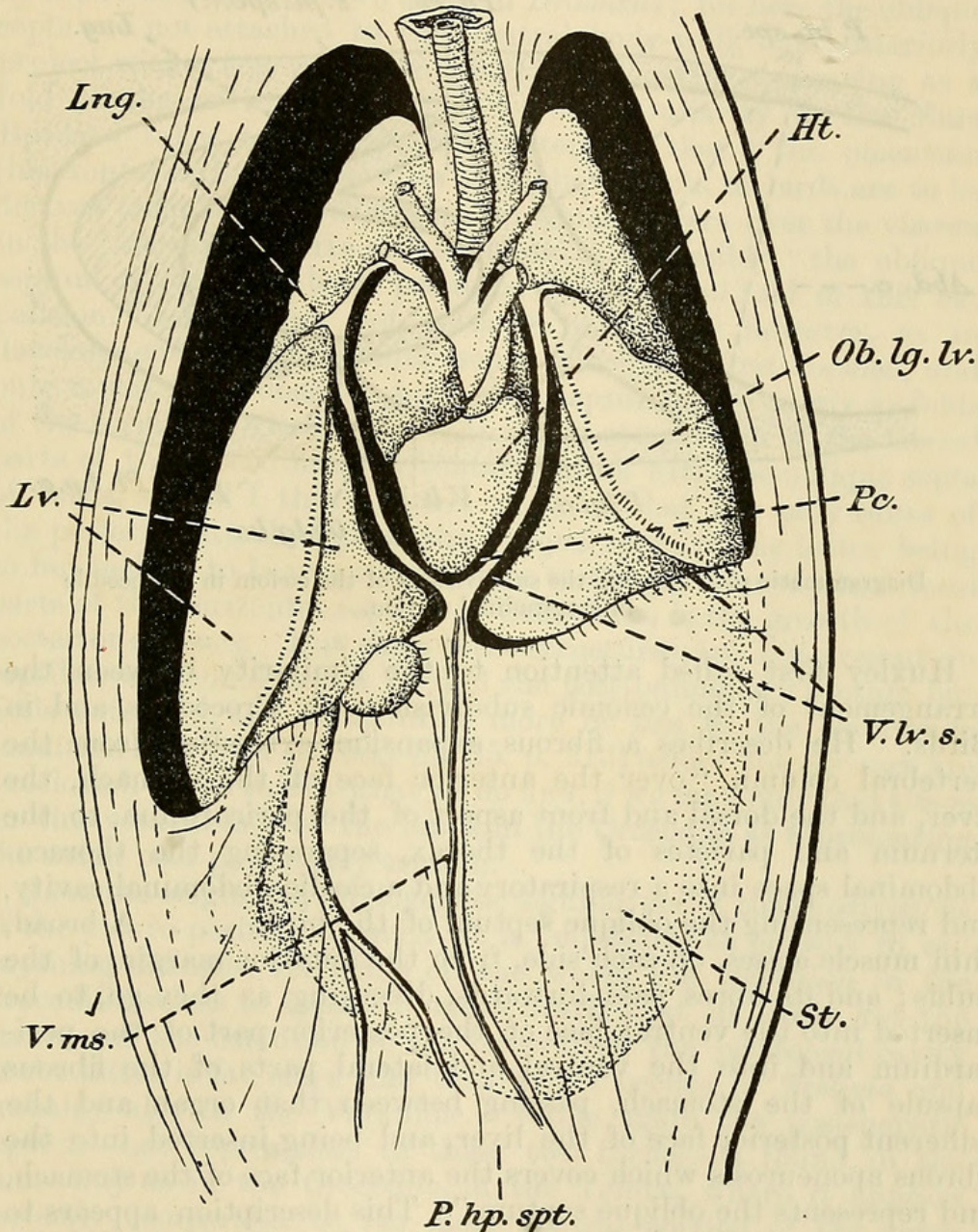


Young Crocodile bisected in the same way as Chick in text-fig. 34, p. 223.

with the oblique ligament of the liver with which it is connected—to shut off the pulmo-hepatic cavity from a subseptal, ventral, post-hepatic space. There is a large pulmo-hepatic cavity extending right round from the dorsal attachment of the post-hepatic septum to the ventral attachments of the oblique ligaments of the liver, perfectly continuous except for a narrow partition projecting a little way inwards from the ventral body-wall. The pulmo-hepatic recesses seem to correspond almost exactly to those spaces in birds, lying as they do between the ventral surfaces of the lungs, the dorsal margins of the liver, and the post-hepatic septum; and I believe that tissue which forms the roof of each recess, and covers the postero-ventral face of each lung, represents the post-pulmonary septum of birds. Text-fig. 36 is a dissection from the ventral side of a young specimen of *Crocodylus palustris*. It shows the continuous pulmo-hepatic cavities closed off behind

by the oblique ligaments of the liver and the more vertical portion of the post-hepatic septum. Nearer the middle line lie the ventral liver-sacs between the posterior wall of the pericardium, the oblique ligaments of the liver, the post-hepatic septum, and the median ventral mesentery. Behind, the post-hepatic septum

Text-fig. 36.

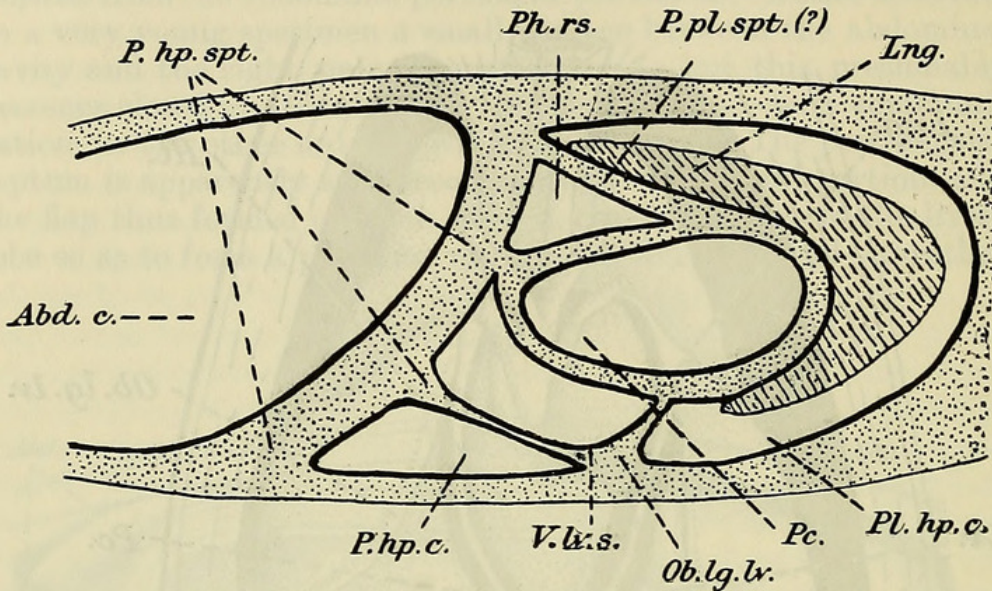


Young Crocodile opened from the ventral side. The ventral walls of the pericardium, pulmo-hepatic cavities, and ventral liver-sacs have been cut away.

lies horizontally over the stomach, attached both posteriorly and laterally to the body-wall (*cf.* text-fig. 32, p. 222, of a bird). Text-fig. 35 is of the same Crocodile bisected longitudinally a little to the left of the middle line. It shows, in addition to the structures seen

in the previous figure, the incomplete ventral partition between the pleural and hepatic regions of the pulmo-hepatic cavity, the position of the left pulmo-hepatic recess, and the possible representative of the avian post-pulmonary septum (*cf.* text-fig. 34 of a bird bisected in the same way, and also text-figs. 33, p. 223, and 37).

Text-fig. 37.



Diagrammatic plan showing the subdivisions of the coelom in a Crocodile in longitudinal section.

Huxley first called attention to the similarity between the arrangement of the coelomic subdivisions in Crocodiles and in Birds. He describes a fibrous expansion extending from the vertebral column "over the anterior face of the stomach, the liver, and the dorsal and front aspect of the pericardium, to the sternum and parietes of the thorax, separating the thoraco-abdominal space into a respiratory and a cardio-abdominal cavity, and representing the oblique septum of the bird. . . . A broad, thin muscle arises, on each side, from the anterior margin of the pubis; and its fibres pass forwards, diverging as they go, to be inserted into the ventral face of the posterior part of the pericardium and into the ventral and lateral parts of the fibrous capsule of the stomach, passing between that organ and the adherent posterior face of the liver, and being inserted into the fibrous aponeurosis which covers the anterior face of the stomach, and represents the oblique septum." This description appears to refer to the whole of that membrane which I have called the post-hepatic septum, together with the roof of the pulmo-hepatic recesses and the oblique ligaments of the liver; and as I have already said, it is only that tissue forming the roof of the pulmo-hepatic recess on each side which I regard as possibly comparable to the oblique septum (post-pulmonary septum) of Birds.

On the other hand, Beddard [2] says with reference to the muscles described by him in the oblique septa of Puffins and

Penguins, that the muscle referred to by Huxley in the Crocodile is the equivalent of this muscle, for in both cases the fibres arise from the pubis. Beddard therefore considers it more justifiable to identify the middle portion of the horizontal septum of the Crocodile with that structure in birds, while the lateral portions containing the muscles he compares with the oblique septa of birds. And this comparison he considers is made more obvious by the relations of the two septa in *Dromæus*; for here the oblique septa are not attached to the ventral body-wall, but posteriorly project with a free edge into the visceral cavity, appearing as a fold of the horizontal septum. This peculiarity in the Emu Beddard takes to support his contention that "the omentum (horizontal septum) as well as the oblique septa of birds are to be derived from the fibrous expansion which covers over the viscera in the Crocodilia." He also suggests that possibly "the oblique septum of birds has been produced by a vertical fold of this expansion." This does not seem to me likely however, as in development it is the oblique septa which are first formed, and only much later does the horizontal septum arise, partly as folds of the former. Also, against the above comparison of the lateral parts of the crocodilian horizontal septum with the oblique septa of birds, should I think be set the fact, that the only cause of the posterior attachment of the oblique septa in the latter being so far back as to bear a resemblance to the position of the lateral parts of the horizontal septum in Crocodiles, is the growth of the posterior air-sacs. But since these structures are not present in reptiles, we should expect to find the post-pulmonary septum but little extended, and comparable more or less to the embryonic condition in a bird (*cf.* text-fig. 25, p. 213) before the air-sacs are developed. And this is what we do find, if we take only that tissue on the ventral face of the lungs in the Crocodile as representing the avian post-pulmonary septum.

As to the origin and phylogenetic significance of the subdivisions of the pleuro-peritoneal cavity, it is impossible at present to say anything definite; for while on the whole the condition in the Crocodilia seems to approach most nearly that in Birds, yet the manner of the exclusion of the lungs from the peritoneal cavity in the latter is far more like that which occurs in *Testudo* and probably also in the Varanidæ. While again the post-hepatic septum—not represented in these two forms—is found, in the same way as in the Crocodile, in the Teiidæ, where it appears perfectly comparable to the more ventral portion of the avian post-hepatic septum; and according to Butler, it is also completely represented in Snakes. Therefore, whether or not the subdivision of the coelom will prove of importance as to the phylogeny of the Reptilia and Aves, must, I think, remain undecided until further embryological work has been done.

List of Works referred to in the text.

1. BEDDARD, F. E.—“Notes on the Visceral Anatomy of Birds. —I. On the so-called Omentum.” Proceedings of the Zoological Society, 1885.
2. BEDDARD, F. E.—“Notes on the Visceral Anatomy of Birds. II. On the Respiratory Organs in certain Diving Birds.” Proceedings of the Zoological Society, 1888.
3. BEDDARD, F. E.—“On certain points in the Visceral Anatomy of the Lacertilia—particularly of *Monitor*.” Proceedings of the Zoological Society, 1888.
4. BEDDARD, F. E.—“On the Oblique Septa in the Passerines and in some other Birds.” Proceedings of the Zoological Society, 1896.
5. BEDDARD, F. E.—The Structure and Classification of Birds. London, 1898.
6. BERTELLI, D.—“Contributo alla morfologia ed alla sviluppo del diaframma ornitico.” *Monitore Zoologico Italiano*, ix. Firenze, 1898.
7. BERTELLI, D.—“Sviluppo dei sacchi aeriferi del pollo. Divisione della cavità celomatica.” *Memorie della Società toscana di Scienze Naturali*, xvii. Pisa, 1899.
8. BERTELLI, D.—“Ricerche di Embriologia e di Anatomia comparata sul diaframma e sull'apparecchio respiratorio dei vertebrati.” *Archivio di Anatomia e di Embriologia*, iv. Firenze, 1905.
9. BUTLER, G. W.—“On the Subdivision of the Body-cavity in Lizards, Crocodiles, and Birds.” Proceedings of the Zoological Society, 1889.
10. BUTLER, G. W.—“On the Relations of the Fat-bodies of the Sauropsida.” Proceedings of the Zoological Society, 1889.
11. BUTLER, G. W.—“On the Subdivision of the Body-cavity in Snakes.” Proceedings of the Zoological Society, 1892.
12. HUXLEY, T. H.—“On the Respiratory Organs of *Apteryx*.” Proceedings of the Zoological Society, 1882.
13. MALL, F.—“Development of the lesser Peritoneal Cavity in Birds and Mammals.” *Journal of Morphology*, v. 1891.
14. MÜLLER, B.—“The Air-sacs of the Pigeon.” *Smithsonian Miscellaneous Collections, Quarterly Issue*, iv. 1908.
15. ROCHÉ, G.—“Contribution à l'étude de l'anatomie comparée des réservoirs aériens d'origine pulmonaire chez les oiseaux.” *Annales des Sciences naturelles*, ser. 7, xi. Paris, 1891.
16. SAPPEY, P.—*Recherches sur l'appareil respiratoire des Oiseaux*. Paris, 1847.
17. WELDON, W. F. R.—“On some points in the Anatomy of *Phoenicopterus* and its Allies.” Proceedings of the Zoological Society, 1883.

See also Hochstetter, F.—“Ueber die Entwicklung der Scheidewandbildung in der Leibeshöhle der Krokodile,” in Voeltzkow's “Reise in Ostafrika,” 1903–1905, Bd. 4; and “Beiträge zur Entwicklungsgeschichte der *Emys lutaria*. 2. Die ersten Entwicklungsstadien der Lungen und die Bildung der sogenannten Nebengekröse,” in the *Denkschriften der Math.-Naturwiss. Klasse der Kais. Akad. der Wiss.*, Bd. 84, Wien, 1908, which I have been unable to consult.



Poole, Margaret. 1909. "The Development of the Subdivisions of the Pleuroperitoneal Cavity in Birds." *Proceedings of the Zoological Society of London* 1909, 210–235. <https://doi.org/10.1111/j.1096-3642.1909.tb01866.x>.

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