1450 does not extend more than a section or two beyond the liver, and is separated by a marked opening from the stem of the umbilical vesicle in this embryo, as is shown in Fig. 1442, *O* (see also No. XII., Fig. 1428, *O*). On the aboral side of the umbilical cord the peritoneal cavities of the two sides unite in both embryos again, marked *O'* in both figures.

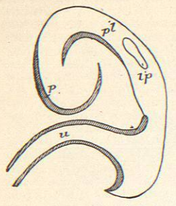

FIG. 1444.—Outline of Cœlom in Embryo No. II. in Sagittal Section. The striated line indicates that the cœlom crosses the median line. *P*, Pericardial space; *pl*, pleural cavity; *l p*, outline of lesser peritoneal cavity.

Development of the Diaphragm.—It has often been stated that the development of the diaphragm, especially in the human embryo, belongs to one of the most difficult problems of embryology, partly because of the difficulty of obtaining the necessary specimens and partly because there are no fixed points from which to calculate. In its development the whole diaphragm wanders from the head to the abdomen, forming as well as modifying the structures and organs along the way. So while von Baer[58] recognized that the diaphragm wandered in its development, picking up its nerve in so doing, a fairly clear picture of the whole process was not given until Cadiat,[59] His,[60] Uskow,[61] and Ravn[62] studied carefully the development of neck, heart, lungs, and intestine. In so doing His especially recognized the anlage of the diaphragm in a mass of tissue located with the heart amongst structures belonging to the head and containing within it the veins to the heart as well as the anlage of the liver. This mass of tissue His termed the septum transversum. His's studies were made upon the human embryo, mainly by the method of reconstruction, and shortly after they were published Uskow made a very careful study of the further growth of the septum transversum. Uskow recognized the great importance of two additional structures in the formation of the pericardium and adult diaphragm from the septum transversum: these he termed the *pleuro-pericardial membrane*, containing the phrenic nerve and the *pillars* which form the dorsal end of the diaphragm. The pillars of Uskow have been termed the *pleuro-peritoneal membranes* by Bracket, and as this term is more appropriate it should be adopted.

My own studies show that the pleuro-pericardial and pleuro-peritoneal membranes arise from a common structure which grows from the lobe of the liver along the dorsal wall of the ductus Cuvieri to the dorsal attachment of the mesocardium. Later it extends toward the head to complete the pleuro-pericardial membrane, and then toward the tail to complete the pleuro-peritoneal membrane. This structure, which I term the *pulmonary ridge*, giving rise to the pleuro-pericardial and pleuro-peritoneal membrane, is located in the sagittal plane of the body cavity with cephalic and caudal horns on its dorsal side. The ductus Cuvieri lies between these horns.

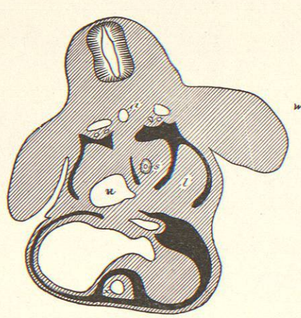

FIG. 1447.

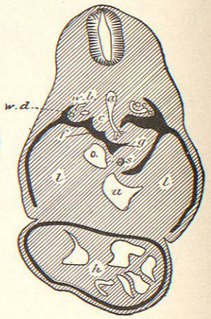

FIG. 1448.

FIGS. 1447 and 1448.—Sections through Embryo No. II. *a*, Aorta; *s*, stomach; *l*, liver; *u*, umbilical vein; *x*, bulbus aortæ; *h*, heart; *o*, omphalomesenteric vein; *g*, lesser peritoneal cavity; *f*, foramen of Winslow; *c*, cœliac axis; *w.b.*, Wolffian body; *w.d.*, Wolffian duct.

In following the fate of the septum transversum it is necessary to consider the division of the body cavity into the pericardial, pleural, and peritoneal cavities. According to His, the body cavity is divided into the *Parietalhöhle* and *Rumpfhöhlen*. The communication between these spaces he has also termed the recessus parietalis. The parietal cavity from its earliest appearance contains the heart and is destined to form the pericardial cavity. This is the pericardial cœlom. A portion of the recessus parietalis forms the pleural cavity; it surrounds the lung buds throughout its development and forms the pleural cœlom. The remainder of the recessus parietalis to the origin of the liver has developed in it the liver and stomach; this is added to the general peritoneal cavity and may be termed the peritoneal cœlom. In the early embryos the whole cœlom lies far out of its final place; in embryo XII. nearly the entire cœlom lies in the region of the head and neck, and in the further development of these parts the cœlom with the surrounding organs wanders away from the head to its permanent location. As long as the serous cavities arising from the cœlom are in the process of wandering and are not fully separated from one another, they may be termed pleural, pericardial, and peritoneal cœlom; when they are fully established they form these cavities.

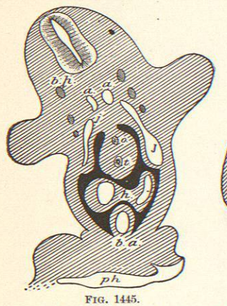

FIG. 1445.

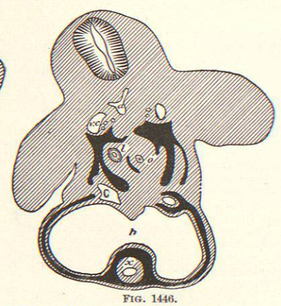

FIG. 1446.

FIGS. 1445 and 1446.—Sections through Embryo No. II. at the Points Indicated in Fig. 1442. Enlarged 22 times. *B p*, Brachial plexus; *a*, aorta; *b a*, bulbus aortæ; *ph*, pharynx; *h*, heart; *t*, trachea; *o*, œsophagus; *j*, jugular vein; *l*, lung; *v c*, cardinal vein; *C*, Cuvierian duct.

In embryo XII., Fig. 1433, the cœlom of the embryo forms a free space encircling the heart and extending on either side of the body over the omphalomesenteric veins to the root of the umbilical vesicle. This canal of communication has developed within it the lung, stomach, and liver, and throughout its earlier development it always measures in length about one-fourth of that of the body. The appearance of the lung and liver marks the subdivision of the cœlom into the pleural and peritoneal cœlom. With the development of the liver, lung, and stomach the cœlom containing them gradually dilates until the embryo is about 9 mm. long, when the containing canal evaginates, so to speak, and turns the liver and stomach out into the general peritoneal cavity. The Wolffian body, which occupies the dorsal wall of the canal, gradually degenerates, and the lung takes its place. From these statements it is readily inferred that the canal extending from the pericardial cœlom, His's recessus parietalis, gives rise to the pleural cœlom on its dorsal side and to the peritoneal cœlom on its ventral side. The line of division is formed by the pleuro-peritoneal membrane extending from the ductus Cuvieri to the adrenal.

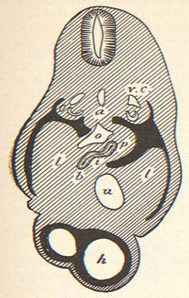

FIG. 1449.

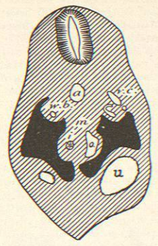

FIG. 1450.

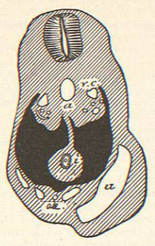

FIG. 1451.

FIGS. 1449–1451.—Sections through Embryo No. II. *a*, Aorta; *v.c.*, cardinal vein; *o*, omphalomesenteric vein; *p*, pancreas; *i*, intestine; *b*, bile duct; *l*, liver; *h*, heart; *u*, umbilical vein; *m*, mesentery; *w.b.*, Wolffian body; *all*, allantois.

It is now no great task for me to give the development of the diaphragm in the human embryo, for I have at my disposal excellent sections, as well as definite knowledge of the anatomy of the surrounding organs contributed by the above-mentioned authors.

While the embryo is still straight it is very easy to locate the various organs and their relations to one another, but through their shifting and the flexion and extension of the embryo the relations are constantly changing, and one must not rely too much upon sections or else erroneous impressions will often be obtained. At first the heart is upon the oral and dorsal side of the septum transversum, then on its ventral side, and finally again on its dorsal side. At first the lungs are on the dorsal side of the heart, then on the lateral side, and finally also on the ventral side of it. At first the liver is on the aboral side of the septum transversum in the head of the embryo, then on the dorsal side of it in the cervical region of the embryo, then as the liver is descending in its excursion it is transferred to the ventral side of the septum and extends into the sacral region. At first the Wolffian body extends high into the thoracic region of the embryo, but while it is degenerating and the diaphragm descends, the upper part of the posterior cardinal vein remains, while the lower part is incorporated with its vena cava inferior, as shown by Hochstetter.[63] As the Cuvierian ducts and cardinal vein descend into the thorax, the segmental veins entering the cardinal veins are gradually shifted, so that veins which originally emptied into the posterior cardinal now empty into the anterior cardinal. While the whole process is taking place the arteries arising from the descending aorta also shift, as I have shown in a previous communication.[64] At that time my collection of human embryos was very limited, and it was necessary to include some observations on lower animals to prove my point, but now I can give a complete table of human embryos in which the point of origin of the cœliac axis is recorded.

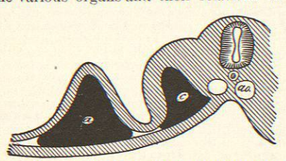

FIG. 1452.—Section of a Chick to Show that the Body Cavity Communicates with the Extra-Embryonic Cœlom. Although the embryo has been injected, the injection masses *a* and *c* are not continuous.

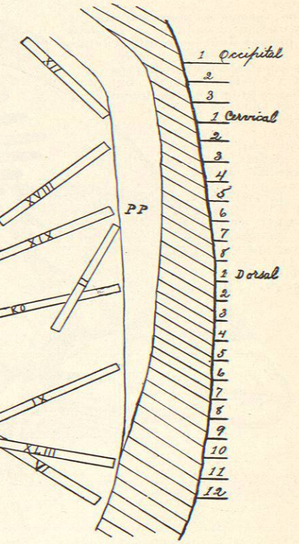

FIG. 1453.—Diagram to Show the Position of the Diaphragm. The numbers on the blocks indicate the embryos from which the diaphragms are taken. *KO* is His's embryo K O: *PP*, the outline of the opening between the pleural and peritoneal cavity, which is finally closed when the diaphragm reaches the tenth dorsal segment.

TABLE SHOWING POINT OF ORIGIN OF CŒLIAC AXIS.

Embryo.	Length in millimetres.	Origin of cœliac axis.
No. XII	2.1	Opposite 4th cervical nerve.*
His's Embryo M	2.6	" 1st dorsal " +
" B	7	" 2d " ‡
No. II	7	" 4th " "
His's Embryo A	7.5	" 6th " " §
No. XLIII	13	" 10th " "
" IX	14	" 11th " "
" XXII	18	" 11th " "
" XVII	16	" 12th " "
" LVII	20	Below 12th " "
Adult	....	" 12th " "

* In the first two embryos the omphalomesenteric artery is noted, and not the cœliac axis.
+ Compare Fig. 15, Pl. vi., His's "Atlas," with M4, Pl. vii.
‡ Compare Fig. 35, Pl. ii., His's "Atlas," with Fig. 1, Pl. i.
§ Compare Figs. 79 and 86, His's "Atlas," with Fig. 4, Pl. i.

The table shows that the arteries arising from the ventral side of the aorta to supply the stomach and intestines are constantly shifting until their definite origin is finally reached. In these specimens the omphalomesenteric artery is shifted ahead of the cœliac axis. In embryo No. II. the omphalomesenteric artery has a double origin from the aorta, which indicates that this movement may be brought about by a new anastomosis forming, which is then followed by an occlusion of the old origin. At any rate it is impossible that the whole aorta shifts with the abdominal viscera, for it is bound to the vertebræ and muscle plates through the segmental arteries.

The various sections and the reconstruction of embryo No. II. show the pleural and pericardial cavities still communicating freely. The same is true in embryos XIX., XVIII., and IV. Immediately after this stage there are no embryos in my collection, so I have no specimen in which the communications between the pleural and pericardial cavities are just closing. In embryos VIII., V., IX., and XLIII. (Figs. 1453–1455), the pleural and pericardial cavities are separated, while the pleural and peritoneal still communicate. In the embryos with a vertex breech measurement exceeding 17 mm. the pleural and peritoneal have been separated completely.

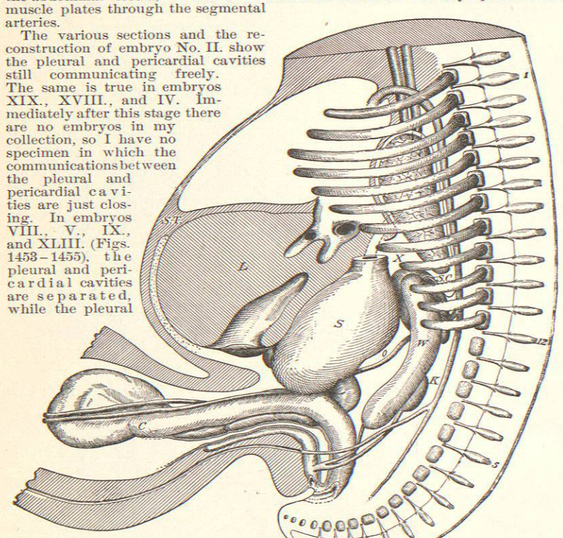

FIG. 1454.—Reconstruction of Embryo No. IX. Enlarged 17 times. *S.T.*, Septum transversum; *L*, liver; *S*, stomach; *C*, cæcum; *W*, Wolffian body; *K*, kidney; *1–12*, dorsal ganglia; *o*, omphalomesenteric artery. The ventral mesentery of the liver is dotted, as it is only a thin membrane; *S.C.*, suprarenal capsule; *X*, point of communication between pleural and peritoneal cavities.

The separation of the pleural from the pericardial cavity is dependent upon the complete development of the diaphragm. At first the septum transversum and the membrana reuniens are on the ventral side of the pleural cavity, and both are still located within the head. As the septum transversum descends into the body it is next located on the dorsal side of the heart. In other words, the dorsal end of the septum transversum has not moved as rapidly as the ventral end, and thus the whole mass of tissue has turned a quarter revolution. This is accompanied by the extreme flexion of the head, as represented in embryo No. II. At this time the septum transversum has descended to the lower part of the cervical region. Now the septum begins to turn in the other direction again, for with the development of the neck the ventral end of the septum becomes the fixed point and the dorsal end moves more rapidly. The successive stages in the movement of the septum are best shown in the diagrammatic Fig. 1453.

Fig. 1454 shows the septum transversum on the ventral side of the stomach and the pleural cavity communicating with the peritoneal at the point *X*. The Wolffian body and the suprarenal capsule, which is very large, have receded markedly, and the pleural cavity already forms a pocket on the dorsal side of them. A sagittal section through this region, somewhat distant from the median line, is given in Fig. 1457. A transverse section of the embryo pictured in Fig. 1454 is given in Fig. 1455. This section is just at the point above the opening, and shows the communication between its pleural and peritoneal cavities closed on one side, but open on the other. There is a ridge on the side of the cavity which projects between the lung and the liver and continues down to the suprarenal capsule. This ridge has been well described by Ravn,[65] who gives an excellent illustration of the opening with the ridge encircling it.

In all the embryos in which the pleural and peritoneal cavities still communicate, the vena cava does not yet communicate with the posterior cardinal vein.

Fig. 1457 is from an embryo slightly larger than the one from which Fig. 1454 was taken. The pleuro-peritoneal communication has just closed by the walls of the ridge having grown together; the extent and shape of the pleural cavity is much as it is in Fig. 1454. The Wolffian body is smaller, and the kidney and suprarenal capsule have come together.

The story, then, is brief: as the diaphragm descends, its dorsal end is in apposition with the suprarenal capsule, and finally, when the capsule approaches the twelfth rib, a ridge of tissue which also includes the capsule unites with a ridge from the septum transversum, and the opening is closed. These two ridges, however, are portions of one and the same ridge, as they form a circle and in section appear as two ridges. The circle is closed much after the fashion of tying up a bag.

All of the abdominal organs, with the exception of the kidney, descend; and the descent is not

completed until the pelvis is formed to admit some of them. In the stages pictured nearly all the small intestine lies in the umbilical cord, as is the case in many

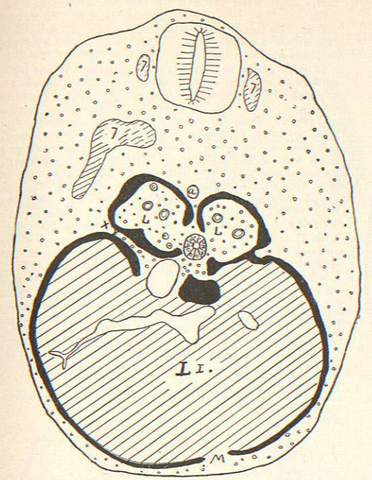

FIG. 1455.—Section through the Point of Communication between the Pleural and Peritoneal Cavities in Embryo No. IX. Enlarged 15 times. *7*, Seventh rib; *L*, lung; *Li*, liver; *M*, ventral mesentery of liver; *a*, aorta. The diaphragm is complete on one side, *X*, while it is incomplete on the other.

mammalian embryos. In embryo X. (Fig. 1457) a large portion of the liver also projects into the cord. I have also observed a hernia of the liver in another embryo somewhat larger. I do not consider the form of embryo X. altogether normal, but this was not noticed until the reconstruction was complete.

Closely associated with the closing of the pleuro-peritoneal opening is the development of the cœliac ganglion. In these young embryos it is extremely large, and can be outlined already, while the septum transversum is still high in the thorax. As the septum descends, the various communicating branches of the nerves are caught up with the cœliac ganglion and dragged along. This accounts for the high origin of the splanchnic nerve.

Fig. 1458 (embryo VI.) shows that all the tissues are becoming more definitely outlined, and the whole structure is firmer than in embryo X. The organs of the abdomen are more firmly clustered together, and the intestine has become more convoluted. The lung is much larger, and the pleural cavity extends to the ventral wall of the embryo, obscuring wholly the outline of the heart. In general it confirms everything given in Fig. 1457.

Minot[66] has stated that the pleural cavities are to be considered a portion of the septum transversum, because they lie on the dorsal side of it. From what has already been said above it will be seen that I consider the septum transversum the mass of tissue between the pericardial cavity, the pleural cavities, and the opening between the two sides of the peritoneal cavity immediately below the liver, marked *O* in Figs. 1428 and 1442. This tissue includes the membrana reuniens, which is really the wings of the septum transversum as described by His. In my account I have employed the term membrana reuniens wherever possible to avoid confusion, and have usually employed the terms septum and primitive diaphragm as synonyms.

There are developed within the region of the septum transversum the whole liver, including its ventral mesentery, the lesser peritoneal cavity, the stomach, and the suprarenal capsule. This same region which I have marked out by these three boundaries as the septum transversum is still sharply defined in the adult. The point *O* in Figs. 1428 and 1442 is still as definably marked as ever by the round ligament, foramen of Winslow, and the duct passing from the liver to the duodenum. The round ligament is developed by the umbilical vein shifting around the side of the abdominal walls into the ventral mesentery of the liver, and then when the liver is retracted from the umbilical cord, the vein and mesentery remain as the round and broad ligaments respectively.

Lesser Peritoneal Cavity.—I have already discussed the lesser peritoneal cavity in a separate paper,[67] and find that I can confirm all that I have stated at that time. I can only add that the portion of it extending up under the lung degenerates, while the omental sac is growing rapidly. I have also found that it is extremely easy for the omentum to find its way over the large intestine. At the time this takes place the large intestine is in the median line, while the stomach and the omentum are on the left side of the body. After the intestine is retracted

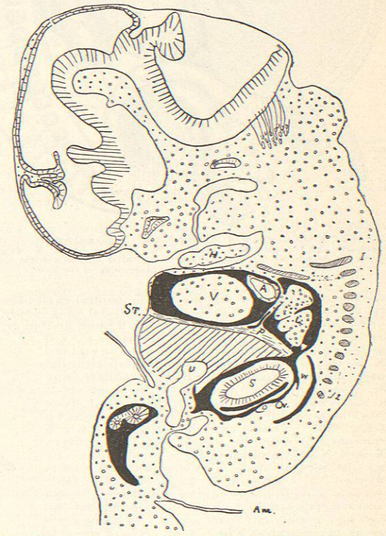

FIG. 1456.—Section through Embryo No. XLIII. Enlarged 8 times. *H*, Hand; *A*, auricle; *V*, ventricle; *L*, lung; *S T*, septum transversum; *P*, phrenic nerve; *U*, umbilical vein; *S*, stomach; *W*, Wolffian body; *Ov*, ovary; *Am*, amnion; *1–12*, ribs.

from the cord the cæcum falls over to the right side of the body, while the descending colon is shifted to the left side, and the omentum then comes to lie on the ventral side of the transverse colon.

Expansion of the Body Cavity and Obliteration of the Extra-Embryonic Cœlom.—After the pleural and pericardial