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ON THE

MORPHOLOGY

OF THE

DIGESTIVE TRACT OF THE CAT

BY

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ON THE MORPHOLOGY OF THE DIGESTIVE TRACT OF THE CAT.

The development of the human alimentary canal has been thoroughly studied by Hertwig, Toldt, Klatsch, Mall, and also by Huntington and others; but, as far as I know, nothing has been written upon the digestive tract of the cat, except when considered in a very broad and general way, as is found in some of the text-books on the adult anatomy of this animal. Among these books may be mentioned the writings of Mivart, Bonnet, and Wilder.

The abdominal cavity of the adult cat differs in several respects from that of the human subject, and perhaps a word as regards these differences will not be out of place, since by keeping them in mind they will be of material aid in the understanding of the subsequent pages.

One of the most striking differences is the absolute lack of all adhesions between the viscera and the abdominal walls. The different divisions of the colon, as well as the great omentum, are in no wise bound down by adhesions but are freely movable. The stomach is very obliquely placed, and its lesser curvature makes a much more acute angle than in the human subject. The duodenum forms a long, free, and very extensive loop, which might well be described as consisting of four portions, as is customary in the description of the human duodenum. The cæcum is well developed, and ends in a narrow pointed extremity. The vermiform appendix is absent. The ascending colon is rather short, the transverse is well developed and terminates in the descending colon. The position of the transverse colon in the cat is totally different from its position in the human subject.

In the former it lies behind the various coils of jejunum and ileum, while in the latter it lies in front of them.

The absence of all adhesions, and the short ascending colon, suggest at once an embryonic type of abdominal cavity.

Method of Investigation.

This investigation was made by means of microscopic sections, and by the dissection of seventy-four embryos, as

well as by the dissection of numerous adult cats. Several of these embryos were very kindly sent me by Profs. Wilder and Gage, of Cornell University. The study of development by means of dissection is a somewhat antique and abandoned method, and yet it was found to be of the greatest possible service in this investigation. If an embryo of only 12 mm. be treated by the progressive alcohol method, the abdominal organs will be sufficiently hardened so that they may be individually removed, and yet they will retain their normal shape; or the body wall of the embryo may be entirely taken away and the viscera al-

Fig. 1.

The body wall of an embryo 34 mm. has been removed. The viscera are seen *in situ*. (Enlarged 5.3 diameters.) *r. v.*, right ventricle. *l. a.*, left auricle. *l. v.*, left ventricle. *l.*, liver. *i.*, intestines. *a. l.*, allantois. *lu.*, lung. *s.*, stomach. *sp.*, spleen. *W. b.*, Wolffian body. *o.*, omentum.

lowed to remain *in situ*. Treated in this manner, the viscera retain perfectly their relations to each other, and can be

studied with the greatest ease. To make such a dissection of the older embryos is a comparatively simple affair, and it is perfectly possible with the smaller ones, although somewhat more difficult. The method has the great advantage of speed, but it is not an economical one, as now and then an embryo is necessarily inadvertently sacrificed. In the study of the younger stages, sections are indispensable, as they are of great aid in the verification of a diagnosis.

The microscopic drawings were made with the camera lucida, and all the others are careful copies of the different specimens. Fig. 1 represents a side view of the abdominal and thoracic viscera of an embryo 34 mm. The body walls have been removed, and all the organs are seen *in situ*. They present no difficulty whatever in their identification. Anteriorly, a coil of intestines is seen which was contained within the cavity of the umbilical cord. In an embryo of this length, one would not expect to find them in this position, but as we shall see later, the date of their entrance into the coelom proper is prone to great variation.

Intestines Extra-Abdominal.

For many years the fact has been recognized that at a certain period in the development of the human embryo, portions of the intestine lie outside of the abdominal cavity proper, within the cavity of the umbilical cord, which at this period is a direct continuation of the coelom. These portions include the ileum, the cæcum, a part of the colon, and a large proportion of the jejunum. They remain for a certain space of time in this position, and then enter the abdominal cavity proper. It seems to me that until recently the full importance and significance of this phenomenon has not been appreciated, since it must necessarily have an important influence on the future position of the abdominal viscera.

The literature on this subject was very meagre before the appearance of two articles by Mall, and it is to him that

we are chiefly indebted for the greater part of our knowledge. (Journal of Morphology, Vol. 12. Archiv. für Anat. u. Entwicklungsgeschichte Jahr. 1897. s. 403.)

He states that this phenomenon occurs in pigs as well as in the human species. This statement I am able to confirm, as well as to assert that it has also been observed by me in

Fig. 2.

Sagittal section of an embryo 15½ mm. *α*, oesophagus. *l. o.*, lesser omentum. *P.*, pylorus. *Pa.*, pancreas. *s. m. a.*, sup. mesenteric artery. *Ht.*, heart. *L.*, liver. *J.*, jejunum. *c. u. c.*, cavity of umbilical cord. *c.*, colon. *p. v.*, portal vein. *g. o.*, great omentum.

cats, dogs, and rabbits, and, as he suggests, it is most probable that it will be proved to be a mammalian characteristic.

Mall attributes the cause of the entrance of the intestines into the cavity of the umbilical cord, in the human embryo, to the descent of various abdominal organs, as well as to the great growth of the liver.

The two following sections show conclusively that in the cat the enormous size of the liver forms the chief factor in forcing the intestines to develop (during a certain period), outside of the abdominal cavity proper, within the cavity of the umbilical cord.

Fig. 2 is a sagittal section of a cat embryo $15\frac{1}{2}$ mm. The plate shows well the continuity between the coelom proper, and the cavity of the umbilical cord. The enormous size of the liver is most striking, as well as the size of the mesenteric vessels. At this stage the superior mesenteric artery is nearly two thirds the size of the intestine, so that it, together with the portal vein, occupies a very appreciable amount of space in the abdomen. The liver grows with great rapidity, and to such an enormous size that it practically fills the abdominal cavity, so that those portions of the intestine which develop at a somewhat later date have no choice, but are forced to grow in the continuation of the coelom, or, in other words, in the cavity of the umbilical cord. The surface of the liver which lies in apposition with the intestines is deeply grooved, which shows the pressure its growth must exert upon them. Moreover, the liver itself often oversteps the boundary line between coelom proper and the cavity of the cord, and a small bit of it, in this section, may be said to be actually contained within the latter cavity. In this embryo this is seen to a very slight degree, but it is not very uncommon to find quite a large expansion of the liver within this cavity, partially surrounding the intestinal coils. We have so frequently observed this phenomenon that at one time the question became a pertinent one as to whether it might not be the normal condition, and if for a brief space of time the liver ought not to be considered as a constant occupant of this cavity. This would seem, however, to be going too far; but to state that the liver is often found there is certainly no exaggeration.

A transverse section of this same stage of development is also instructive. Fig. 3 represents a transverse section of a cat embryo $15\frac{3}{8}$ mm. The section passes through the

coelom and the cavity of the umbilical cord. In the former cavity, the stomach, duodenum, and liver are closely packed together, while in the latter the coils of jejunum, ileum, and colon are recognized. The surface of the liver is deeply

Fig. 3.

Transverse section of an embryo 15 $\frac{3}{8}$ mm. *Pv.*, portal vein. *L.*, liver. *D.*, duodenum. *J.*, jejunum. *Al. a.* allantoic artery. *Al.*, allantois. *U. v.*, umbilical vein. *S.*, stomach. *Spi.*, spigelian lobe. *C.*, colon. *s. m. a.*, sup. mesenteric artery. *c. u. c.*, cavity of umbilical cord.

grooved by the intestines, as was seen in the previous sagittal section.

It seems to me that after an examination of these two sections one is forced to conclude that, in the cat, the liver

is chiefly responsible for the presence of the intestines in the cavity of the umbilical cord.

Although the sections demonstrate this point clearly, they fail to give us as complete an understanding of the relations of the different viscera within the abdominal cavity proper at this particular stage of development, as can be obtained by the dissection of an embryo.

Fig. 4.

The ventral wall removed from an embryo $17\frac{3}{8}$ mm. (Enlarged 10.6 diameters.) *L.*, liver. *J.*, jejunum. *C.*, colon. *c. ext.*, coils extra-abdominal. *O.*, omentum. *Sp.*, spleen.

Fig. 4 represents the abdominal cavity of an embryo $17\frac{3}{8}$ mm. after the removal of the ventral wall.

The enormous size of the liver is its most striking feature, together with the coil of intestine which was situated within the cavity of the umbilical cord. A stretch of

jejunum is seen going to this coil, and the colon coming from it. The cæcum is extra-abdominal, but it is hidden by one of the coils of the small intestine. A glance at Fig. 1 will make these relations quite comprehensible.

Fig. 5 represents a drawing of the abdominal cavity of an embryo $20\frac{2}{3}$ mm. The stage of development is the same

Fig. 5.

The ventral wall removed from an embryo $20\frac{2}{3}$ mm. The intestines which were in the cavity of the umbilical cord have been cut away. (Enlarged 10.6 diameters.) *L.*, liver. *J.*, jejunum. *D.*, duodenum. *S.*, stomach. *o.*, omentum. *Sp.*, spleen. *C.*, colon.

as the last, but the embryo is a trifle larger. The abdominal wall has been removed and the coil of intestines, which was so prominent in the last plate, has been cut away at the umbilicus, or, in other words, at the point of junction of the cavity of the coelom with that of the umbilical cord, in order

to show more accurately the relation of the jejunum and colon to the liver. One sees with great distinctness how deeply both of these portions of the intestine groove that organ; in fact, at one point they are both actually surrounded by liver tissue. The liver of this embryo, however, does not

Fig. 6.

Continued dissection of the embryo $20\frac{2}{5}$ mm. (Enlarged 10.6 diameters.)
L., liver. *J.*, jejunum. *D.*, duodenum. *S.*, stomach. *C.*, colon. *O.*, omentum. *Sp.*, spleen.

seem to present quite such colossal dimensions as in the embryo of $17\frac{3}{5}$ mm., as on the right a small bit of the duodenum is visible, and on the left the greater curvature of the stomach, both of which were completely concealed by it in the former embryo.

The following five plates are progressive dissections of this same embryo.

In Fig. 6 those portions of the liver have been removed which previously concealed the greater part of the stomach and duodenum, while the rest of the organ remains undisturbed. The stomach, the great omentum attached to its

Fig. 7.

Dissection of the embryo 20 $\frac{2}{3}$ mm. (Enlarged 10.6 diameters.) *L.*, liver. *D.*, duodenum. *J.*, jejunum. *S.*, stomach. *s.m.a.*, sup. mesenteric artery. *O.*, omentum. *Sp.*, spleen. *C.*, colon. *Cæ.*, caecum.

greater curvature, and the spleen, are clearly defined. The lesser omentum has been taken away, which brings to light the Spigelian lobe of the liver in close relation with the lesser curvature of the stomach. The pylorus, as well as the first part of the duodenum lie posterior to the jejunum and colon.

The second portion of the duodenum rests upon the caudate lobe of the liver, while the beginning of its third portion (the dotted line) disappears behind the jejunum and its mesentery. The + on the jejunum in Fig. 6 corresponds in position with the + on the jejunum in Fig. 7.

Fig. 8.

Continued dissection of the embryo 20 $\frac{2}{3}$ mm. (Enlarged 10.6 diameters.)
D., duodenum. *s. m. a.*, sup. mesenteric artery. *J.*, jejunum. *L.*, liver.
S., stomach. *O.*, omentum. *Sp.*, spleen.

This figure is the same stage of dissection as the last, except that the coils of intestine have been turned down, instead of being removed, so as to bring the mesenteries and the cæcum into view. The mesentery of the duodenum may be seen resting upon the caudate lobe, and the huge

superior mesenteric artery lying between the jejunum and the colon, but within the mesentery of the former. The cæcum, which was previously hidden by the intestinal coils, is readily recognized.

In Fig. 8 the jejunum and its mesentery have been divided at the + pictured in Figs. 6 and 7, and the colon where it is seen to be bent in the last plate. The stomach and the first and second portions of the duodenum are clearly defined, while the third and fourth portions are still hidden from view. The exact position and course of the intra-abdominal portion of the jejunum may now be studied. It begins at the termination of the duodenum, close to the cut superior mesenteric artery, proceeds caudad and then ascends to the umbilicus. A loop is thus formed whose convexity faces caudad and to the left. The jejunum then crosses the third portion of the duodenum and ascends parallel to and to the left of its second portion, resting all the time upon its mesentery. This loop of jejunum is absolutely constant, although, as we shall see later, its length depends upon the stage of development of the embryo.

In order to follow the duodenum throughout its entire course, it is necessary to separate the jejunum from its mesentery and to turn it caudad (Fig. 9). This brings the duodenum into view, and shows clearly the exact position of its four divisions. The first portion is the continuation of the pyloric extremity of the stomach, and rests upon the right central lobe of the liver. The second (D) is the descending portion, the third is represented by its bend, whose convexity faces caudad and to the right, while the fourth is the ascending portion which terminates where the jejunum begins, close to and just below the superior mesenteric artery.

The last three divisions of the duodenum all rest upon the caudate lobe.

The dissection of this embryo has given us the relations of the intra-abdominal divisions of the digestive tract at that period when the greater proportion of the intestines lie extra-abdominal. Let me briefly recapitulate them. The stomach

is rounded in form, much more vertical in position, and nearer the median line of the body than in an older embryo. The liver conceals it, as well as the duodenum. The duodenum makes a horseshoe like bend which may be divided into four portions, and at its termination it is fixed, and is

Fig. 9.

Concluded dissection of the embryo 20 $\frac{2}{3}$ mm. (Enlarged 10.6 diameters.)
D., duodenum. *s. m. a.*, sup. mesenteric artery. *J.*, jejunum. *L.*, liver. *S.*, stomach. *O.*, omentum. *Sp.*, spleen.

in relation with the superior mesenteric artery. This point marks the commencement of the jejunum which curves caudad and to the left, and then ascends to the umbilicus, which is situated a trifle cephalad from the pylorus. The jejunum then enters the cavity of the umbilical cord, and lies

here in coils together with the ileum, cæcum, and a portion of the colon. The colon may be traced into the abdominal cavity proper, where it takes its position just to the left of the median line of the body.

As we have already seen, the presence of the intestines within the cavity of the umbilical cord is chiefly due to a rapid and tremendous growth of the liver. Unfortunately, it has been impossible for me to determine the exact force, or conditions, which cause their entrance into the abdominal cavity. The period of their entrance is certainly a very variable one, and, indeed, one is tempted to think that it is almost ungoverned by the size or the length of the embryo, and possibly only by a certain stage of development. At one time it seemed to me as though it might possibly be explained by means of the mesenteric attachment. The mesenteries of a 15 mm. embryo have exactly the same attachment as in the adult cat. It is a curious fact that, were it possible to exert traction upon that part of the jejunal loop which crosses the third portion of the duodenum on its way to the cavity of the umbilical cord, and should this be continued until the jejunum, ileum, cæcum, and colon were drawn within the abdominal cavity proper, and then if at a given moment this traction should cease, one would find the intestines arranged as they are in the adult animal, with this exception, that the cæcum and colon, being the last to enter the abdomen, would naturally lie ventrad from the other coils of intestine, whereas in the adult cat they lie dorsad from them. And not only this, but the arrangement of the mesenteries would be found to be identical with those of the adult cat. Although it is impossible to give at present the reason of the entrance of the intestines into the abdomen, it is my belief that they have a definite order of entrance, and obviously it cannot be the theoretical one just described, although it seems to me possible that at some later date this order may be found to be applicable to the human embryo.

Fig. 10 represents the dissection of an embryo 62 mm.,

and in spite of its size a large coil of intestines was contained within the cavity of the umbilical cord (I). The abdominal wall was removed as well as those portions of the liver which

Fig. 10.

Dissection of an embryo 62 mm. A portion of the liver has been removed. (Enlarged 4 diameters.) *I.*, intestinal coil. *D.*, duodenum. *J.*, jejunum. *L.*, liver. *Il.*, ileum. *S.*, stomach. *Sp.*, spleen. *O.*, omentum. *K.*, kidney. *C.*, colon. *Al.*, allantois.

obscured any of the divisions of the alimentary canal. One sees at a glance that the stomach is more obliquely placed than in the previous younger embryos, that the great omen-

tum is more developed, and that the spleen is situated much farther to the left side of the body. In a word, this embryo represents a more advanced stage of development than the previous ones. The jejunum forms a long, extensive loop, which, together with its mesentery, almost completely conceals the duodenum. The cæcum lies in the median line of the body, close to and caudad from the pyloric extremity of the stomach. The terminal portion of the ileum takes a straight course to the umbilicus, where it joins the remaining portion of the small intestine to form the numerous coils contained within the cavity of the umbilical cord. The colon descends, makes a curve with its convexity to the left, and lies between the kidney and the jejunal loop, and close to its termination seeks once more the median line of the body. In this plate the outline of the cæcum is not distinctly defined, on account of its position. It lies with its mesenteric border facing dorsad, and this would seem to be the most natural position for it to occupy directly after its entrance into the abdominal cavity.

It will be remembered that in the former embryo the jejunum formed a short loop ventrad from the duodenum, and that the cæcum was extra-abdominal. In this embryo the jejunal loop is much more extensive, and the cæcum is intra-abdominal as well as the colon, and a short stretch of the ileum. The extra length of the jejunal loop approximately corresponds to the length of the colon, cæcum, and ileum which were previously extra-abdominal; hence it seems reasonable to conclude that the first step in the entrance of the intestine is a simultaneous entrance of its extremities.

It has been my fortune to observe several embryos whose intestines were entirely intra-abdominal, with the exception of a small coil of the ileum, which was situated from one to three cm. from the cæcum. These embryos varied greatly in size, and the variation is quite sufficient to account for the range of from one to three cm.

Hence we conclude that there exists in the cat a definite

order of entrance of the intestines into the abdominal cavity. First, a simultaneous entrance of the two extremities; secondly, an entrance of the jejunum, and thirdly, of the remaining portion of the ileum.

Formation of the Transverse and Ascending Colon.

The cæcum seems to remain in this position, with its mesenteric border turned dorsad (Fig. 10), until all the intestines have entered the abdominal cavity. It then turns so that its mesenteric border faces caudad, but it still retains its position in the median line of the body. Fig. 11 shows this relation well. It represents the opened abdominal cavity of an embryo 44 mm. All the intestines were of course intra-abdominal. Those portions of the liver which concealed the stomach and duodenum were removed, as well as the spleen, the greater part of the omentum, and the jejunum and ileum with their mesenteries, in order that the exact position and relations of the cæcum and colon might be observed. The cæcum is seen in the median line close to the pylorus, and rests upon the mesentery of the duodenum. The colon in the first part of its course is closely applied to the greater curvature of the stomach, and then turns caudad between the junction of the duodenum and jejunum on the one hand, and the Wolffian body on the other. The position of the stomach is distinctly more oblique than in the former younger embryos, and it is curious to notice that the terminal portion of the ileum occupies with great regularity the future site of the ascending colon.

Fig. 12 represents an embryo 65½ mm. The dissection is the same as the last; namely, a removal of the abdominal walls, portions of the liver, the spleen, great omentum, and the greater part of the jejunum and ileum with their mesenteries. The position of the stomach is not very different from that represented in the last plate, but as we shall see later, its obliquity seems to chiefly depend upon the develop-

ment of the Spigelian lobe of the liver, rather than upon the size of the embryo. The position of the cæcum is now quite different. It is situated to the left of the median line, but still retains its position close to the greater curvature. The

Fig. 11.

Dissection of an embryo 44 mm. A portion of the liver has been removed, as well as the jejunum and ileum. (Enlarged 5.3 diameters.) *L.*, liver. *D.*, duodenum. *Il.*, ileum. *J.*, jejunum. *S.*, stomach. *cæ.*, cæcum. *O.*, omentum. *W. b.*, Wolffian body. *C.*, colon.

relations of the colon are about the same as in the last plate. It winds around the point of junction of the duodenum and jejunum, and then seeks the median line. The terminal por-

tion of the ileum may be seen in the future position of the ascending and transverse colons.

It is difficult to say with certainty why the cæcum should here be found on the left side of the body, but the following explanation seems to me to be a plausible one: During the period of this migration of the cæcum there must

Fig. 12.

The dissection of an embryo 65 $\frac{2}{3}$ mm. (Enlarged 4 diameters.) *L.*, liver. *Il.*, ileum. *D.*, duodenum. *S.*, stomach. *cæ.*, cæcum. *O.*, omentum. *K.*, kidney. *d. c.*, desc. colon.

necessarily have been very little increase in the length of the colon. This is confirmed by a glance at Figs. 11 and 12. In the former, the colon makes a gentle curve, whereas in the latter it makes a sharp one. Now, had the colon been subject to either a continuous growth, or to a growth which

was in proportion to the growth of the embryo, one would not expect to find a diminution, but distinctly an increase in this curve. In a word, the colon in Fig. 12 is much shorter

Fig. 13.

The dissection of an embryo 70 mm. (Enlarged 4 diameters.) *L.*, liver. *t. c.*, transverse colon. *cæ.*, caecum. *il.*, ileum. *S.*, stomach. *Sp.*, spleen. *O.*, omentum. *D.*, duodenum. *s. m. a.*, sup. mesenteric artery. *k.*, kidney. *d. c.*, descending colon.

in proportion to the length of the embryo than in Fig. 11. Moreover, the loop formed by the junction of duodenum and jejunum is exerting no little pressure upon the colon as it

winds about it, and this pressure tends to push the colon and cæcum as far to the left side of the body as is possible. It seems to me that this pressure, together with a disproportionate growth of the colon, presents a probable explanation for the strange position of the cæcum to the left of the median line of the body. The migration of the cæcum to the left does not seem likely to be a curious coincidence or an anomaly, for this relation has been repeatedly observed, each case differing only in degree.

Fig. 13 represents the opened abdominal cavity of an embryo 70 mm. The dissection is exactly the same as the last one, but the embryo is not only larger, but is also more advanced in development. We now find that the colon has materially increased in length. At this stage the stomach, spleen, great omentum, and kidney prevent its further growth to the left. The stomach and liver interfere with its extension cephalad, the coils of jejunum and ileum as well as the liver lie ventrad from it, and the fixed point of junction of the duodenum and jejunum prevent its bodily movement to the right. The cæcum has no choice but to grow in a transverse direction, and thus the colon is elongated and the so-called tranverse colon is formed.

Fig. 14 represents the opened abdominal cavity of an embryo 73 mm. The dissection is the same as of the last two embryos, except that the great omentum has been opened in such a manner as to show the extremity of the Spigelian lobe of the liver, and its relation to the stomach. This organ is very obliquely placed, and so reminds one more of the adult than of the embryo.

Parts of the liver, spleen, and omentum have been removed, as well as the greater portion of the jejunum and ileum. The remaining organs present no difficulty in their identification. This embryo differs materially in one respect from the others, in that it possesses an ascending colon.

The cæcum continued its tranverse growth to the right until it encountered certain obstacles, which forced it to change this direction of growth. It met the duodenum,

which in itself was no slight obstacle to pass, and if the relations of the neighboring organs be carefully examined, other and possibly still more potent obstacles will be found,

Fig. 14.

The dissection of an embryo 73 mm. (Enlarged 4 diameters.) *L.*, liver. *t. c.*, transverse colon. *a. c.*, ascending colon. *D.*, duodenum. *cæ.*, caecum. *Il.*, ileum. *S.*, stomach. *Spi.*, Spigelian lobe. *O.*, omentum. *J.*, jejunum. *Sp.*, spleen. *s. m. a.*, sup. mesenteric artery. *d. c.*, descending colon. *K.*, kidney.

which must have obstructed its path. At this stage of development, the duodenum and its mesentery are resting upon the caudate lobe of the liver. This lobe is wedge-shaped, it is thicker externally than it is internally, consequently the duodenum and its mesentery rest upon an inclined plane which slopes to the left. The cæcum in its growth is obliged to ascend this inclined plane, and when it reaches the top it encounters the edge of the caudate, as well as at times the edge of the right central lobe of the liver, which obstacles obstruct its further growth to the right. The liver prevents its growth either cephalad or ventrad, and besides this, the coils of the jejunum and ileum lie ventrad from it. For these reasons, the cæcum is forced to grow caudad, parallel and to the left of the second portion of the duodenum. It is in this manner that the ascending colon is formed, and that the cæcum attains its usual adult position, to the right of the median line, and in close relation with the duodenum.

Intestinal Coils in the Embryo.

Is there a constant arrangement of the coils of jejunum and ileum either in the embryo or in the adult cat?

The embryos were treated by the progressive alcohol method, which sufficiently hardened their intestines and mesenteries, so that they would remain in place while being studied.

Five embryos were first chosen, of 69, 71, 74, 75, and 80 millimetres in length. The coils of jejunum and ileum were sketched, and at the same time a wire model was made, in order to determine if there was any general resemblance in the position of the individual coils. It was surprising to see that there was almost no resemblance whatever between any two of the models.

Feeling that this work was not sufficiently accurate, two embryos were chosen from the same litter which resembled each other in the period of development, in that the cæcum

in each was situated in the median line of the body, but they differed from each other in length, one measuring $45\frac{2}{5}$ mm., and the other $52\frac{2}{5}$ mm. Moreover, the length of their jejunum and ileum was very different; the former measured 63, and the latter 86 mm. The abdomens were opened, and

Fig. 15.

St., stomach. cæ., caecum. Du., duodenum.

drawings were made of the liver and of the intestinal coils *in situ*. The anterior portion of the liver was then removed, which brought the stomach and other intestinal coils previously hidden by it into view, and a second drawing was now made of all the superficial intestinal coils. The coils were followed by beginning with the termination of the ileum and ending with the beginning of the jejunum, and at the same time the deeper coils were sketched beneath the already

drawn superficial ones. The various coils were numbered, beginning with the termination of the ileum and ending with the beginning of the jejunum, and the corresponding

Fig. 16.

St., stomach. *cæ.*, caecum. *Du.*, duodenum.

superficial coils in both drawings were marked with the same letter.

There was no similarity in the arrangement of the individual coils of intestine in these two embryos.

It seemed to me that this might have been caused by the great difference in their length, so three embryos were chosen, as nearly as possible the same length, $63\frac{2}{5}$, $65\frac{2}{5}$, and 66 mm. These were drawn and studied after the method just described. The $63\frac{2}{5}$ embryo was not as far advanced in intestinal development as the other two. Its caecum was in

the median line, and its total length of jejunum and ileum was only 104 mm.

Embryos $65\frac{2}{3}$ and 66 mm. resembled each other very closely. In each case a short ascending colon was present, and the length of jejunum and ileum was almost identical, 119 and 120 mm. respectively. The allantois in both was fully distended.

In spite of the close resemblance existing between these two embryos, the coils of intestine differed materially from each other, as can be seen on referring to Figs. 15 and 16, but it should also be added that the arrangement of their intestinal coils resembled each other more closely than any of the previous embryos, and for this reason it seemed to me to be worth while to publish them, although there is, to say the least, very little similarity between them.

The following description applies to Figs. 15 and 16. Fig. 15 is an embryo of $65\frac{2}{3}$ mm., and Fig. 16 an embryo of 66 mm. (enlarged 5.3 diameters). These plates represent the arrangement of the intestinal coils as seen after the removal of the ventral lobes of the liver. The different coils are numbered, beginning with the termination of the ileum and ending with the beginning of the jejunum. The superficial coils are marked with a letter.

In the embryo cat the individual coils of jejunum and ileum have no definite arrangement, and it seems to me that it would be even going too far to state that the ileum was more apt to be situated on the right side of the body than on the left, although in many cases it is found there.

Intestinal Coils in the Adult Cat.

The thoracic aorta of five cats was injected with seventy per cent alcohol, and they were allowed to remain in fluid of the same strength for a week, and then their abdominal cavities were opened. The intestines had been sufficiently fixed by the alcohol to allow a satisfactory study of the coils of jejunum and ileum.

As soon as the abdomen was opened, an accurate draw-

ing was made of the superficial intestinal coils, and then a tracing of this drawing. The coils were followed throughout the entire length of the jejunum and ileum, and the deeper ones sketched in beneath the already traced superficial coils. So that there were two drawings for each animal, one of the superficial coils, the other of the superficial and deep ones.

On comparing the drawings thus made of the five cats, it was impossible to discover the slightest resemblance between them.

I therefore conclude that there is no fixed relation of the individual coils of the jejunum and ileum in the adult cat, and consequently that no constant arrangement exists in the position of these divisions of the small intestine. The intestinal coils were, of course, much more complicated in the adult animals than in the embryos, which is presumably due to the greater length of the adult intestine.

The Liver.

The development of this organ has an important influence on the adult position of certain divisions of the alimentary canal.

The cat's liver differs in so many respects from the human liver that a brief description of its lobes may be useful, before we consider the effect of its growth upon the neighboring organs.

If a liver which has been previously hardened *in situ* is removed from the body and viewed by its ventral surface, it will be seen to present a dome-like form.

The summit of the dome corresponds to its cephalic surface and is in connection with the highest part of the diaphragm. Its base represents the caudal surface, and is in relation with the different viscera. The longitudinal fissure divides the organ into two unequal halves. The right half is distinctly the larger of the two. An oblique fissure subdivides the left half of the liver into the so-called left central

and left lateral lobes. The former aids in the formation of the summit of the dome, and is in relation with the diaphragm and with the ventral abdominal wall. The left lateral is a much larger lobe. It is in relation with the ventral and lateral walls of the abdomen, while its caudal surface is closely applied to the stomach.

The right half of the liver comprises four lobes and is much less regular in shape. The right central and caudate are the only lobes to be seen in a ventral view. The former is very extensive and forms the right half of the dome. Its cephalic surface is in relation with the diaphragm, its ventral and lateral surfaces with the abdominal walls, and it is

Fig. 17.

2. The ventral surface of the liver of an adult cat. (Natural size.) *r. c.*, right central lobe. *g. b.*, gall bladder. *l. c.*, left central lobe. *l. l.*, left lateral lobe. *c.*, caudate lobe.

partially subdivided by a deep fissure, in which the gall bladder is lodged. Its caudal surface is in relation with the pylorus, and with the junction of the first and second portions of the duodenum.

The right lateral is a small lobe, and one which varies very much in size.

It is wedged in between the right central and caudate lobes, usually separated from each by a fissure, and its dorsal surface is overlapped by the former and its ventral sur-

face by the latter lobe. The dorsal surface of the right lateral lobe is consequently in relation with the right central lobe, and with the dorsal abdominal wall. Its ventral surface is apt to be hidden to a variable extent by the caudate lobe, with the exception of a small area which is in relation with the cephalic extremity of the kidney.

The caudate lobe usually presents three surfaces: A ventral surface upon which rests from one quarter to one third of the second portion of the duodenum and its mesentery; a

Fig. 18.

The caudal surface of the liver of an adult cat. (Natural size.) *r. c.*, right central lobe. *g. b.*, gall bladder. *d.*, duodenal groove. *c.*, caudate lobe. *k.*, kidney impression. *r. l.*, right lateral lobe. *l. l.*, left lateral lobe. *f.*, fundus of stomach. *x.*, apex of Spigelian lobe. *v.*, portal vein. *v. a.*, in relation with vertical arm of the lesser curvature of stomach. *s.*, Spigelian lobe. *p.*, in relation with the pylorus.

caudal surface, which covers the cephalic extremity and a part of the ventral surface of the kidney, and a dorsal surface, which is in relation with the right lateral, and often with the right central lobe as well.

Lastly, the Spigelian lobe remains to be described. This lobe seems especially liable to variations in form, but is fairly constant in size. It is most frequently pyramidal in shape. Its base is attached to the junction of the right central and caudate lobes, while the rest of the lobe is free, and extends

ventrad and to the left, to terminate in an apex. It has three surfaces. The ventral surface is in relation with the lesser omentum. The two lateral surfaces face somewhat obliquely. The right surface looks ventrad and to the right, and upon it rests the pylorus. The left surface looks caudad and to the left, and is in relation with the œsophagus, and with the vertical arm of the lesser curvature of the stomach.

The lesser curvature of the stomach forms an angle, which for convenience may be described as being composed of a vertical and of an oblique arm.

Fig. 19 is a diagrammatic sketch of the stomach, showing its approximate relation to the Spigelian lobe in the adult and in the embryo cat. The interrupted line represents the

Fig. 19.

Diagram of the stomach showing its relation to the Spigelian lobe in the embryo and in the adult. V. A., vertical arm of the lesser curvature. O. A., oblique arm of the lesser curvature.

outline of this lobe in the adult, and the dotted line as it appears at a certain stage of development in the embryo. In the adult cat, the apex of the lobe rarely meets the point of junction of the two arms of the lesser curvature, but sometimes (as is shown in the figure) lies close to it.

The liver is a fixed organ, and it is important to bear this in mind when considering the influence it exerts on the

position of the other viscera. It is attached to the diaphragm, and is also connected to the stomach by means of the lesser omentum. Its tissue is soft, the adjoining organs press against it, so as to produce permanent impressions upon it, and perhaps even to affect the growth of single lobes, but they are incapable of moving it bodily in any direction. On the examination of a number of livers which have been hardened *in situ*, one cannot fail to be impressed by the great extent of their normal variation. Not only do they differ in shape when considered as a whole, but there is also an enormous variation in the individual lobes, and some of them seem to be more prone to it than others.

It is difficult to explain why there should be so much more variation in the size and shape of this organ in the cat than in the human species, but such is certainly the case, and these variations are not confined to the adult animal, but are found in the embryo as well.

The liver grows with great rapidity, and it is natural to suppose that its increase in size would take place in the direction of least resistance, which I believe to be the case.

The individual variation in the external form of an embryo might tend to favor the development of one lobe to the detriment of another, and, as has been stated above, it is not very rare to find a portion of the liver within the cavity of the umbilical cord. It would seem quite possible that this might occur either if the point of communication between the coelom and the cavity of the cord was actually more capacious than usual, or if its contents were not quite as fully developed in one case as in another.

Furthermore, one lobe has the power to supplement a deficiency of growth which may exist in an adjoining lobe, and this is especially true of the embryo. For example, on opening the abdominal cavity of an embryo one would expect to differentiate a right lateral from a caudate lobe, but often there is no fissure visible. On a closer examination the caudate lobe will be found to be undeveloped, and to lie entirely concealed beneath the duodenum, whereas the lateral lobe

appears much larger than is usual, and occupies the normal position and relations of the undeveloped caudate lobe. This is perhaps the most striking example of this phenomenon, and seems to corroborate the theory that the liver develops in the direction of least resistance. The cause of resistance is, of course, often quite unknown.

There is no difficulty whatever in the identification of the liver lobes in a dissected embryo of 14 mm., and yet the proportion that these lobes bear to each other in the embryo is very different from their proportions in the adult. We have already seen that in the latter the right lateral is a very much smaller lobe than the right central. On the other

Fig. 20.

The caudal surface of liver and stomach of a 50 mm. cat embryo. (Enlarged 5.3 diameters.) *r. c.*, right central lobe. *i.*, intestinal groove. *d.*, duodenum. *r. l.*, right lateral lobe. *c.*, caudate lobe. *s.*, Spigelian lobe. *l. l.*, left lateral lobe. *p.*, pylorus. *f.*, fundus.

hand, in the embryo, it is one of the largest of all the lobes. In the adult, the Spigelian lobe seems to be of little importance, and yet, during development, it plays a most prominent part in the position of the stomach. The individual lobes not only differ in their proportions in the embryo and in the adult, but they also differ in the direct influence they exert upon the adult position of certain abdominal organs.

Fig. 20 shows the relation of the stomach and duode-

num to the liver, in an embryo of 50 mm. It may facilitate an understanding of the subsequent figures (in determining the position of the stomach, which in them has been removed), especially if a comparison be made between them and this one.

The fundus of the stomach lies in the concavity of the left lateral lobe, the pylorus rests upon the Spigelian lobe, and the duodenum deeply grooves the right central, the right lateral, and the caudate lobes. A groove is also seen on the right central and right lateral lobes which was occupied by a piece of the small intestine.

Fig. 21.

The caudal surface of the liver of a cat embryo $17\frac{2}{5}$ mm. (Enlarged 10.6 diameters.) *r. c.*, right central lobe. *j.*, jejunal groove. *r. l.*, right lateral lobe. *d.*, duodenal groove. *k.*, kidney impression. *c.*, caudate lobe. *c. o.*, colon groove. *l. l.*, left lateral lobe. *x.*, apex of Spigelian lobe. *f.*, groove for fundus. *v. a.*, in relation with the vertical arm of lesser curvature of stomach. *æ.*, oesophagus groove. *s.*, Spigelian lobe.

Fig. 21 represents the caudal surface of the liver of an embryo $17\frac{2}{5}$ mm., whose intestinal coils were extra-abdominal.

The various lobes can be easily identified. In the median line, close to the junction of the left lateral and right central lobes, two grooves are seen. The one on the left of

the embryo was occupied by the colon as it entered the abdomen from the cavity of the umbilical cord. The one on the right by the jejunum as it was about to leave the body cavity. This portion of the intestine also grooves the right lateral lobe. From this point of view, the right lateral appears to be actually larger than the right central lobe, although in reality this is not the case, but it is very much larger in proportion, as compared with the adult.

The left lateral lobe is deeply concave for the fundus of the stomach, and the œsophageal groove is seen close to the median line of the organ.

The pylorus rests upon the Spigelian lobe, and gently grooves it to the right of the cross, which marks the apex of this lobe. The apex touches the lesser curvature of the stomach, or possibly reaches a hair's breadth caudad from it. The lesser omentum lies ventrad from the lobe. It will be noticed that at this stage the relation of the Spigelian lobe to the stomach closely resembles that of the adult cat.

The duodenum begins close to the median line, and its second portion is situated to the left of the jejunum, in front of, and to the right of, the pylorus. It grooves the right central, the right lateral, and caudate lobes, and its loop, or third portion, rests upon the latter lobe. Its position is quite different from that of the adult, for it will be remembered that in the adult from one quarter to one third of the upper part of the second portion of the duodenum rested upon the caudate lobe, whereas in this embryo its third portion is in relation to it.

Fig. 22 represents the caudal surface of the liver of an embryo 61 mm. in length. The different lobes can be easily differentiated, and it will be observed that the caudate and Spigelian lobes are at this stage of development particularly prominent.

The fundus of the stomach is contained in a deep fossa formed by the left lateral lobe, while its pyloric extremity rests upon and grooves the Spigelian lobe. The duodenal groove is well marked as it curves over the right central and

caudate lobes. The depression for the kidney, as well as two grooves for the small intestine, are to be noticed.

It is at about this stage of development, it seems to me, that the liver is most influential in its effect upon the position of the neighboring organs.

In this embryo the cæcum lay to the right of the median line, close to the duodenum, so that a transverse but no ascending colon was present. The œsophageal opening of the stomach was well to the left of the median line. The

Fig. 22.

The caudal surface of the liver of a cat embryo 61 mm. (Enlarged 5.3 diameters.) *d.*, duodenal groove. *r. c.*, right central lobe. *c.*, caudate lobe. *k.*, kidney impression. *r. l.*, right lateral lobe. *i.*, intestinal grooves. *l. l.*, left lateral lobe. *x.*, apex of Spigelian lobe. *f.*, groove for fundus. *v. a.*, in relation with the vertical arm of the lesser curvature of the stomach. *œ.*, œsophageal groove. *s.*, Spigelian lobe. *p.*, groove for pylorus. *v.*, portal vein.

stomach rested upon the Spigelian lobe, whose apex extended caudad from the lesser curvature, and was in close relation with the greater curvature. The dotted line in Fig. 19 indicates the boundary of this Spigelian lobe, and gives its relation to the stomach. Fig. 14 also shows this from a different point of view. The great omentum has been opened, and so the apex of the Spigelian lobe is seen appearing dorsad from the stomach. A glance at Fig. 20, which

shows the relation of the stomach to the liver, will facilitate the understanding of these relations. The third portion of the duodenum rested upon the lower border of the caudate lobe, as in the 17 $\frac{2}{5}$ mm. embryo.

Fig. 23 represents the caudal surface of the liver of an embryo 111 mm. The appearance of this liver is quite different from the two preceding ones. The caudate and Spigelian lobes are not as prominent; the fossa occupied by the fundus of the stomach is much less pronounced, the groove for the œsophagus is better developed, and, in two words,

Fig 23.

Caudal surface of the liver of an embryo cat 111 mm. (Enlarged 2.6 diameters.) *d.*, duodenal groove. *r.c.*, right central lobe. *c.*, caudate lobe. *k.*, kidney impression. *r.l.*, right lateral lobe. *l.l.*, left lateral lobe. *f.*, groove for fundus. *x.*, apex of Spigelian lobe. *v.*, portal vein. *v.a.*, groove for the vertical arm of the lesser curvature of the stomach. *œ.*, œsophageal groove. *S.*, Spigelian lobe. *p.*, groove for pylorus.

this liver reminds one of the adult quite as much as of the embryo. In this embryo the hair was beginning to appear on the surface of the body, the ascending colon was perfectly formed, the third portion of the duodenum was some distance below the caudate lobe (possibly rather less than one half of its second portion rested upon it), and lastly, the Spigelian lobe extended a very short distance behind the stomach as

compared to the 61 mm. embryo (Fig. 22). It reached about one fifth of the distance between the broken and dotted lines, as shown in Fig. 19.

The Effect of the Growth of Certain Lobes upon the Neighboring Organs.

Now that we have examined each of these livers individually, let us consider certain points wherein they differ from each other, and the manner in which these differences affect the adjoining organs.

In Fig. 21, embryo $17\frac{2}{3}$ mm., the stomach and duodenum might be described as being contained in a great fossa which is almost surrounded by liver tissue. In Fig. 22, 61 mm. embryo, these borders have grown apart and the fossa is disappearing. In Fig. 23, 111 mm. embryo, the separation of the liver borders is still more marked, until finally in the adult, Fig. 18, the fossa may be said, comparatively speaking, to have disappeared. This transformation in the shape of the liver is probably largely due to the development of the intestines. In embryo $17\frac{2}{3}$ mm., the intestines were extra-abdominal, and so the liver only enclosed the stomach and duodenum, whereas in all the other embryos they were intra-abdominal, and were steadily growing in size as well as in length. The body of the embryo was of course also subject to growth, and so the liver was allowed to change its shape, to accommodate itself on the one hand with the growth of the intestines and on the other with the growth of the abdominal cavity. As has already been stated, the shape of the liver is prone to great variation, and when one reflects that the coils of intestine are pressing upon its caudal surface, it is reasonable to conclude that any change in the shape of this organ would affect the arrangement of these coils. It consequently might seem far more curious had we been able to determine any definite arrangement of them than an absolute lack of it.

A glance at the four liver plates shows that the caudate

lobe presents in each a very different appearance. In the 17 $\frac{2}{5}$ mm. embryo it is comparatively insignificant. On the other hand, in the embryo of 61 mm., it is very large and prominent. Its outer edge is much thicker than its inner edge, in consequence of which it forms an inclined plane, sloping to the left, upon which rests the duodenum and its mesentery.

This lobe in the 111 mm. embryo and in the adult do not differ materially from each other.

In the 61 mm. embryo the ascending colon was unformed, but the transverse was fully developed. The cæcum, in its growth from left to right, rested upon the mesentery of the duodenum which lay upon the caudate lobe. It is clear that the cæcum in its growth was forced to ascend this inclined plane until it reached the duodenum, and then these structures, together with the overhanging edges of the right central and caudate lobes, forced the cæcum to change the direction of its growth.

Hence the caudate and right central lobes play an active part in the limitation of the transverse and in the formation of the ascending colon.

In the 17 $\frac{2}{5}$ mm. embryo the extent of protrusion of the Spigelian lobe is very limited, and as has already been stated, its apex was not far from the lesser curvature of the stomach. This is quite different in the 61 mm. embryo. Here this lobe is most prominent, and as we have already seen, it gives the stomach great support. It is far less conspicuous both in the embryo of 111 mm. and in the adult than in the embryo of 61 mm. This is not due to an atrophy of the lobe, but to an increase in the growth of both stomach and liver, so that the proportions are entirely changed.

A glance at the œsophageal groove in the different drawings, shows a gradual change from the median line toward the left. The change is most marked on comparing the embryo of 17 $\frac{2}{5}$ mm. with the embryo of 61 mm. This corresponds to the period when the Spigelian lobe is most prominent. The deep groove on its surface is seen with great

distinctness in the latter embryo, as well as in the embryo of 111 mm.

We know that the stomach is obliquely placed in the adult cat, as well as that the œsophagus enters it obliquely. The cause of both is presumably due to the growth of the Spigelian lobe, chiefly, it would seem to me, at the stage of development that would correspond to the 61 mm. embryo. The liver groove, in which the œsophagus lies, is actually more pronounced at a later date, but this is probably caused by a slight additional growth of the left lateral lobe.

Hence we conclude that certain lobes of the liver, by means of their peculiar mode of growth, have a direct influence upon the obliquity of the terminal end of the œsophagus, the position of the stomach, the arrangement of the coils of the jejunum and ileum, the formation of the ascending colon, and in the limitation of the transverse colon of the adult cat.

Finally, I should like to acknowledge my indebtedness to Prof. C. S. Minot for many valuable suggestions, and especially for calling my attention to the advantages of dissection over other methods in the pursuance of this investigation.

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