

## **Studies on the Alimentary Tract of Sheep in South Africa.**

### **III. The Influence of Bowel Anastomosis on the General Nutritional State of Merino Sheep.**

By

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#### INTRODUCTION.

IN his "Mechanics of the Digestive Tract", Alvarez aptly quotes Billings to the effect that "a good reliable sett ov bowels iz wurth more tu a man than enny quantity of brains". Loss of moderate portions of this tract leaves the individual with little disturbance. Ileo-transversostomy is an operation of common occurrence and on the whole well-borne in man. Resections of small gut pass by unnoticed. When however extensive portions of small intestine are sacrificed a margin of safety is approached beyond which health and vigour may become severely impaired. Observations of this type are equally numerous and varying, varying for the simple reason that all measurement of bowel in vivo is relative. The standard anatomical length of 22 feet of small gut in the human can only be adhered to as a post-mortem fact. Attached to its fan-shaped mesenterium, and subject to the play of varying degrees of tonus at operation, it is possible to estimate the same length of bowel at the most divergent figures. Thus the cadaver length of 5.6 metres of small intestine is reduced to a total length of 2.5-2.75 metres from mouth to anus by swallowing of tubes in the experiments of Schembra and v. d. Reis. Moreover the normal divergence in bowel length in different individuals is such that the effects of extensive resection can rarely be gauged by measuring the excised length of bowel, and therefore only careful consideration of the remaining length of functioning tract can act as a guide to the re-establishment of equilibrium.

It would appear that loss of anything above half the length of small bowel can lead to metabolic disturbances. Numerous such cases are reported after resection of 2 meters of small gut (strangulations and lesions post abortum occurring frequently). Even loss of shorter stretches has led to disturbance, the subsequent autopsy revealing that the patient had originally had a much shorter intestinal tract than the classical length. In general the vast majority of extensive resections appertain to small gut with subsequent anastomosis of upper to lower small intestine.

The occasion for intestinal exclusion necessitating an anastomosis between jejunum and colon is doubtless rare, and as such the problem of the permissibility of joining a minimum functional length of the small intestine to a given part of the colon has received scant attention. The experience of such a case stimulated our interest in this question. Briefly, a man aged 58, had recently before admission into hospital recovered under conservative treatment from a subacute attack of ileus. The abdomen was still moderately distended, and there was still evidence of bowel-distension. Barium enemas proved negative. Oral administration revealed that a blind pouch became filled from the upper coils of the small bowel, and this in conjunction with a scar in the left hypochondrium from draining some cystic cavity 15 years previous, seemed to establish the diagnosis of a pancreatic cyst which might by adhesions be causing an incomplete obstruction. Laparotomy was agreed upon. At the operation one found practically all the distal  $\frac{2}{3}$  of the small intestine embedded in one extensive mass of adhesions, superimposed upon countless cysts of the appearance of extremely thin walled dermoid cysts situated throughout the mesenterium of the small gut, and binding down the whole conglomerate mass to the caecum and ascending colon. At one spot a definite kink in the whorls of intestine had caused obstruction, as was evidenced by the dilatation of gut extending three feet proximally. Three courses were open to pursue:—

1. A radical resection of all involved gut and proximal colon in the presence of partial ileus would have meant certain death;
2. separation of such adhesions as were causing the bowel obstruction was a rational, safe line to follow, but uncertain in its effect and the duration thereof;
3. an anastomosis between the free proximal small intestine to the colon could not be applied in the form of a jejuno-caecostomy, the whole mass preventing such approximation, and would of necessity have had to become a jejuno-transversostomy.

In view of the extreme uncertainty of such a procedure, recourse had to be taken to the second choice, that of liberating the strictured gut. A cyst excised intact for examination revealed a laminated membrane of echinococcal cyst with sterile debris as contents.

In view of the above case it was decided to perform a series of investigations upon animals to attempt to ascertain whether the proximal half of the colon was of essential value in cases with a minimal residue of small intestine, in casu, jejunum. There seemed reason to believe that the function of the proximal colon is of sufficient importance to provide different results in jejuno-caecostomy as compared to jejuno-transversostomy.

The hind-gut, in man and in most animals, has repeatedly been shown to act mainly as a faecal reservoir with comparatively little absorptive or excretory function to perform. In man the hind-gut commences at the junction of the middle and distal third of the transverse colon. That part of the large intestine which would be

excluded in a jejuno-transversostomy forms the distal part of the mid-gut. It has far greater significance than the distal colon or hind-gut. Such is already evidenced by its greater diameter, the faecal end of the colon having a diameter of 6 c.m. as compared to 2.5 c.m. at the distal sigmoid. The greater volume corresponds to the pre-eminently absorptive function of the proximal colon. Intestinal contents are discharged into the caecum in fluid state, and in the distal third of the transverse colon, that is on entering the hind-gut, are transformed into inspissated faecal balls. Nature effects this transformation over a short course by various ingenious manoeuvres of this portion of the gut, which has lately been intensively elucidated by X-ray cinematography (Wildegans). Chief of these is that peculiar movement of antiperistalsis, almost exclusively confined to this portion of the alimentary canal, and only questionably present in the sigmoid colon under other than pathological conditions. Antiperistalsis, moreover, is responsible for faecal tumor formation in the proximal colon in cases of intestinal exclusion, a subject upon which Tonnis offers considerable elucidation.

The extreme difference in the size and shape of the proximal colon in carnivorous and herbivorous animals is sufficient proof of its function of digesting cellulose products in addition to its condenser action. Man, the omnivorous forms an intermediate, with a haustrated colonic structure resembling the herbivorous type. Its comparative shortness in man on the other hand shows that it is designed for handling only small amounts of cellulose. Primitive man was a hunter and fisherman thousands of years before he learned to till the soil (Alvarez).

The question therefore arises: can the proximal colon cope with semi-digested intestinal contents from the jejunum in the sense of its normal function, and thus ameliorate the extreme digestive deficit of a jejuno-transversostomy? And, alternatively, does the proximal colon, in virtue of its antiperistaltic function possibly still function by retrograde filling from a jejuno-transversostomy in such cases of intestinal exclusion? Do such experiments shed any further light on faecal tumor formation in the proximal colon?

The choice of animal would fall on monkeys, which, however, could not be obtained in sufficient number and similarity for such experiments. Carnivora with their extremely short colon would not justify any comparison to man, although the intestines of the dog are most favourable for manipulation and measurement. Pigs would suit the purpose but for the difficulty in handling them. Rabbits were tried as a first attempt at herbivora, but it appeared that the mortality from shock within 24 hours (without technical deficiencies at the anastomosis) proved too great. It was therefore decided to select sheep.

The colon in man corresponds mostly to that of the herbivorous animal, which is blessed with an extensive large bowel for the digestion of its cellulose nourishment. One felt too, that if there was no appreciable divergence between jejuno-caecostomy and jejuno-colostomy in herbivora one would be justified in concluding that the divergence should be relatively equally small in man. Unfortunately



the measurement of small intestine is exceptionally difficult in the proximal length of jejunum in the sheep, where the mesenterium is so short, and the bowel so deepseated that the utmost care is required to avoid mesenterial haemorrhage. As a point corresponding to the distal part of the transverse colon in man, one selected the mid-point of the ansa spiralis in the sheep, a point easily recognisable and constant, and a point moreover where the ingesta have become completely "balled". Absorption must therefore have been practically completely effected before reaching this point.

#### OPERATIVE PROCEDURE.

As experimental animals were selected 4-tooth Merino lambs in good condition and of clinically healthy appearance. All animals had been kept under laboratory conditions for some months prior to being placed in experiment. The ration both before and after operation consisted of good quality veld hay, green barley or green lucerne and a small daily allowance of yellow crushed maize, with drinking water ad lib. Records were kept of the appetite shown by animals at different times, although the actual daily quantities consumed were not recorded. At first all animals were weighed twice weekly although later on this was changed to one weighing weekly. Furthermore faeces were collected from all animals twice weekly in linen bags strapped round the anus, and the amount, consistence and other characteristics described. For the rest, the animals were kept under constant clinical observation and post-mortem examination carried out on all animals lost, special attention being paid to the measurements of the different parts of intestine.

After 48 hours total starvation and prior to operation, the abdomen of the animal was shorn, shaved and washed and disinfected. Choral hydrate 60 to 80 c.c. 10 per cent. intravenously was used throughout as a general anaesthetic, the results on the whole being very satisfactory. All operations were performed under aseptic precautions. The first step was a paramedian laparotomy extending from the level of the umbilicus 5 to 6 inches backwards. Following this, the caecum was partly withdrawn and the ileo caecal junction and lower ileum made out. Starting either from the ileo caecal opening or from the duodenum, certain lengths of small intestine were measured off in approximately 6-inch loops caught up progressively between the thumb and forefinger of the two hands. This measurement as can be understood was at best only relative, seeing that the intestines are extremely elastic and festooned on the mesentery. Next the bowel was caught up in a rubber protected intestinal clamp over a length of  $\pm 6$  inches at a level previously decided upon. Depending on the anastomosis to be performed, a second clamp was placed either on the upper blind end of the caecum for a jejuno-caecostomy or on to the ansa spiralis, i.e. at the junction of upper and middle third of the colon for a jejuno-colostomy.

Previous measurements of the intestines of 4-tooth sheep gave values of 55 to 60 feet for the whole length of small intestine and 13 feet for the large intestine, taken immediately after slaughtering of the animals.

After drawing up the clamps closely parallel to each other, a side-to-side anastomosis was made with an opening of approximately 2 to 3 c.ms. between the two loops of intestines which was united by a single layer of a continuous cat gut suture. Following this, the small intestine was doubly ligated just distal to the anastomosis and severed between the ligatures, the two stumps being buried by purse-string sutures. In this manner a direct passage could be established between any level of the small intestine and any part of the large intestine, the portion of small intestine distal to the anastomosis being left in situ with its upper end blind.

The abdominal wound was closed with the usual three layers of sutures and collodion iodoform dressing applied to the skin.

#### EXPERIMENTAL FINDINGS.

Altogether 18 sheep were used in these experiments, being divided into two main groups of 8 each and one small group consisting of only 2 sheep.

##### *Group 1.*

In this group, comprising 8 sheep, the proximal 30 ft. of the small intestine as measured at the time of the operation, was anastomosed on to the tip of the caecum, the rest of the small intestine being left intact except for a closure and invagination of its upper stump. In the following table details are given concerning the bowel lengths as measured at autopsy, the ratio of anastomosed small intestine to the distal closed portion, and also the time of death after operation.

TABLE 1.

Sheep No.	Proximal small intestine anastomosed.	Distal small intestine.	Ratio of prox. to distal small intestine.	Large intestine.	Time of death.
41014	24 ft.	28 ft.	1 to 1.17	—	7 weeks.
40596	25 ft.	36 ft.	1 to 1.44	13½ ft.	8½ weeks.
40697	14 ft.	25 ft.	1 to 1.8	13 ft.	10 weeks.
40585	21 ft.	29 ft.	1 to 1.4	11½ ft.	10 weeks.
40893	29 ft.	33 ft.	1 to 1.1	13 ft.	19 weeks.
41051	23 ft.	41 ft.	1 to 1.8	—	1 day (shock).
40846	30 ft as measured at operation	—	—	—	Alive after 31 weeks.
38246	25 ft. as measured at operation anastomosed on to ileum 3 ins. above ileo-caecal opening	—	—	—	Alive after 44 weeks.

As will be seen from the above table, the total length of small intestines in the different sheep showed considerable variation although the length of large intestine was fairly uniform throughout. Furthermore in all the sheep which died, the length of small intestine anastomosed was shorter than that excluded, i.e. in every case actually less than half of the whole small intestine was kept in full function. In some cases this was only 4 ft. less than the distal portion excluded while in others it was considerable and measured as much as 11 ft. However, by anastomosing on to the tip of the caecum the whole large intestine was kept in function. Of the 8 animals only 2 are still alive, 5 of the others having died at intervals ranging from 7 to 19 weeks after operation, while 1 died from shock 24 hours after operation.

*Clinical Symptoms.*—The only symptoms of interest during the experimental period were those in connection with the general nutritional condition including the body weights and the amount and nature of the faeces passed.

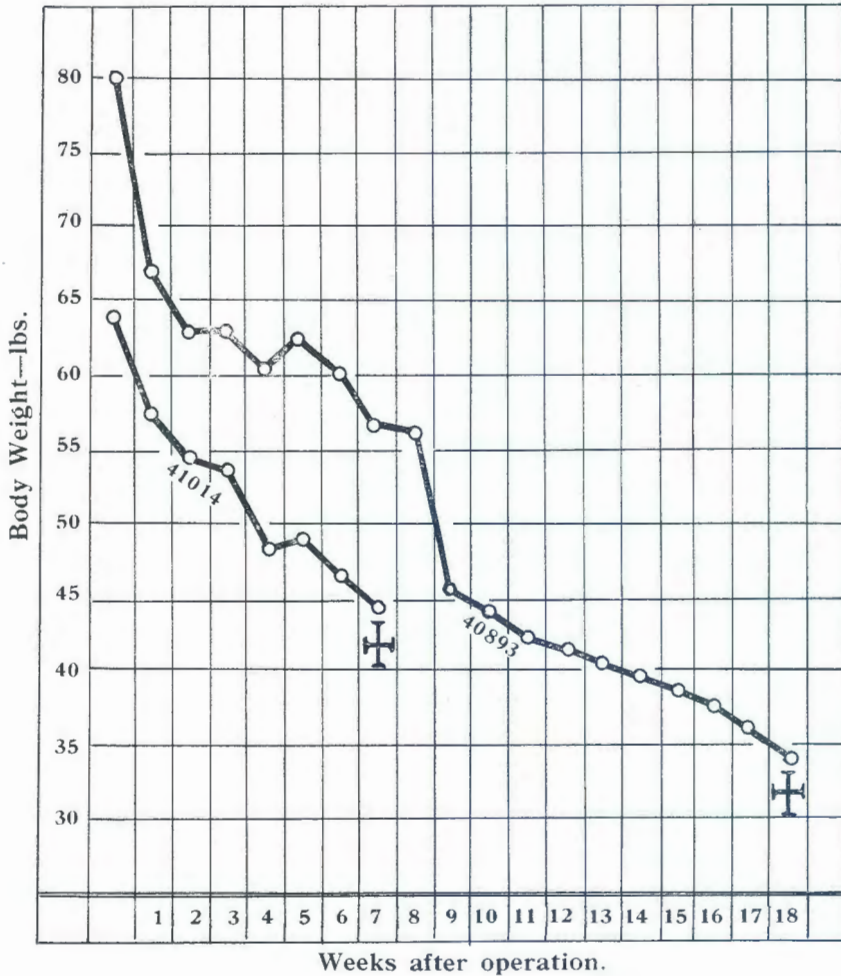
*Faeces.*—All animals, except one, stood the operation very satisfactorily, and usually commenced feeding on the second or third day. In every case, however, a severe watery diarrhoea made its appearance within 5 days after operation. A similar attack of severe diarrhoea was repeatedly noticed to affect some of the animals at intervals of one to three weeks, the consistence of the faeces being very fluid, clear or only slightly turbid, brownish, and at worst only mildly catarrhal. With the disappearance of the diarrhoea, usually after 2 to 3 days, the consistence of the faeces rapidly increased to that of a fairly thin to thick pultaceous mass. At times there were even signs of the normal pellet formation. The colour remained fairly constant ranging from a light yellowish green to the dark green of normal sheep's faeces. The coarseness of the faecal matter showed little change and small pieces of undigested maize were at times observed in the excreta.

*Body Weight.*—In each of the 5 animals that died, there was a progressive decrease in the body weight up to the time of death as will be seen from graph 1, taken from the two sheep that died in 7 weeks and 19 weeks respectively. In every case there was progressive emaciation, and weakness, the animal frequently appearing huddled up and with the back arched. Towards the end, profound weakness was followed by prostration with decubitus. Animals found in this state were slaughtered for post-mortem examination.

In the two animals that survived, a sharp initial decrease in the body weight was followed by a gradually progressive recovery. Thus as shown in graph 2 one sheep has practically reached its original body weight after 31 weeks, while the other after 43 weeks shows considerable gain on its weight prior to the operation. Both animals appear lively, they feed well and the faeces passed is normally formed.

GRAPH 1.—Sheep 40893 and 41014.

Proximal part of small intestine anastomosed on to tip of Caecum. Both dead.



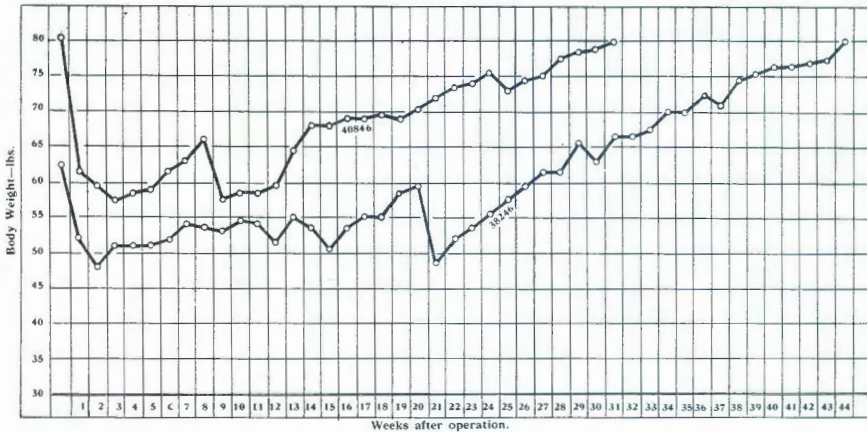
*Post-mortem Findings.*—In all five carcasses examined, the pathological changes noted were very uniform, varying slightly in degree only. Thus in every case there was definite cachexia, general atrophy of skeletal muscle and fatty tissues, gelatinous infiltration of subcutaneous tissue, varying degrees of atrophy of the internal organs, especially the liver and kidneys, accompanied by brown pigmentation, also general pallor of the carcass. The forestomachs and abomasum appeared small and in some cases badly filled and with signs of atony of the muscular wall. The proximal (anastomosed) portion of the small intestines in every case appeared to have suffered little or no change, being of the usual thickness and colour and containing apparently normal ingesta. The distal (excluded) part of



the small intestines, however, was materially altered in every sheep, being pale, markedly atrophic and threadlike. The lumen of the bowel was very small and contained only traces of a thick, creamy inspissated secretion. No food residues whatever were found in this part, neither did any retrograde filling take place from the caecum through the ileo-caecal opening. In every case the anastomosis was found widely patent, easily admitting the index finger. It appeared well healed and without signs of any leakage. The large intestine appeared well filled, the ingesta showing little change from the normal. No morphological change was detected in the walls of the large gut. In two cases there was evidence of skeletal change, e.g. rib fractures followed by poor callus formation. In these cases the ribs were found to be rather easily broken between the fingers. Samples of the different bones were collected for further examination.

GRAPH 2.—Sheep 40846 and 38246.

Proximal part of small intestine anastomosed on to tip of Caecum. Both alive.



### Group II.

In this group, again consisting of 8 animals, the proximal half of the small intestine, measured off as being approximately 30 ft., was anastomosed on to the middle of the ansa spiralis, a point found to correspond to the junction of the proximal and middle thirds of the large intestine. It should be indicated that at this level the faecal pellets are already fairly well formed and of firm consistence proving that water absorption and consequently the dehydration of the faecal mass is largely conducted in the upper third of the large intestine. Thus in this series approximately the lower half of the small intestine as well as the upper third of the large intestine was excluded by the anastomosis.

The following table indicates the different bowel lengths as found at autopsy, also the time of death after operation.



TABLE II.

Sheep No.	Prox. small intestine (anastomosed).	Distal small intestine (excluded).	Prox. large intestine (excluded).	Distal large intestine (anastomosed.)	Time of death.
40511	19 ft.	30 ft.	4½ ft.	10 ft.	3 days (obstruction).
40880	25 ft.	—	—	—	10 days (diarrhoea).
39466	18 ft.	30 ft.	4 ft.	9 ft.	11 weeks.
32865	28½ ft.	23½ ft.	5 ft.	8½ ft.	12 weeks.
39412	22 ft.	23¼ ft.	5⅔ ft.	8 ft.	21½ weeks.
40902	24½ ft.	30½ ft.	4½ ft.	8½ ft.	21½ weeks.
41089	23½ ft.	20 ft.	4½ ft.	8 ft.	30½ weeks.
38632	25 ft. as measured at operation	—	±4 ft.	±8½ ft.	Alive after 52 weeks.

As shown in Table II only 1 out of the 8 animals still survives. Two animals were lost within a few days after operation, one as the result of acute ileus following oedematous closure of the anastomosis wound in the intestines. The other sheep died as the result of a severe and obstinate diarrhoea appearing on the second day after the operation and lasting up to the time of death. None of the sedatives and astringents administered effectively stopped the condition. As in the previous group, the total length of small intestines in the different animals showed considerable variation, although the large intestine was of closely uniform length in all the sheep. Except in the case of two animals, the length of small intestine excluded was again greater than that which was anastomosed. With regard to the large intestine, the upper 4 to 5 feet was regularly excluded in every animal while approximately twice this length was retained through the anastomosis. Five animals succumbed over a period ranging from 11 to 30½ weeks after being operated. One sheep is still alive after 12 months.

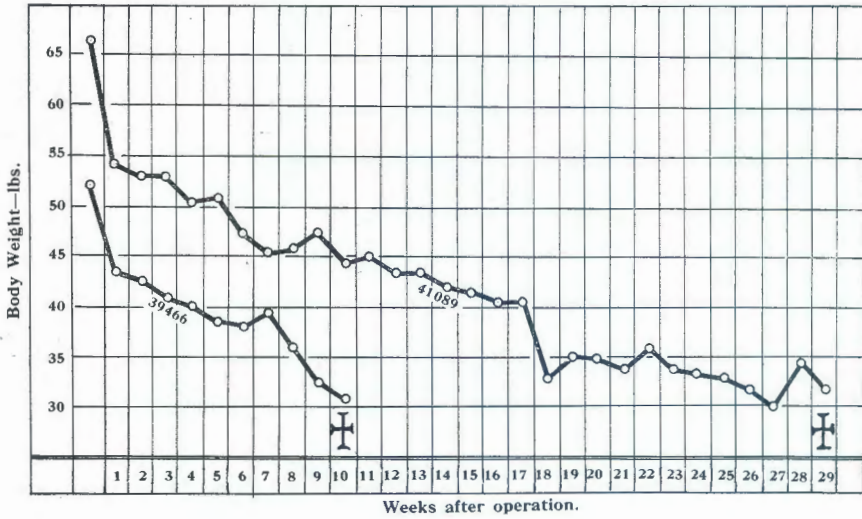
*Clinical Symptoms.*—The symptoms shown by all animals in this group, except for the two acute cases, were very closely similar to those seen in the first group. In every case, however, the diarrhoea was more persistent, although the degree of wateriness of the faeces varied from time to time. Normally formed solid faecal pellets were never collected from any of these sheep. Even the one animal which is still alive after 12 months, has shown a diarrhoea during the whole period, at times so severe as to provoke extreme exhaustion verging on prostration.

The weight curves too are very similar to those shown by the first group. Graph No. 3 is that of the sheep which died after 11 weeks and 30½ weeks respectively, while the animal still surviving is represented on graph No. 4. This latter animal has shown remarkable tenacity in spite of the severe and repeated attacks of diarrhoea, which are clearly represented on the graph by the numerous sharp decreases in its body weight. Whereas none of the other animals appear to have made any serious attempt at accommodating themselves to the new conditions of digestion, this one sheep has not only succeeded in adapting itself to existing conditions but has actually gained 14 lb. on its original weight as registered at the time of operation.

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GRAPH 3.—Sheep 41089 and 39466.

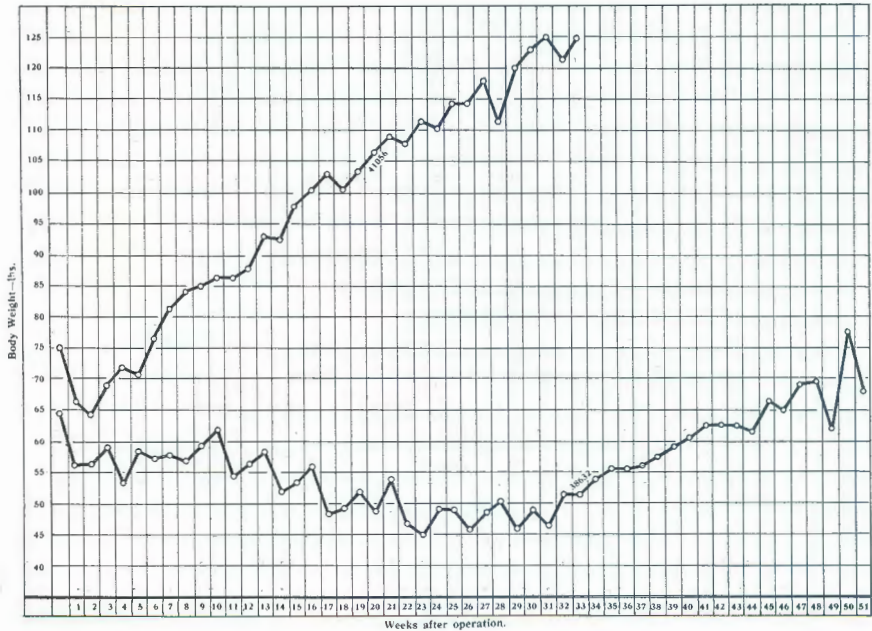
Proximal part of small intestine anastomosed onto ansa spiralis. Both dead.



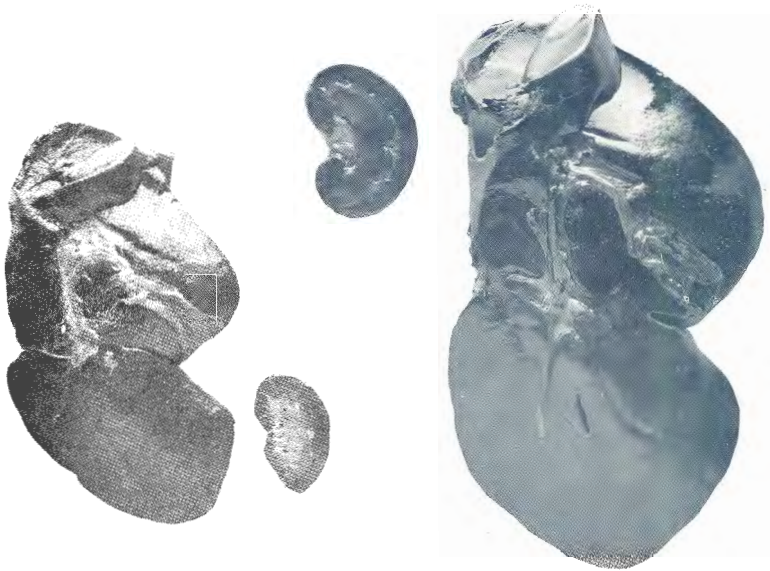
GRAPH 4.

Sheep 41056. Lower ileum anastomosed onto ansa spiralis

Sheep 38632. Proximal part of small intestine anastomosed onto ansa spiralis.



*Post-mortem Findings.*—On the whole the pathological lesions are in accord with those described for the first group. The degree of cachexia and atrophy was particularly severe in those animals dying after the longest interval. The skeleton appeared small and stunted. The internal organs especially the liver, kidneys and spleen showed well marked atrophic changes. Thus the liver of sheep No. 41089 weighed 180 grams compared with the liver of a healthy sheep of the same age weighing 550 grams. (See photograph No. 1.) The distal part of the small intestines excluded from the anastomosis was again found to be pale, atrophied and empty except for small amounts of inspissated secretion. The caecum and upper colon proximal to the anastomosis in every case contained a thick pasty, greyish inspissated material probably composed of various substances such as mucins, cholesterol and mineral salts. Further analytical work is being conducted on these materials. The mucous membrane of this part showed no change from the normal. In none of the animals examined at post-mortem were there any signs of retrograde filling of the colon cranial to the anastomosis, whereas the rest of the colon distal to the anastomosis in each case contained soft pultaceous faecal masses. Although all these animals frequently showed diarrhoea, no signs of enteritis were to be noted at post-mortem.



PHOTOGRAPH NO. 1.

*Left.*—Liver and kidney of sheep 41089 showing severe atrophy after loss of 20 ft. small intestine and 4½ ft. large intestine, 6½ months previously.

*Right.*—Liver and kidney of normal sheep of same age.

### *Group III.*

In order to ascertain what rôle the ileocaecal sphincter played in controlling the passage of ingesta from the small intestine to the caecum, the lower ileum in one sheep ( $\pm 6$  inches above the sphincter)



was anastomosed on to the tip of the caecum, i.e. a widely open passage was established between the small intestine and the large intestine the ends of the intestine distal to the anastomosis being closed. Regular examination of the faeces showed that this animal never suffered even a single attack of diarrhoea while the consistency of the excreta remained normal over a period of 10 months. The weight curve has also gradually risen, the animal having more than doubled its weight prior to operation. In the second sheep of this group, the lower ileum was anastomosed on to the ansa spiralis thus excluding not only the ileo caecal sphincter but also the caecum and upper third of the colon. As will be seen from its weight curve (graph No. 4) a sharp decrease immediately after the operation, was followed by a steady and progressive increase until after a period of 7 months the animal had practically doubled its original weight. Throughout the whole period the faeces were soft, thickly pulpaecous and at times appeared as partly formed pellets lumped together, i.e. the degree of dehydration has constantly remained somewhat below the normal.

#### DISCUSSION.

Experiments were carried out on Merino sheep (4 tooth old), with the object of ascertaining firstly, the effect of anastomosing the upper half of the small intestines on to the caecum and secondly, by anastomosing the same portions of small intestines on to the ansa spiralis, corresponding to the junction of upper and middle thirds of the large intestines. For this purpose two main groups were formed of eight sheep each. On the whole the operation was well stood, only three sheep being lost within the first week, one from shock, another from ileus through oedematous swelling and closure of the anastomosis and a third from acute and persistent diarrhoea. Of the remaining thirteen sheep, 10 died over a period of 12 months. The main difficulty encountered in the operation was in connection with the proper measurement of the lengths of intestines especially of the small intestine, due to the varying degrees of tonus and also to the festooned attachment of the intestine on to the mesentery. In all cases the object was to preserve approximately half the small intestine through the anastomosis and to exclude the other (distal) half. However, post-mortem examination and measurement of the intestines of the 10 sheep revealed the fact that in the majority of cases considerably more than half of the small intestine was excluded from the functional tract, a fact which definitely contributed to the high mortality. However, as all the carcasses showed varying degrees of cachectic and atrophic changes in which the intestines were also involved, the measurement of the latter at post-mortem may to some extent have been influenced by these processes. Thus whereas the functioning portion of the intestine appeared normal, the excluded part was definitely atrophied, pale, and atonic, which to some extent might have accounted for the greater lengths obtained as compared with those of the functioning portions. No suitable method has been devised for a more accurate measurement of intestinal length, although this point is being investigated in connection with a further series of experiments about to be undertaken.

All the operated animals lost weight very rapidly in spite of their good appetites. The 10 animals which died, never even seemed to make an attempt to adapt themselves to the shorter intestinal lengths and thus inhibit the progressive body wastage. Of the three surviving animals a preliminary period of severe wasting was followed by a second phase during which gradual adaptation took place. The animals not only maintained their weight during this period but were actually able to show a steady gain under the new conditions of digestion and absorption. Unfortunately no detailed study of the metabolism of these animals was possible at the time of the experiment.

Of the two groups, the animals in the first group, in which only the lower half of the small intestine was excluded, showed no significant advantage over the second group in which the proximal part of the large intestine was in addition also excluded from the anastomosed tract. In no instance was there retrograde filling of the lower half of the small intestine from the caecum, neither did the caecum and proximal part of the colon become filled where the anastomosis was made on to the *ansa spiralis*. This fact indicates that retroperistalsis is extremely feeble or perhaps completely absent in the upper third of the large intestine of the sheep. The large amount of inspissated non-faecal material regularly found in the caecum and upper colon indicates that this is an area of active excretion and secretion. Complete analyses of these materials are at present being carried out. Although the caecum and upper colon must be regarded as of great importance in the absorption of water, the lower levels of the colon are to some extent capable of compensating for the loss of the caecum and upper colon. This however is largely a matter of individuality as some animals suffer heavy loss of water through a persistent diarrhoea while others minimise this loss by passing less watery faeces. The diarrhoea so often noticed in the animals, was however not related to any form of colitis as no pathological lesions were found in the large colon post-mortem. In two animals operated upon, the loss of the ileocaecal sphincter only or the ileocaecal sphincter together with the caecum and upper colon, led to no untoward effects whatsoever.

#### SUMMARY.

1. Exclusion of the lower half of the small intestines alone (see graphs 1 and 2), or in addition exclusion of the caecum and upper colon through bowel anastomosis causes progressive atrophy, extreme cachexia and even death in Merino sheep (see graphs 3 and 4).

2. No retrograde filling takes place of any of the portions of intestine excluded, hence the absorptive surface is decreased by the length so excluded from anastomosis.

3. There is considerable disturbance in the water metabolism of such animals, the degree of adaptation and compensation depending in some measure on the individual characteristics of the animal itself.

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