

3. On the Anatomy of *Antechinomys* and some other Marsupials, with special reference to the Intestinal Tract and Mesenteries of these and other Mammals. By FRANK E. BEDDARD, M.A., F.R.S., F.Z.S.

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(Text-figures 111-124.)

CONTENTS.

- I. On some Points in the Anatomy of *Antechinomys*, p. 561.
- II. On some Points in the Anatomy of *Phascologale*, p. 564.
- III. On the Intestinal Tract in some Marsupials, compared with that of other Mammals, p. 567.
- IV. On the Existence of a Suprarenal Portal System in Marsupials, p. 600.
- V. Resumé of new facts, p. 603.

I. *On some Points in the Anatomy of Antechinomys laniger.*

An example of this rare Marsupial was kindly placed in my hands some time since by Mr. Beck of this Society, with the request that I would examine its anatomy. The specimen consisted of the carcass after the skin had been removed, and was therefore incomplete as regards many of the muscles. But the viscera were intact, and I am able therefore to contribute something towards a fuller knowledge of this small Polyprotodont Marsupial. The only memoir known to me which deals with its anatomy is one by the late Mr. Alston in the 'Proceedings'\* of this Society, written nearly thirty years ago. In this paper a number of facts is given relating to the internal organs of the body and there is also an account of its osteology. The viscera are somewhat summarily described by Mr. Alston; and there is thus some scope for a fuller account of certain organs in the light of later work upon the anatomy of mammals.

The *stomach* of this Marsupial has been figured by Alston, who has compared it with that of *Antechinus*†. He has, moreover, divided other related genera by the more globular or more transversely elongate form of that organ. I submit herewith (text-fig. 111) a drawing of the stomach of the specimen of *Antechinomys* which I have myself dissected and which I hope is accurate. It will be seen that it agrees more nearly with *Antechinus* as represented by Mr. Alston than with *Antechinomys* as figured by that naturalist. In particular I would call attention to the considerable calibre of the duodenum where it leaves the stomach, and to the fact that the cardiac half of that organ is considerably prolonged beyond and to the left of the entrance of the œsophagus. I am led, therefore, to doubt the value of the

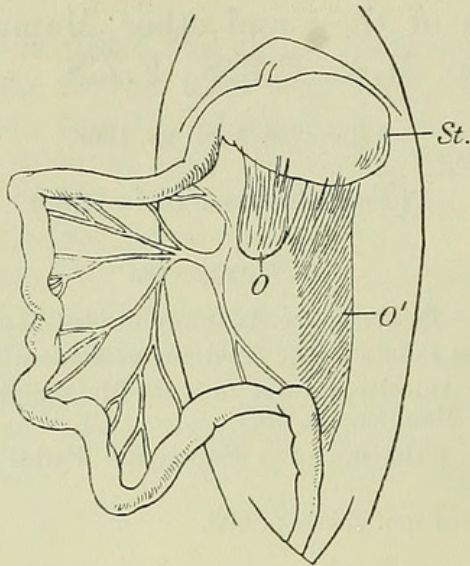
\* P. Z. S. 1880, p. 454.

† Now referred to *Phascologale* (Thomas, Cat. Marsupials Brit. Mus. 1885).



characters of that organ in discriminating between these allied genera.

Text-fig. 111.



Alimentary tract of *Antechinomys laniger*.

O. Omentum. O'. Splenic omentum. St. Stomach.

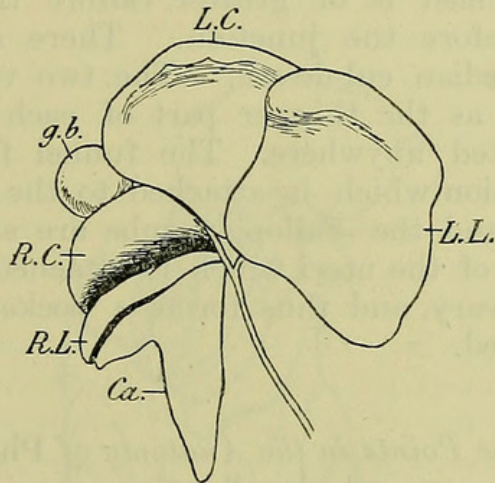
The *intestine* presents a number of features of interest. It is in the first place very short, as Mr. Alston has pointed out. Furthermore, there is no external differentiation into sections. The tube has the same bore throughout, and the absence of any trace of a cæcum renders it impossible to fix the delimitation between ileum and colon. The alimentary tract is not only short but, comparatively speaking, rather wide. There is no duodenal loop to be distinguished from the rest of the tube. The interesting fact about the intestine is that the whole tube is suspended from the middle line of the dorsal parietes by a single continuous mesentery. This is absolutely uncomplicated by any secondary attachments of any sections of the gut to each other, or to the parietes. In other mammals there is at least (in the majority of cases at any rate) one folding of the gut upon itself. That is, in the region of the stomach the transverse colon lies above the duodenum just after it issues from the stomach, and there is in this region a more or less direct mesenteric secondary connection between the duodenum and the colon or mesocolon. There is nothing of the kind in *Antechinomys*.

Another point of importance to be noted in relation to the intestine is that the loops into which it is thrown are not fixed. The whole intestine can be straightened, or rather of course thrown into a continuous curve, and thus differs markedly from many forms where the foldings of the intestine are permanent foldings and cannot be straightened out without tearing the supporting mesentery. Indeed, it is not too much to say that the alimentary tract of this mammal is as simple as that of any Lizard.



Mr. Alston's figure of the *liver* of *Antechinomys* does not agree entirely with the appearances which I have observed, and the description which he gives is very brief. I find (text-fig. 112) no Spigelian lobe, but the caudate lobe is deeply bifid and largely covers the right kidney. The gall-bladder, which Alston has correctly stated to be present, appears to me to occupy an unusual position. Instead of lying in a cleft in the middle of the right central lobe, as is at any rate often the case among mammals, it lies, as in some other Marsupials\*, to the median side of the right central lobe almost between it and the left central. I did not find the right lateral lobe quite so large as Alston has figured it. It is closely fitted to the caudate. The liver "formula" of this Marsupial seems to me to be fairly accurately expressible as follows:—viz.,  $LL\frac{1}{2} > LC = RC > RL = Ca$ .

Text-fig. 112.

Liver of *Antechinomys laniger*, abdominal aspect.

Ca. Caudate lobe. g.b. Gall-bladder. L.C. Left central lobe. L.L. Left lateral lobe. R.C. Right central lobe. R.L. Right lateral lobe.

The *spleen* is of large size and shows no indication of a triradiate form; it is wider at the duodenal end and narrower at the opposite extremity. The wide extremity of the spleen is marked by two parallel longitudinal furrows which divide up this extremity into several finger-shaped lobes not detached from each other.

The *pancreas* is very diffuse and scattered, consisting of numerous small lobules; it forms a more or less continuous mass which lies partly in the mesoduodenum and partly in the splenic omentum. It reaches also to the other side of the stomach and a piece of it lies to the left of the cystic duct between that duct and the duodenal end of the stomach.

The *omentum* (text-fig. 111, O) is very short and ends in pulled out ragged edges as is shown in the drawing. It is

\* E. g. *Dendrolagus* and *Petrogale*, Beddard, P. Z. S. 1895, p. 131.



nowhere attached to the alimentary canal. The splenic omentum (text-fig. 111, *O'*) extends a little beyond the left kidney in its insertion on to the median dorsal line.

The left *kidney* is well below the right, and in fact its anterior end is only just a trifle above the level of the posterior end of the right kidney. The kidneys are rather large, about 10 mm. long.

The *organs of reproduction* are not widely different from those of other Marsupials. The example of *Antechinomys* dissected by myself was a female and apparently fully formed in the organs of sex. I am able to fill up a lacuna in our knowledge of those organs in the Marsupialia. The uterus of each side was swollen into an almost spherical dilatation near to the origin of the Fallopian tube into which it abruptly contracted. At the other extremity this dilatation lessened more gradually, though at the same time with some abruptness, into the rest of the uterus. At the junction of the two uteri in the middle line the common chamber thus formed is of greater calibre than is either of the uteri just before the junction. There seemed to be a rudiment of a median cul-de-sac. The two vaginæ are about the same calibre as the thinner part of each uterus and are not specially dilated anywhere. The funnel forms the usual fimbriated expansion which is attached to the ovary for a very short space. It and the Fallopian tube are supported by the anterior ligament of the uteri which is attached to the parietes in front of the ovary, and thus forms a pocket into which the ovary can be pushed.

## II. *On some Points in the Anatomy of Phascologale macdonellensis.*

I also owe to the kindness of Mr. Beck a complete example of this recently described species of *Phascologale*, which presents several features of interest in its anatomy. The genus itself is not well known anatomically. So far as I have been able to ascertain, there are only two recent memoirs extant which deal with the visceral structures of species of *Phascologale*. The first of these is in a paper upon *Antechinomys laniger* by the late Mr. Alston to which reference has already been made, and in which the stomach of *Antechinus* (= *Phascologale*) *swainsoni* and *Phascologale penicillata* are described, and in the case of the former figured, as well as some other viscera. In the second paper—Dr. D. J. Cunningham's Report upon the Marsupials collected during the voyage of H.M.S. 'Challenger,'\* some notes are given upon the thoracic viscera (*not* the abdominal) of *Phascologale calura* and concerning the azygos vein.

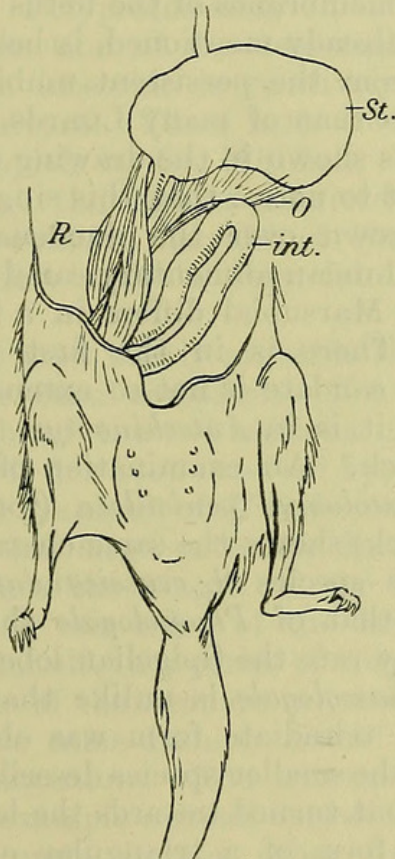
The example which I dissected was a fully adult female with no signs of immaturity. The teats (3 on each side) were large,

\* Vol. v. of the Reports.



indeed so large as to suggest that the animal had recently borne young. Neither were there any signs of immaturity about the organs of reproduction. Nevertheless, there was a large persistent urachus or umbilical cord. There is no question here of mere traces or of a minute rudiment of this structure. It was large and conspicuous, as is plainly shown in the accompanying figure (text-fig. 113). Whether this umbilical cord does or does not contain any functional blood-vessels I cannot say. All vestiges of blood-vessels were invisible on dissection. Moreover, although I have used the term "cord" to express this structure, it is by no means an exactly descriptive word. When the animal was dissected under water the membrane forming the umbilical cord floated out loosely, being merely gathered together at the point where it perforates the rectus abdominis muscle to be attached to the skin.

Text-fig. 113.



"Umbilical cord" and adjacent viscera of *Phascologale macdonellensis*.

int. Intestine. O. Omentum. R. Rectus muscle perforated by umbilical cord. St. Stomach.

The attachment of this membrane to the intestine fixes that tube, as is natural, in a definite position; if it were not for this persistent umbilical cord the intestine could be, as I imagine, laid out in a continuous curve as in *Antechinomys*. The point where the umbilical membrane is attached to the gut represents,



I presume, the position of Meckel's diverticulum. In this case the greater part of the intestine will be referable to the small intestine and the colon will be short. The umbilical membrane, however, is not limited to that portion of it which is attached to the intestine. It spreads out and is continuous with the omenta both great and small; there is absolute continuity between the umbilical membrane and the stomach and spleen. It would appear therefore, that *Phascologale macdonellensis*, like the majority of Marsupials, has an umbilical placenta. In relation to this I may say that there was no connection whatever between this umbilical cord and the bladder. The umbilicus itself lies rather in front of the last rib, and is situated 10 mm. from the end of the sternum; it is, on the other hand, 28 mm. from the anus.

One cannot but think that the case described here is exceptional, and that the genus or species generally is not characterised by this persistent umbilical cord. It will be, however, interesting to enquire how far the omentum is really connected with the membranes of the fœtus in development.

The *intestine*, as already mentioned, is held in position by the ligament derived from the persistent umbilical vesicle. It has a simple course like that of many Lizards, and forms only one loop upon itself as is shown in the drawing (text-fig. 113). It is not without interest to notice that this single loop is rather like the single loop thrown over the duodenal region during the development of the human alimentary canal.

The *liver* of this Marsupial differs in a few points from that of *Antechinomys*. There is in the first place a considerable Spigelian lobe; the caudate is not so extensively prolonged over the right kidney as it is in *Antechinomys*. Otherwise the liver does not differ much. An examination of an example of the larger species *Phascologale penicillata* (for which I am also indebted to Mr. Beck) shows the same characters. The liver of *Sminthopsis* (of the species *S. crassicaudata* and *S. larapinta*) agrees more with that of *Phascologale* than of *Antechinomys*. In the former at any rate the Spigelian lobe was obvious.

The *spleen* of *Phascologale* is unlike that of *Antechinomys* in that the Marsupial triradiate form was obvious, particularly in *P. penicillata*. In the smaller species described here the bifurcate end of the spleen, that turned towards the left side of the body, was rather in the form of a triangular expansion of the end of the spleen, the base of the triangle lying towards the right. In *Sminthopsis* the spleen is more like that of *Antechinomys*, the right expansion being little marked.

As in *Antechinomys* the right kidney is much above the left, and the same asymmetry is seen in *Sminthopsis*. I examined the female generative organs of *P. penicillata* as well as of the species which forms the subject of the present notes. The same very strong dilatation of the distal end of each uterus that I have described in *Antechinomys* was to be seen in both of these species. It was very marked indeed in both. In the larger



*Phascologale penicillata* there was also a considerable dilatation at about the middle of each vagina. The two vaginæ and the bladder open into the common external canal at about the same level. I did not notice any trace of a median cul-de-sac of the uteri in the larger species, whose genitalia appeared to be rather more mature and were in any case larger than those of *P. macdonellensis*.

### III. On the Intestinal Tract in some Marsupials, compared with that of other Mammals.

Some of the general features of the intestinal tract in many Marsupials are already well known. It is well known through the investigations of many (*e. g.*, Owen\*, Forbes†, Beddard‡, Parsons§, Lönnberg||, Klaatsch¶, Mitchell\*\*, &c.) that the large intestine of the Diprotodont Marsupials is as a rule †† very long relatively, even—it may be—much longer than the small intestine. In those Polyprotodontia in which a cæcum is present to mark the junction of the two regions of the gut, it is plain that the large intestine is relatively shorter, but not so short as in the Carnivora. These facts are shown graphically for six species of Marsupials by Dr. Mitchell. Though doubtless it is not asserted that the figures referred to exhibit with absolute accuracy the relative lengths of the large and small gut, it is clear that they make a very fair approximation to accuracy.

Furthermore, it is at least highly probable that more accurate figures could not have been compiled. For it is well known that the relative lengths of the two sections of the gut are apt to vary. For example it has been asserted by Brants (quoted by Tullberg ‡‡) that in 30 examples of *Mus decumanus* the relative lengths of the small and large intestine fluctuated between a small intestine ten times the length of the large, and a large intestine which was only one third of the length of the small intestine. Tullberg himself, in a series of very careful measurements of eight examples of the common rat, made upon specimens prepared in exactly the same fashion, found not so great but yet a considerable fluctuation. The extremes in two rats of equal size were in one example a small intestine of 808 mm. and a large intestine 201 mm., in the other the small intestine 835 mm. and the large intestine 186 mm. It is therefore

\* *Dendrolagus inustus*, P. Z. S. 1852, p. 103.

† *Phascolarctos cinereus*, P. Z. S. 1881, p. 180.

‡ *Dendrolagus bennetti*, P. Z. S. 1895, p. 131.

§ P. Z. S. 1896, p. 683.

|| Several species, P. Z. S. 1902, i. p. 12.

¶ Morph. JB. 1892.

\*\* Several species, Tr. Z. S. 1905, vol. xvii. p. 437.

†† To which at any rate *Petaurus breviceps*, an insect-eating Diprotodont, is an exception. See Lönnberg, *loc. cit.* p. 14.

‡‡ "Ueber das System der Nagethiere," Nova Acta Reg. Soc. Upsala, ser. ii. 1899.



impossible, as it would appear, to suggest any improvement in the figures of Dr. Mitchell from this side of the question.

	Small Int.	Large Int.	Cæcum.
<i>Dendrolagus inustus</i> ♀ .....	117	73	4
<i>Trichosurus vulpecula</i> ♂ .....	70 $\frac{3}{4}$	81	15 $\frac{1}{4}$
<i>Macropus melanops</i> ♂ .....	156	162	18
„ <i>giganteus</i> ♀ .....	172	54	7
„ <i>brachyurus</i> ♀ .....	52	21	2 $\frac{1}{2}$
„ <i>billardieri</i> .....	146	30	2 $\frac{1}{2}$
<i>Hypsiprymnus cuniculus</i> ♀ ...	24	10	1 $\frac{1}{2}$
„ <i>gaimardi</i> ♂ ...	40	28	2

Apart from the relative lengths of the small and large intestines and the form of the cæcum, or its absence, upon which I have no new facts of my own to record in the present paper, but concerning which I take the opportunity of utilising a series of measurements recorded by my predecessor Mr. W. A. Forbes (see list above), the intestinal tract of mammals exhibits a series of modifications in different groups and in members of those groups, which may be considered under the following headings, viz. :—

(1) The relationship of the various coils of the intestine to each other. (2) The fixity or freedom of the loops of the small intestine. (3) The permanent loops of the colon.

Under all of these headings I have a few new facts to record with respect to the Marsupials and to certain other mammals.

(1) *The relations of the coils of the intestine to each other.*—It is clear from the descriptions given by Owen\*, that as a rule at any rate† the intestinal tract in the Marsupials is a freely movable tract throughout, having no mesenteric connections between the colon and other regions. As Sir Richard Owen was particular to describe such folds and connections when they occur in other mammals (as for example Rodents), the absence of any such statements in his papers upon Marsupials leads to the inference that such do not exist in those mammals; a statement which I am able to confirm from my own dissections. Other observers have noted a similar series of facts. Prof. Grant in describing the anatomy of *Perameles nasuta*‡ has noted the dimensions of the several tracts of the intestine but has made no comment upon any folds of the gut, which would certainly have been mentioned (one assumes) had they been present, since the same observer almost at the same time§ carefully described such folds in the Paca. Vrolik, in describing the anatomy|| of *Dasyurus ursinus*, does not appear to have said anything about

\* On *Dasyurus macrourus* (= *D. maculatus*), P. Z. S. 1835, p. 7; on *Macropus parryi*, ibid. 1834, p. 152; on *Dendrolagus inustus*, ibid. 1852, p. 103.

† This does not, however, seem to apply to the Wombat (see Owen, P. Z. S. 1836, p. 49) which requires re-examination from this point of view.

‡ Mem. Wernerian Soc. vi. 1832, p. 184.

§ Loc. cit. & t. cit. p. 133.

|| Tijdschr. wis- en natuurk. Wetensch. 1851, p. 153; briefly abstracted in Ann. Mag. Nat. Hist. ix. 1852, p. 245.



the presence of any folds in the gut, but gives measurements of the lengths of the several parts of the gut.

The late Sir William Flower \* by implication makes the same statement; for he remarks of the alimentary tract of the Opossum (*Didelphys virginiana*) that "the colon forms a single arch and then passes directly down to the pelvis; but being very loosely attached by mesentery it is very movable."

None of these writers, however †, with the exception of Sir Richard Owen, refers to the fact that among the Marsupialia there are two grades in the complication of the alimentary tract to be met with. That author says of *Dasyurus maculatus*—"The mesentery was one continuous duplicature of the peritoneum extending from the pylorus to the end of the colon as in the Reptilia."

It appears to me that by this phraseology is indicated an intestine like that of *Antechinomys* described in the present paper ‡, comparable to an early stage in the development of the alimentary tract of man before the hinder part of the gut has been folded over the anterior part. In his Treatise on Comparative Anatomy the "reptilian" condition of the gut in certain Marsupials is more plainly stated.

These two stages in the development of the intestine are figured in Flower's Lectures on the organs of digestion in the Mammalia already referred to and in any textbook of human anatomy. It is obvious that the conditions obtaining in *Antechinomys* represent the first stage persistently retained. There are not many positive facts which lead to the supposition that any other Marsupial shows the same. The only figures of the entire alimentary tract of a series of Marsupials known to me are those of Mitchell already referred to, and of Klaatsch §. But there is no indication here of differentiation between the lower and higher types in the direction referred to. Klaatsch, indeed, figures *Dasyurus viverrinus* as *not* possessing the "reptilian" form of gut, since it possesses the cavo-duodenal ligament. I can quite confirm him from an examination of *D. maugai*.

That this simple form of gut is not due merely to its shortness and to the mechanical difficulty implied by a folding over, is proved by the occurrence of the same type in animals belonging to other orders of mammals. In *Centetes caudatus*, for example, among the Insectivora, there is precisely the same type. The continuous mesentery of the gut is nowhere folded over, and the whole intestine is arranged exactly on the plan of that of *Antechinomys*, though it is much longer. Dr. Mitchell's figure of *Centetes* might at first sight appear to bear out my statement. But if this figure be compared, *e. g.*, with that of *Phalangista*

\* In his Lectures on the Alimentary System of Mammals reported in Med. Times and Gazette, 1872.

† Nor is the fact adverted to by Cunningham in his description of the gut of the Thylacine, &c., Rep. Zool. Challenger, vol. v.

‡ *Supra*, p. 562.

§ Morph. Jahrb. xviii. 1892, p. 622, fig. 2, p. 664, fig. 10, pl. xxii. fig. 7.



*vulpina*, no difference in this particular between the two forms is there discernible. Now in *Phalangista* there is the typical folding over of the hinder part of the alimentary tube upon the anterior. The two figures, therefore, which have been referred to, only hide the essential differences between the two types, informing us merely of the existence in one and the absence in the other of a cæcum—a fact already well known. It is interesting to note that *Centetes* has not always this simple arrangement of the gut. I found it in one example but not in another, where there was one folding over, but no further specialisation. This is also interesting not merely from the point of view of fixity of characters, but because in the Hedgehog the gut is folded over upon itself as in most mammals, and is not a simple coil on a continuous mesentery\*.

I am not quite clear from his description and interpretation of Zoerner's † results, whether Klaatsch places the Edentate *Myrmecophaga* in the same category as *Antechinomys*. But I imagine not, since *Tarsius* is described as showing "die einfachsten Mesenterialverhältnisse" among the Mammalia. In any case, I can assert that some of the American Edentata also show a very simple gut, comparable to that of *Tarsius* and *Antechinomys*. In *Myrmecophaga jubata* and *Tamandua tetradactyla* the gut can be laid out without removal from the body in a continuous loop, precisely like the figure given of the same by Mitchell ‡. In this feature the genera mentioned are to be contrasted with *Dasypus* and other Armadillos. There is, however, no indication of the differences in the figures of Mitchell excepting, indeed, that the mesocolon is drawn on one side of the colon in one form, and on the other in the other types. This cannot, however, imply any such difference as is here recorded, since, as already referred to, the different conditions obtaining in *Centetes* and *Phalangista* are indicated by a diagram which would imply complete similarity, while *Phalangista* and *Macropus* are

\* It is possible, however, that Dr. Mitchell (Tr. Z. S. 1905, vol. xvii. p. 532) may have forestalled me and have met with the same variation in this rather important feature which I have noted above. In his "Summary of Systematic Inferences" he writes that "in most . . . Insectivora . . . the intestinal tract . . . (is) suspended by a continuous mesentery." This would seem to imply the condition which I have described above. On the other hand, he does not in the same section say the same of the American Anteaters, which in this respect resemble *Centetes*, so far as one of the specimens of the latter which I dissected is concerned. And again in the special section dealing with mammals individually, Dr. Mitchell makes no mention of a continuous mesentery, but remarks that *Erinaceus* is practically identical with *Centetes*. It may well be that the recollection of more than one example led to these two not precisely contradictory, but not altogether concordant statements. I may recall the fact that some years ago I described (Novit. Zool. vol. viii. 1901, p. 91) a continuous mesentery in two other examples of *Centetes ecaudatus*, and did not meet with the important variation recorded here.

† "Bau und Entwicklung des Peritoneum &c. von einiger Edentaten," Inaug.-Diss. Halle, 1881. Not seen by me.

‡ It is important to settle this matter definitely, for Flower is not conclusive in his statements. On an early page of the "Lectures," already quoted, he remarks that the reptilian character of the gut is "only found among Mammals in some Insectivora and insectivorous Marsupials." Later, however, he refers to it as also existing in Whales and in *Myrmecophaga*.



represented as different. I am disposed to believe from its shortness that the gut of *Bradypus* will be found also to conform to this plan \*. The simple colon of all these forms of moderate length, neither excessively long nor excessively reduced, is, as I think, in agreement with Dr. Mitchell, a mark of low position in the series, especially since no modification traceable to different feeding-habits is recognisable.

On a superficial inspection the intestinal tract of many Carnivora appears to be constituted on the same simple plan as that of *Antechinomys*, *Myrmecophaga*, *Centetes*, &c. That is to say, the gut can be laid out in one continuous coil without removing it from the body or cutting any mesentery. There are, however, variations in the degree of freedom of the gut. In *Cercoleptes caudivolvulus* for example, the gut can be readily laid out either to the left or to the right, and then forms a continuous coil apparently with a continuous mesentery throughout. It would seem in fact to have retained the primitive arrangement altogether. In *Ictonyx capensis*, on the other hand, this spreading out into a continuous fold is only possible on the left side; the gut cannot be thus spread out on the right side. So too with *Nandinia binotata*. In *Ursus syriacus* the gut can be readily laid out on the left side; but I have unfortunately no note as to whether it can be also spread out to the right so as to present the appearance of a continuous mesentery like that of the simplest mammals. In *Genetta rubiginosa*, however, the gut can, as in *Cercoleptes*, be laid out on either side of the middle line without tearing or unduly stretching any mesenteries. The disposition of the gut, however, in these animals, though superficially as has been said that of the simplest forms in the order, is in reality different. It will be seen that where the end of the duodenal loop comes near to the middle dorsal line, it is actually fastened to the mesocolon by a short mesentery, as is shown in the accompanying figure (text-fig. 120 B on p. 591). The comparative freedom which the whole intestinal tract enjoys is clearly due to the partial disappearance of this particular mesentery, the ligamentum cavo-duodenale. If more extensive, the arrangement of the intestine in a continuous coiled line from stomach to rectum would be impossible. If, on the other hand, the mesentery disappeared altogether, there would be actually a continuous mesentery from end to end of the gut. I am inclined, therefore, to believe that the intestine has in these forms undergone a simplification approximating to the primitive state of the gut with its mesentery. And indeed it may well be that even the apparently simple forms like *Antechinomys* are in reality the terminal stage in such a reduction, and not evidence of the persistence of a primitive state of affairs. I believe, however, that the coincidence of this apparently primitive state in such widely removed types as *Centetes* and *Tamandua* is evidence in

\* As to *Choloepus*, however, Klaatsch observes that "das Lig. hepatocavoduodenale ist schwach entwickelt."



the contrary direction. The conditions obtaining in the Carnivora, and as it would appear in the whole of that group, cannot be looked upon as a reduction due to small size. For it will have been noted that the large Bear is quite on a level with the small *Cercoleptes* or *Ictonyx*. It is not only the Carnivora which show this simplification of the gut. For I have already remarked that the same state of the intestine and its mesentery is to be seen alternatively in *Centetes*. Even among the Primates it exists; for in *Chrysothrix sciureus*, as I point out later (p. 577), the intestine can equally well be laid out along a comparatively straight mesentery to either right or left side. It must be noted, however, that in this animal and in the Carnivora the colon is very short. It is, in the specimen which I dissected, only  $6\frac{1}{2}$  inches in length, a measurement which agrees exactly with that of Martin\*.

Although the above facts concerning the Carnivora are I believe correct, and indeed quite bear out Klaatsch's figure† of the intestinal tract of the Cat, where the mesentery attached to the duodenum and to the middle line is figured and termed "ligamentum cavoduodenale," and his statements concerning other genera. Max Weber has, however, described and figured a different state of affairs in the Bear‡. The species examined was *Ursus arctos*, and the gut is figured as turned over to right and left without a trace of this ligament, and described in the following words:—"Der ganze übrige Darm an einer einfachen Mesenterialplatte (Mesenterium commune) die mit einfacher radix mesenterii an der Wirbelsäule wurzelt aufgehängt ist." There may of course be this difference between the two species of *Ursus*, or the case may be analogous to that which I have described above in *Centetes ecaudatus*. In any case it is clear that the majority of the Carnivora (whether Arctoid or Æluroid) do not bear out the statement of Max Weber with reference to *Ursus arctos*.

In more differentiated forms a further complexity is introduced in the existence of a special ligament joining the commencing duodenum with the proximal end of the colon. For this Klaatsch adopts Krause's term *ligamentum colicoduodenale*. It is figured by Klaatsch in several forms, in *Myoxus*, *Stenops*, and human embryo. Nor has Tullberg neglected this connection between the small and large intestine in his figures of certain Rodents. This structure is so persistent in the Rodents that it even occurs in the case of the small *Arvicanthus*, where the colic coils are reduced to a minimum; as indeed they are according to Klaatsch's figures in *Myoxus*. It is very important to note that even the Marsupials with their little specialised gut show traces of the same; in *Trichosurus vulpecula* and *Pseudochirus peregrinus*

\* P. Z. S. 1833, p. 89.

† "Zur Morphologie der Mesenterialbildungen, &c. ii Theil," *Morph. Jahrb.* xvii. 1892, p. 646, fig. 4.

‡ Die Säugethiere, p. 212.



I found this membrane, and I may take this opportunity of remarking that the omentum also is attached, though for a very short space, to the colon as in the genus *Macropus*. Neither of the facts is represented in Klaatsch's figure of the gut of *Trichosurus vulpecula* \*. There remains, however, a substantial difference between *Trichosurus* and *Pseudochirus* on the one hand and *Macropus* on the other, in that in the latter the connection between omentum and colon is extensive, as is duly figured by Klaatsch for *Macropus bennettii*. I cannot agree with Dr. Mitchell in finding no connection of this kind between the duodenum and colon in *Hyrax*. In examples of this "Subungulate" which I dissected some time since, the duodenum near to its exit from the stomach was adherent to the colon in the neighbourhood of (distal to) the paired cæca by a ligament of some length. Moreover, there was also a fixation of the omentum upon the same region of the colon. I take this opportunity of remarking that *Hyrax* shows a particular point of likeness to the Perissodactyle Ungulates as I venture to think. In the latter group without exception, as has been shown by many anatomists, the cæcum is immediately followed by a single simple loop of the colon. The same occurs in *Hyrax*, though it is in that animal not quite so well-marked. The colon immediately after leaving the single cæcum, which I regard as the equivalent of the Perissodactyle cæcum, is folded back along the cæcum and connected with it by a ligament; the distal limb of this loop is not quite so well established as in the Perissodactyle, however. I discuss these facts more in detail on a subsequent page.†.

The attachment of the great omentum to the colon is well-known as an anatomical fact. Klaatsch has figured this in several forms. Later in this communication I direct attention to the same attachments in various Rodents and Lemurs.

I have found no such attachment in Carnivora ‡, nor in American Edentates (in which I am in accord with Klaatsch). In *Orycteropus*, however,—and this emphasises the distinctness of that type from its alleged relatives in the New World—there is a fixation of the omentum along two separated lines. The most anterior is on to the cæcum and the very commencement of the colon. Then follows a considerable area of colon unattached to the omentum which is again attached to it further along. This state of affairs reminds us of the transitory condition in the human foetus figured by Klaatsch (*cf. loc. cit.* p. 694, fig. 16), which is, however, permanent in *Cebus* as he has pointed out. For other facts relating to the attachment of the omentum and of other ligaments reference may be made to subsequent pages, where they are described in several animals.

\* *Loc. cit.* pl. xxii. fig. 7.

† See below, p. 579.

‡ Except in one or two cases where it appeared to me to be distinctly pathological. The non-attachment of the omentum in Carnivora is not, of course, put forward as a new fact. I confirm it by fresh instances.



It is possible that the secondary attachment of the omentum to the colon bears some relation to the formation of the permanent loops of the colon. For this attachment at least offers a fixed and more or less immovable area or length, which would permit of unequal growth in this as compared with neighbouring tracts of intestine. Further contractions of the omentum during its growth would obviously tend to emphasise such loops and would act in the direction of rendering them more permanent. In any case it is important to notice that where there are no fixed ansæ coli, there is at least frequently no secondary attachment of the omentum to the colon. This is the case for example with Carnivora, and with Carnivorous Marsupials, with Armadillos, and Insectivora\*. This rule, however, is not universal in its application; for among the Apes, where there are no definite ansæ coli, there is an attachment of the omentum to the colon. On the other hand, where there are well-defined ansæ the omentum is as a rule found to be inserted upon one of the ansæ. The more exact relations in a number of Mammals are as follows:—Among the Lemurs where there is one colic fold, whether simple or forming a spiral, the omentum is invariably attached to the distal limb of the loop or spiral†. Among Rodents I found that in *Lagostomus* the omentum was attached along the colon from the beginning of the distal limb of the *ansa paracæcalis* to the end of the proximal limb of the *ansa coli dextra*. In *Hystrix cristata* the omentum is attached along one half of the distal limb of the *ansa coli dextra*, the *ansa coli sinistra* having no such connection. In *Sciurus maximus*, however, where the same two ansæ are present, there is no such insertion of the omentum. These facts do not appear to have been dealt with by Tullberg in the Rodents.

The lesser omentum of human anatomists is called by Klaatsch ligamentum hepatogastro-duodenale. It is the ventral membrane of the gut. This is universally represented among Mammals. The posterior continuation of this, however, the ligamentum hepato-cavoduodenale, is not universal. The cavo-duodenal part of this has already been referred to in various mammals. The ventral portion of the membrane, the hepatoduodenale, now requires some consideration. This is described by Klaatsch in *Echidna*, and sought for without finding it in certain Marsupials. On the other hand, it is stated to be present in various Carnivora, Rodents, and Lemurs. I found this as a distinct membrane very plainly to be seen in *Ursus syriacus*. It is to be noted that in this Carnivore the caudate lobe of the liver is prolonged down to the level of the duodenal loop. And thus there was a possibility, so to speak, of finding the membrane, which indeed was slight though unmistakable and connected the extremity

\* I do not, of course, put forward this non-attachment of the omentum as an entirely new fact.

† Klaatsch, *loc. cit.* p. 667, fig. 11, would regard the omentum as occupying the interspace of the loop also. I am not convinced of this.



of the liver-lobe with the ligamentum cavoduodenale. The two mesenteries were quite continuous. In *Echidna* also and other types in which this membrane exists, the liver descended to the level of the recurrent duodenal loop, where it was attached by the ligamentum cavoduodenale. In *Hyrax*, however, the extreme end of the liver is distant from the end of the duodenal loop by a space of fully three inches. There is thus an impossibility of finding a state of affairs like that described above in *Ursus*. In *Hyrax* the duodenum in the ascending limb courses over the right kidney, to which it is firmly attached by membrane; the same kidney is equally attached to the liver by an hepato-renal ligament. Thus we have a series of membranes connecting the liver with the ligamentum cavoduodenale. Klaatsch has regarded this as the equivalent of the entire ligamentum hepato-cavoduodenale, the arrangement of which with respect to its several elements will evidently depend upon the relative positions of the several viscera concerned.

(2) *The Permanent Loops of the Colon.*—As a rule, with but few exceptions, the Marsupials possess none of those permanent loops of the colon which have been termed by Tullberg “ansæ coli,” and by Klaatsch “flexuræ coli.” This is evident from the figures given by Klaatsch and Mitchell and from the descriptions of others, to some of which I have referred above. Nevertheless, the group is not absolutely to be characterised thus. I have found in one example of *Didelphys virginiana* a distinct permanent loop which was rather wide and lay at a considerable distance behind the cæcum. The specimen in which this occurred was a male, and in a female of the same species there was no such loop. I do not connect the variation with sex, but note its presence as indicative of the commencing formation of these special loops in the Marsupialia. I also observed something of the same kind in an individual of *Trichosurus vulpecula*. Furthermore, in several species of *Macropus*\* (i. e. *M. woodwardi*, *M. melanops*, and *M. hagenbecki*) the colon shortly after it issues from the cæcum and just below the stomach is slightly flexed, and permanently so, into a wavy outline of one or two undulations. This again is perhaps to be looked upon as a commencement of the ansæ coli of more highly differentiated forms.

The permanent loops of the colon have been described in a great many mammals and by many zoologists. I have, however, in the course of the past year accumulated a considerable number of facts in this department of anatomy which partly confirm the results obtained by others, are partly new (so far as I am aware), and in some cases enable me to distinguish between already published descriptions that do not happen to be in entire harmony. As to the latter section it must be borne in mind

\* Quite possibly in others; but I have no notes on the point except of the species mentioned above.



that there is apt to be some variation in these loops, as I point out more particularly in the case of the Vizcacha (*Lagostomus trichodactylus*) and the Cape Hyrax (*Hyrax capensis*). Of the latter species I have examined an unusually large number of examples, a fact which naturally gives me some confidence in detailing the characteristics of the alimentary canal and mesenteries of this interesting form. My notes refer to the Anthropeidea, the Lemuroidea, the Hyracoidea, and the Rodentia, which I consider in the order named.

#### ANTHROPEIDEA.

Of the Primates I only report upon two or three species, which happen to be remarkable in various ways. In the Gelada Baboon (*Theropithecus gelada*, sometimes called *Gelada rueppelli*) the intestinal tract as well as other details in its anatomy have been described by the late Mr. A. H. Garrod\*. In a male and female dissected by him, the proportions between the small and large intestines differed greatly. In the male the colon was  $\frac{2}{3}$  of the length of the small intestine, in the female the proportion was much less, *i. e.*,  $\frac{5}{13}$  nearer to  $\frac{1}{3}$ . The example dissected by myself was also a female; but the proportions in length of the two sections of the gut were much nearer equality, though I have, I regret to say, no exact measurements. The ascending colon from its very beginning (*i. e.*, opposite to the entrance of the ileum) and a large portion of the transverse colon were attached to the great omentum. Moreover, the greater part of the ascending colon was bound down by a mesentery to the dorsal parietes. The colon had of course no fixed loops, which indeed do not occur among the Anthropeidea.

In *Semnopithecus melalophus* (a species of which the Society has possessed no previous examples) the small intestine was thrown into few wide and more or less fixed coils owing to the shortening of the mesentery. The colon was long, about double the length relatively of a *Cynocephalus porcarius* examined for purposes of comparison on the same day. Its arrangement was remarkable. The ascending colon and a portion of the transverse colon were sacculated in the usual way along three bands; and the greater portion of the descending colon was similar in its sacculatation. Between the two, and corresponding to the greater part of the transverse colon, was a tract of uniform and small calibre entirely without sacculatations. The omentum was attached to the mesocolon of the anterior sacculated region of the colon, but at a considerable distance from the colon.

The cessation followed after an interval by the resumption of a sacculatation in the course of the colon, recalls a quite similar state of affairs in the colic loop of the *Rhinoceros sondaicus*, figured some years ago by Sir Frederick Treves and myself in that animal†. Although the colon has not, as in *Theropithecus*,

\* P. Z. S. 1879, p. 451.

† Trans. Z. S. vol. xii. pl. xxxiv. figs. 1, 2.



a special mesentery not to be confused with the mesocolon, and attaching it to the parietes of the right side of the body, there is something of the same kind present. For the cæcum of this *Semnopithecus*, which is quite blunt at the apex, is fixed by a membrane to the parietes in the inguinal region on the right side. This had not the look of a former pathological adherence, which would, I think, have presented a more irregular appearance. There were of course no fixed loops in the colon. This special attachment of the cæcum is also found in some other Monkeys. The general anatomy of the Squirrel Monkey, *Chrysotrrix sciureus*, has been described by Martin\*, who pointed out the existence of an extremely short colon, which he found to be only  $6\frac{1}{2}$  inches in length. I can confirm this and add some details which bear upon the subject of the present investigation. The colon, rectum, and short cæcum presented almost exactly the appearance of those viscera in a Viverrid, the large intestine being slightly curved to the right, and thus showing as in many Viverrids a rudimentary transverse colon. It is an exaggeration of the condition observable in *Ateles melanochir*, where the whole of the colon is disposed in one bold curve rather more than semicircular and precisely like that of Armadillos. In *Ateles*, in fact, there is a well developed transverse colon, but hardly an ascending colon. The whole gut appears at first sight to be suspended on a continuous mesentery, for it can be laid out in a continuous curve either on the right or left side without removing it from the body, just as in such types. A closer inspection, however, shows the presence of a *ligamentum cavo-duodenale*, so that the conditions obtaining in this Monkey are just like those which have been described above in the Carnivora. This simplification can hardly be due to reduction in size. For in the smaller *Hapale penicillata* the gut cannot be turned over freely to right or left, and has the normal syphon shape.

#### LEMUROIDEA.

The *ansa coli* of the Lemurs offers some particularly interesting modifications.

The simplest form of colon of those which I have examined is shown in *Microcebus smithii*. Of this Lemur the general anatomy has been described by Martin†. The colon shows no special *ansa* or *ansæ*, but is comparatively short and reaches the terminal straight portion by a boldly curved tract in which there are no permanent folds. This arrangement was identical in two examples of the Lemur which I dissected. This is very similar to the conditions figured in *Cheirogaleus coquereli* by Dr. Mitchell, though I am not quite certain from his description and figure taken together, whether there is or is not a well defined colic loop such as occurs in the genus *Lemur*. Dr. Mitchell speaks of "a colic loop . . . . relatively much shorter in *Cheiro-*

\* P. Z. S. 1833, p. 88.

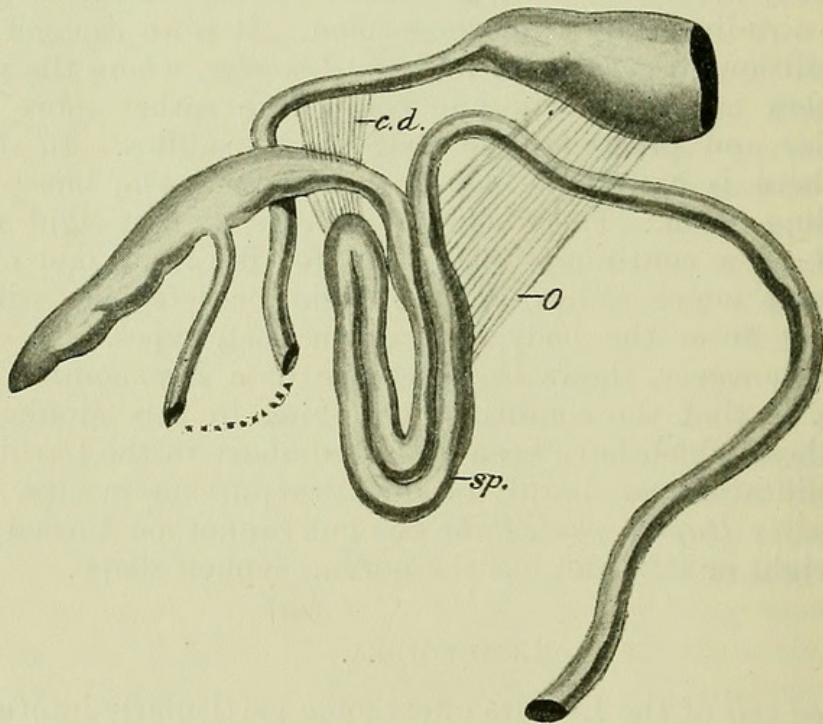
† P. Z. S. 1835, p. 125.



*galeus*," but figures a state of affairs like, for instance, *Dasypus* where there is no defined colic loop. It would be, as I think, convenient to restrict the term colic loop to such a defined loop as occurs in the genus *Lemur*, to which I shall now refer.

Sir W. Flower has figured the single ansa coli in the genus *Lemur* (in *L. flavifrons*) and Dr. Klaatsch has figured an identical loop in *Hapalemur*, and Dr. Mitchell (without referring to Flower's figure or to that of Klaatsch) has figured an identical loop in *L. mongoz*, var. *nigrifrons*. They are indeed obviously identical. I can confirm from my own dissections the existence of this loop in *L. mongoz*, which seems to me to correspond to the *ansa coli dextra* of Tullberg, but of which the constituent limbs were closer together than is figured by Mitchell, agreeing therefore more closely with the figure of Flower. In *L. macaco*

Text-fig. 114.

Cæcum, colic spiral, &c. of *Galago garnetti*.

*c.d.* Ligamentum colico-duodenale, which lies opposite to a ligament binding extremity of colic spiral to commencement of colon. *O.* Omentum. *sp.* Colic spiral. The cut ends of the small intestine are joined by dotted lines.

was the same ansa coli. In *L. albifrons* again the same; but the two limbs were a little further apart in both of two examples. *Lemur sclateri* was the same. The genus *Galago* shows an interesting further development of this simple *ansa* of *Lemur*. I have ascertained that this loop has been figured previously in *Galago crassicaudata* by Flower; but I cannot accept the figure given by Dr. Mitchell as representing the facts in even an approximate fashion. I have lately examined two examples of *Galago garnetti* (the species described by Dr. Mitchell), and some



years ago a single specimen of *G. maholi*. In all of these the *ansa coli dextra* (if I am right in so identifying the loop) is coiled as is shown in the accompanying figure (text-fig. 114) into a short spiral exactly like that of certain Rodents and most if not all Artiodactyles, though much simpler than the spiral of the vast majority of the latter. This characteristic spiral arrangement is entirely lost in the figure given by Dr. Mitchell\*, to which I here refer, though accurately represented by Flower. The matter is of special interest because the same spiral arrangement of the *ansa coli dextra* is to be seen in the genus *Nycticebus* of the subfamily Lorisinae, as is abundantly shown in the figures and descriptions of Vrolik† and Schröder van der Kolk‡, which I am able to confirm by the dissection of two examples of *Nycticebus tardigradus*. The resemblance to *Galago* is exact. I am disposed to think that Dr. Mitchell's figure of the Potto requires revision, in which animal he represents two adjacent ansæ coli disposed like those of many Rodents. Dr. Mitchell has not referred to the papers cited below.

The dissection of an example of *Indris* enables me to confirm the figures of Milne-Edwards§ as to the existence of a colic spiral in the Indrisinae which is more elaborate than in the other types just dealt with. I may be permitted to point out another relation between these Lemurs with a spirally twisted *ansa coli*|| which has not been insisted upon. In the genera where this occurs, *i. e.*, in *Galago*, *Loris*, *Nycticebus*, *Indris*, and, I imagine, *Perodicticus*, the characteristic carpal vibrissæ are absent; they are present in the remaining Lemurs with no *ansa coli* or only a simple one. Specialisation of structure has occurred concurrently in two features of their organisation. It is important to notice that in these Lemurs with a simple or a spirally twisted *ansa coli*, the omentum is attached to the loop or spiral. Furthermore, the opposite side of the spiral is attached to the cæcum, or to the colon just where it leaves the cæcum, by a ligament, and the duodenum is attached to the colon just opposite to this latter ligament by a colico-duodenal ligament.

#### HYRACOIDEA<sup>¶</sup>

I have examined several examples of *Hyrax capensis* and have more particularly studied two specimens of which one was specially favourable for study. This example was not more

\* *Loc. cit.* fig. 41, p. 506.

† N. Verhandel. Nederlandsche Inst. Amsterdam, vol. x. 1844, p. 75.

‡ Tijdschr. Natuurk. Gesch. Leiden, viii. 1841, p. 277, pl.v. figs. vi., vii.; and a joint paper by these two anatomists in *Bijdragen tot de Dierk.* i. 1848-1854, p. 29. Gegenbaur also (*Vergl. Anat. Wirbelth.* ii. 1901, p. 178) figures the spiral in *Loris gracilis*. So also does Klaatsch, though not, as I think, quite accurately in *Nycticebus*.

§ *Hist. Nat. Phys. et Polit. de Madagascar.*

|| I cannot understand Klaatsch's statement that "die rechte Colonflexar ist . . bei *Lemur* relativ noch mächtiger entfaltet als bei *Stenops*."



than half grown, measuring not more than a foot in extreme length. The alimentary tract of this animal has been described at considerable length by Dr. Mitchell, but I find myself in grave disagreement with him, the disagreement extending to matters of fact as well as to interpretations of the value of certain structures. I furthermore deal with certain points which are not dealt with by Dr. Mitchell.

When the body-wall is cut and the halves reflected, the intestinal tract is seen to be represented by the large cæcum which occupies the greater portion of the left moiety, and by the paired cæca and the immediately preceding and succeeding sections of the colon which occupy the right moiety of the superficial part of the abdominal cavity thus disclosed. Above, a few coils of the small intestine are visible, but very few. As Dr. Mitchell has correctly stated, the duodenal loop is longer than he has represented in his figure\*. It extends in the very general fashion down to about the middle of the lumbar region below the kidneys, and is there attached by the usual ligamentum cavoduodenale. This loop of the duodenum shows on the opposite side another remarkable mesenteric fold. When the single cæcum is turned forwards, it is seen that a mesentery with a free edge directed forwards runs over the duodenal loop, being attached on the left to the colon where it emerges from the single cæcum, and on the right to the colon where it passes towards the paired cæca. As this fold has a free edge, a pocket is formed which appears to be imperforate at the bottom. I have no facts to offer for the purposes of a comparison of this mesenteric recess with possibly similar structures in other mammals. The coils of the small intestine, with the exception of the duodenal loop, are, as usual, temporary coils, and the intestine can be straightened bit by bit as it is passed through the fingers. The ileum opens into the single cæcum, the resemblance of which to the cæcum of the Perissodactyles is apparent from the descriptions of others and from an inspection of this portion of the gut which has been somewhat confused by Dr. Mitchell's figure. He represents it as a bilobed dilatation on the course of "Meckel's Intestine." It is, in fact, almost a facsimile of the cæcum of a Rhinoceros, the chief difference being that it has a much blunter termination than in the Perissodactyle. It is moreover sacculated, and the relations to it of the small and large intestines respectively are exactly as in the Rhinoceros' cæcum. Moreover, the large intestine which emerges from it is of greater calibre than the small intestine which enters it. Finally Dr. Mitchell has taken no account of certain mesenteries related to this cæcum which unquestionably suggest its homology with the usual unpaired cæcum of mammals. That the paired appendages of the gut which arise further down may be the equivalents of the Edentate paired cæcum is quite possible. But if so, it is only in my opinion further evidence that the latter are not the equivalents of the usual unpaired cæcum of other

\* Trans. Z. S. 1905, xvii, p. 461, fig. 14.



mammals. The paired cæca of *Hyrax* have no mesenteries of any kind attached to them. They hang perfectly free of peritoneum folds into the body-cavity. I do not think that any true unpaired cæcum, even the small one of the Carnivora, is thus free of mesentery.

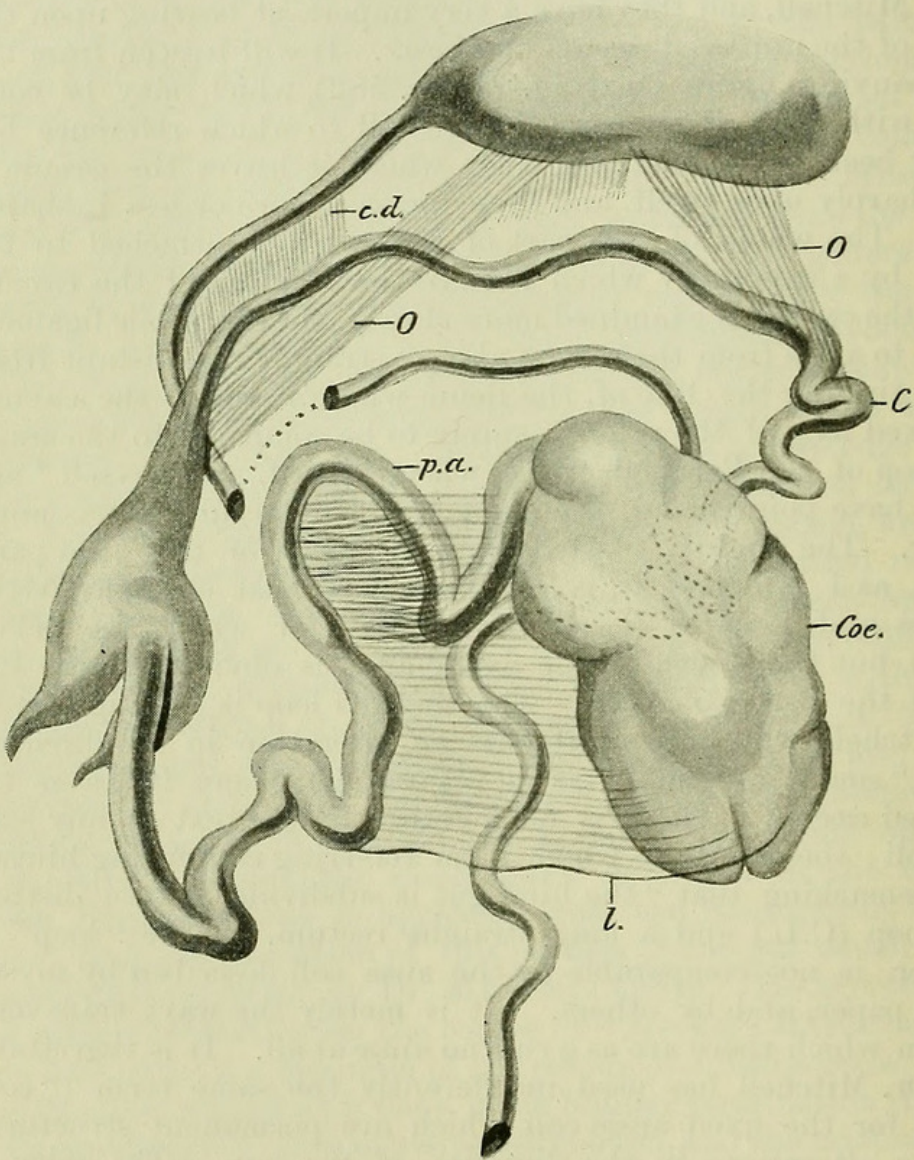
The only other Mammals known to me in which the cæcum or cæca are thus entirely free of peritoneal folds, are the American Edentates. On the other hand, the unpaired cæcum of *Hyrax* has peritoneal folds connected with it. These are not mentioned by Dr. Mitchell, and they have a very important bearing upon the nature of the unpaired cæcum of *Hyrax*. It will be seen from the accompanying figure (text-fig. 115, p. 582), which may be compared with that given by Dr. Mitchell to which reference has already been made, that the colon where it leaves the cæcum is bent sharply upon itself, and then forms a more or less L-shaped curve. The whole of this part of the colon is attached to the cæcum by a mesentery which runs to the very tip of the cæcum. When the cæcum is examined more closely, the cæco-colic ligament is seen to arise from the cæcum along a straight line distant from, but continuing the line of, the ileum where it enters the cæcum. This fixed loop of the colon is surely to be compared to the single colic loop of the Perissodactyles, where indeed, as I myself\* and others have pointed out, the same ligament occurs but is much shorter. The slightly twisted commencement of this ansa paracæcalis, as I interpret it, is reminiscent of that of many Artiodactyles and Rodents (e. g. *Arvicanthis*: for which see below, p. 589), but the length of the entire ansa is obviously more like that of the Perissodactyles. This marked loop is not figured by Dr. Mitchell, who only represents an alteration in the direction of the "small intestine" (as he regards it) where it leaves the unpaired cæcum. There is no mention in the text of any such ansa coli; the author to whom I am referring contenting himself with remarking that "the hind gut is subdivided into a distinct colic loop (C.L.) and a long straight rectum." The "loop" in question is not comparable to the ansa coli described by myself in this paper, and by others. It is merely the wavy transverse colon in which there are as a rule no ansæ at all. It is regrettable that Dr. Mitchell has used indifferently the same term ("colic loop") for the fixed ansæ coli which are permanent structures, and for alterations in the direction of the gut. The colon of *Hyrax* in fact, after leaving the ansa paracæcalis referred to, has no further ansæ coli. It has an irregularly looped course owing to its great length, and passes upwards giving off the paired cæca in an ascending colon, then runs across the body-cavity as the transverse colon, and descends in a series of wavy convolutions as the descending colon into the rectum. As is the case in all of the more specialised Mammalia, the omentum is attached to the transverse colon. And the mode of its attachment is

\* "The Anatomy of the American Tapir," P. Z. S. 1889, p. 254.



very interesting. The colon where it leaves the region of the two paired cæca is attached to the stomach by a fold of the omentum. After this follows a section of the colon to which there is no such omental attachment, and again at the commencement of the descending colon the omentum is for a second time inserted upon it. This arrangement of the omental

Text-fig. 115.

Alimentary tract of *Hyrax capensis*.

*Cae.* Cæcum. *C.* Region of colon in which fixed loops occasionally occur. *c.d.* Ligamentum colico-duodenale. *l.* Ligament uniting cæcum and commencement of colon. *O.* Omentum. *p.a.* Ansa paracæcalis.

attachments is precisely like that of *Orycteropus* as I have described on p. 573. And, as I point out in describing this feature in *Orycteropus*, there is a likeness with the foetal condition in man. There is furthermore, as the figure cited shows, a well-marked colico-duodenal ligament attaching the duodenum



immediately after it has left the stomach to the colon opposite to the attachment of the first part of the omentum. It may be that the attachments respectively to the colon immediately after it has left the paired cæca, is an argument in favour of regarding those cæca as the equivalents of the unpaired cæca in other forms. For in Rodents the attachments of the membranes in question are sometimes to the colon immediately after it has emerged from the cæcum in those animals, and the same relations are to be found in Lemurs. But against this resemblance may be placed the facts of the attachment of the membranes in question in *Dasyprocta*. In that Rodent, as I point out, the omentum and the duodenum are inserted upon the ansa coli, which lies at a considerable distance from the point of emergence of the colon from the cæcum. The evidence therefore cannot be regarded as very strong. Whereas the evidence already dealt with against the identification is very strong.

It will be clear from the foregoing that Dr. Mitchell's statement that "the hind gut divided into a simple colon and rectum merely conforms to the fundamental mammalian plan" is not correct. Nor can I agree with him in the further observation that "the general pattern of the intestinal tract in *Hyrax*, however, suggests no affinity with the patterns exhibited by Rodents and Ungulates." It appears to me to resemble both. But this is of course a matter of opinion. It is not without importance to observe that *Hyrax* shows some variation in certain of the features described above. Since writing the account which I have just given of this Ungulate I have dissected three other specimens, all of small size like that from which the above account has been practically entirely drawn. In one of them, the colon at the end of the transverse section at the further attachment of the omentum is fixed into a short ansa coli which is not very narrow, *i. e.*, the two limbs are not closely approximated. This corresponds in position to the splenic flexure of human anatomy, and is very like the ansa coli sinistra of *Tamias striata* described under my account of the ansæ coli of Rodents. The two other specimens did not show this specialised loop. Furthermore, the mesocolon undergoes some variations in its region of attachment to the dorsal parietes. I did not observe the exact arrangement in the first example dissected. But in the three now under consideration there were three different modes of attachment, thus clearly showing a great variation. In the individual just referred to, this mesentery was attached altogether outside of the left kidney. In a second individual, the left kidney lay for the greater part to the left of, *i. e.* outside of, the mesocolon, but the attachment of the latter was in part to the kidney and cut off an angle of that viscus anteriorly and to the right. In the third example, the line of attachment of the mesocolon divided the kidney into two longitudinal areas, of which the inner lay within the mesocolon area and the outer lay outside of the mesocolon. The pocket of peritoneum referred to was



present in at least two of the subsequently dissected examples of *Hyrax capensis*, but the actual excavation to form a pocket was hardly at all marked. I may further remark that the cavoduodenal ligament ended some little way in front of the posterior angle of the duodenum\*. In all the other points treated of in the above description of the intestinal tract of *Hyrax*, I found these three examples precisely like those originally dissected. It will be observed that my account substantially bears out that of George †, though adding some details.

#### RODENTIA.

As I have dissected a considerable number of Rodents with a view to the accurate mapping of their intestinal resemblances and differences, I may be permitted the following remarks, which, however, contain observations that are partly in accord with those stated at first hand, or as a result of agreement with others, by Tullberg.

Among the Sciuroidea I have examined the following species, viz.: *Cynomys ludovicianus*, *Tamias striatus*, *Sciurus maximus*, *Sciurus macrurus*, and *Sciurus cinereus* (text-fig. 116), of which the second has been also examined by Tullberg as well as the Common Squirrel and some genera which I have not seen. Tullberg has not described or figured the ansæ coli of *Cynomys*. They are typically like those of other Squirrels. That is, there are two permanent loops, of which the first is very much the longer. In *Tamias striata* I find conditions rather different from those described and figured by Tullberg. He describes "nur ein rechte parallelschlinge," but figures two such loops of which the first, *i. e.* that nearest to the cæcum, is the shorter, though both are not so marked as in his figure of *Sciurus vulgaris*. I find in an example of this species two loops, the usual arrangement in Squirrels. Of these the first, that nearest to the cæcum, is of considerable length; and the second is much shorter and also much wider, its constituent tracts of colon being further away from each other than is the case with the anterior ansa coli. Apart from the shortness of both ansæ, especially the second, the colic loops of this Squirrel are like those of *Sciurus maximus*, where there are two; the longer of these next to the cæcum is actually six inches in length, with the two lengths of intestine closely approximated; the second loop is very much shorter but much wider; thereafter the rectum is nearly straight. In *Sciurus macrurus* the arrangement is nearly identical, but the shorter loop is composed of more closely approximated limbs; so too with *Sciurus tennanti* (W. A. Forbes MS.). In *Sciurus*

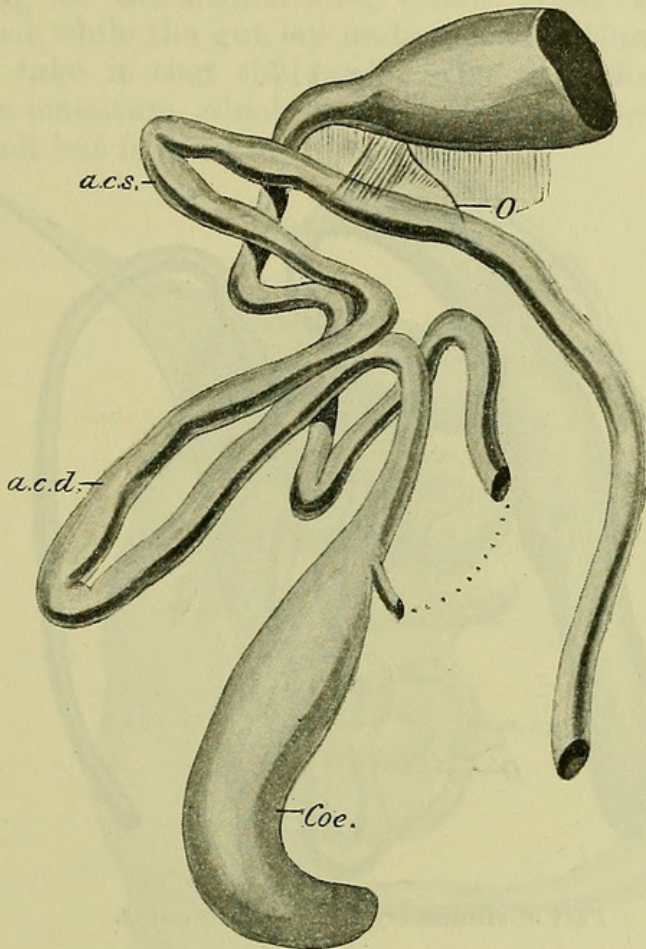
\* This state of affairs would seem to be impossible until it is recollected that the ascending limb is tightly fastened down to the right kidney as it passes over the viscus. (See above, p. 580.)

† Ann. Sci. Nat. (6) i. 1874.



*vulgaris* Tullberg shows a somewhat different state of affairs; there are two well developed and narrow loops close together which are, however, of nearly the same length. This agrees with a figure given by Mitchell of *Xerus capensis*, and by Gegenbaur of *Cynomys ludovicianus*\*, and W. A. Forbes (MS.) of *Arctomys marmotta*.

Text-fig. 116.

Part of alimentary tract of *Sciurus cinereus*.

*a.c.d.* Ansa coli dextra. *a.c.s.* Ansa coli sinistra. *Cœ.* Cæcum. *O.* Omentum.

One of the Hystricomorph Rodents not figured by Tullberg is the Vizcacha, *Lagostomus trichodactylus*. It is stated, however, to resemble *Chinchilla* in possessing an *ansa coli dextra* and an *ansa paracæcalis*, which however is more free from the cæcum than in *Chinchilla*.

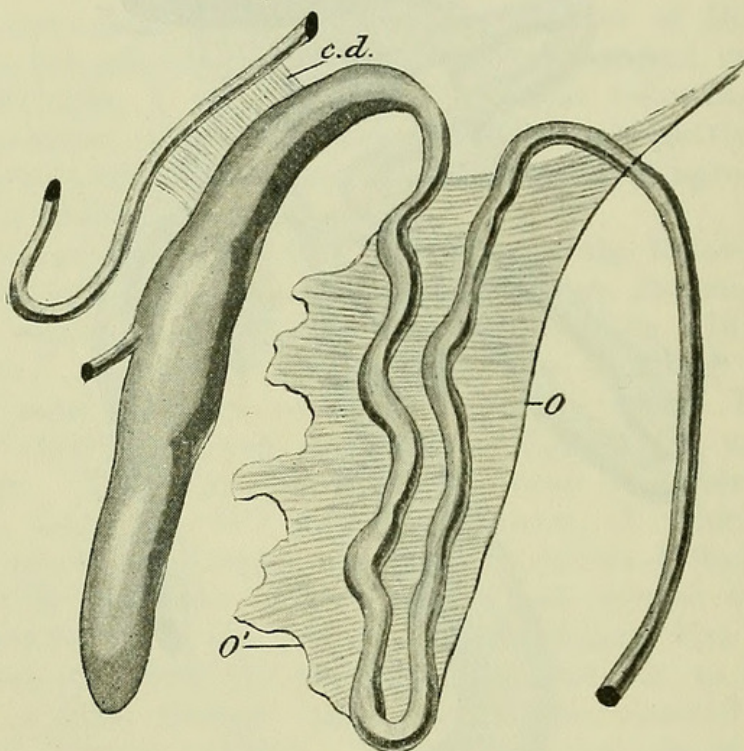
In the two examples which I have dissected there are differences from each other, but I am not clear how far—if at all—either of them differs from the example described by Tullberg. In the one, a female, the *ansa paracæcalis* was a very short, but rather wide loop, totally unlike that figured by Tullberg for *Chinchilla*. The *ansa coli dextra* was long and

\* Vergl. Anat. d. Wirbelthiere.



narrow, and beyond the colon and rectum lay in loosely coiled folds which could of course be straightened out. In the other example, a male, the *ansa paracæcalis* was very large and wide and commenced immediately after the cæcum, ending only with the commencement of the *ansa coli dextra*; the latter was long and narrow as usual, and the rest of the colon, instead of being gathered into temporary folds in a comparatively limited space, ranged, so to speak, throughout the entire colon in a series of broad loops.

Text-fig. 117.

Part of alimentary tract of *Aulacodus*.

*c.d.* Ligamentum colico-duodenale. *O, O'*. Omentum.

*Aulacodus swindernianus* is one of the types of Hystricomorphs not dealt with by Tullberg as regards the points under discussion. I may therefore record the results of a dissection of two examples of this Rodent. Immediately after the cæcum there is a single enormous loop measuring quite a foot long, which is followed by a nearly straight colon and rectum. I am uncertain whether this fold is to be looked upon as the paracæcalis or one of the ansæ coli, dextra or sinistra. Garrod does not seem to have mentioned it in his account of the viscera of this animal\*.

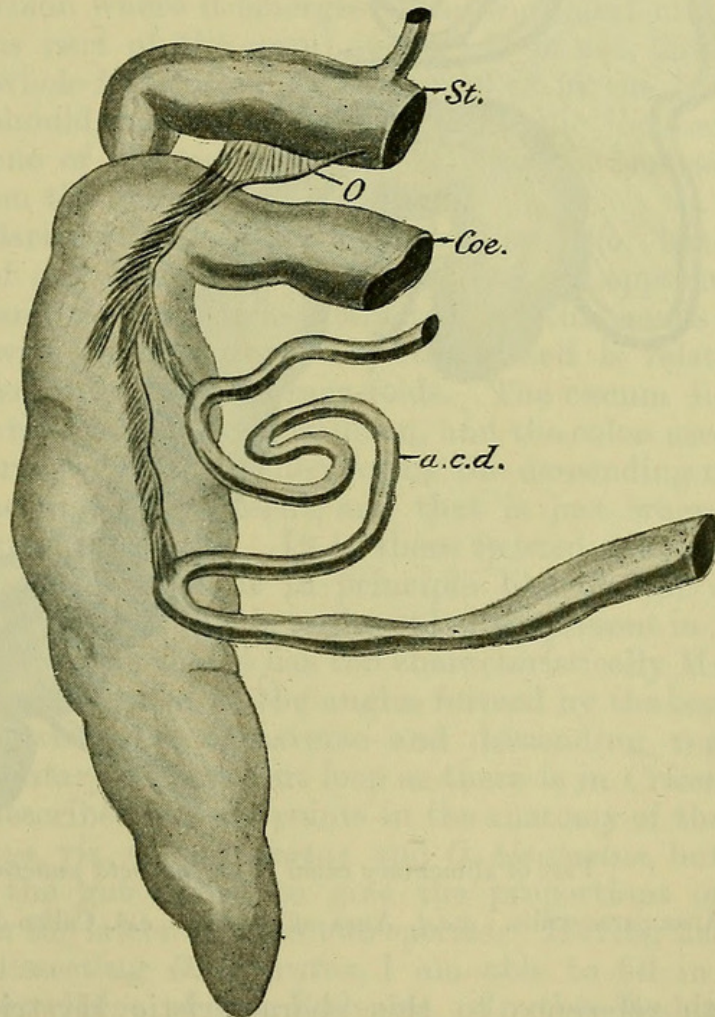
I figure this loop of *Aulacodus* (text-fig. 117) since it differs in various details from that of any other Rodent known to me. It will be observed that the two limbs of the loop running parallel to each other and at no great distance are fringed on

\* P Z. S. 1873, p. 786.



both sides by a membrane with a free edge. On the one side, the membrane has a clearly marked perfectly straight edge, and traced up to the beginning of the loop this is seen to be continuous with the great omentum. The omentum is thus attached to the whole of the ansa coli. On the other side is an equally free fold of membrane, but here the membrane has not a clear cut edge. It ends raggedly and unequally as is shown in the figure. I should say that the figure is made without any cutting of the membranes, which preserve the condition they showed while the gut lay undisturbed within the abdominal cavity. I take it that the ragged edge is really the actual free edge of the omentum, which does not therefore actually end upon the ansa coli but is continued beyond it.

Text-fig. 118.

Part of alimentary tract of *Hydrochoerus capybara*.

*a.c.d.* Ansi coli dextra. *Cœ.* Cæcum, cut through at about the middle of its course. *O.* Omentum. *St.* Stomach.

Although Grant\* and Martin† as well as Tullberg have described the gut of the Paca, *Cœlogenys paca*, I think it worth

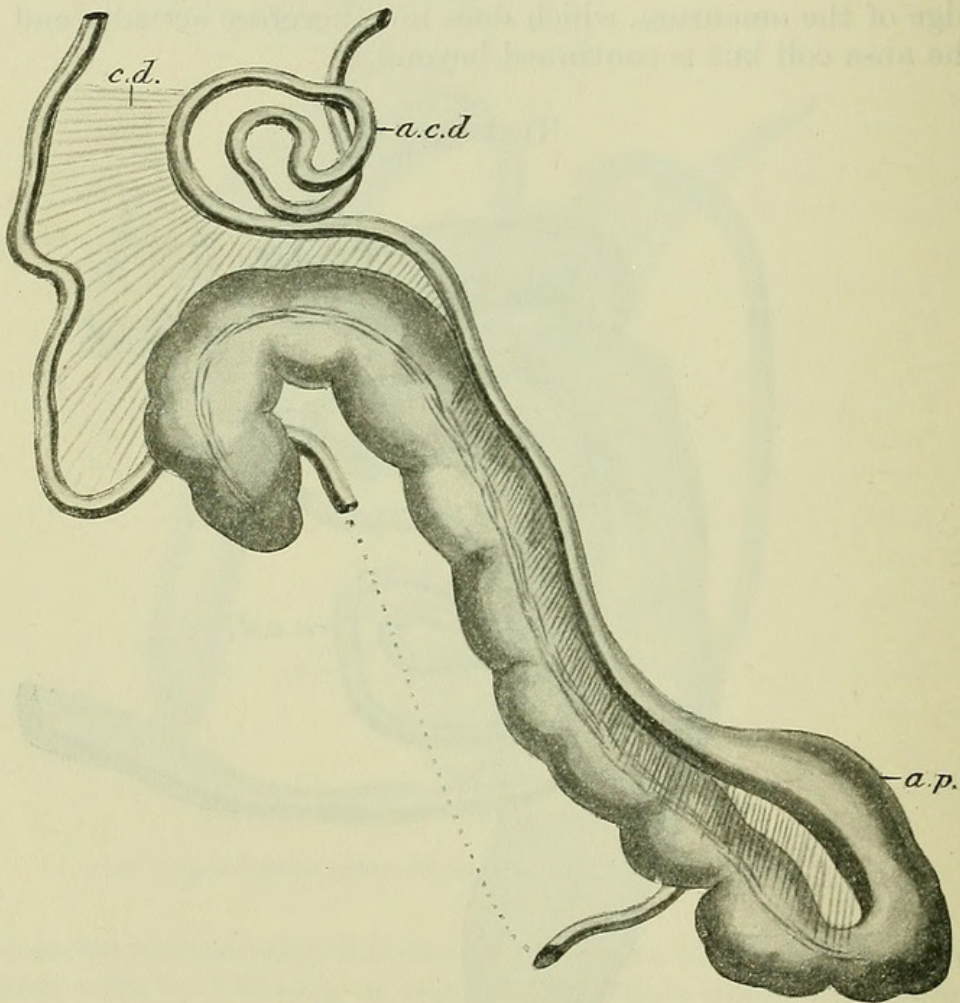
\* Trans. Wern. Soc. *loc. cit.*

† P. Z. S. 1838, p. 54.



while to record my own notes as a contribution towards possible variations in the nature of the spirally coiled ansa paracæcalis. The example which I dissected was coiled in a rather complicated fashion. There are altogether eight limbs in the spiral, and the figure given by Tullberg appears to me to represent rather fewer. That is to say, the loop originally a straight loop has been folded upon itself five times as will be seen from the number of "limbs."

Text-fig. 119.

Part of alimentary canal of *Dasyprocta punctata*.

*a.p.* Ansa paracæcalis. *a.c.d.* Ansa coli dextra. *c.d.* Colico-duodenal ligament.

With reference to this characteristic Hystricomorph spiral, I may mention that in *Hydrochoerus* it is apparently a late growth. I have dissected two examples of about half the full size to which the animal attains, and in both of them there was no complete spiral but merely a loop with a slight twist upon itself at the distal extremity (see text-fig. 118, p. 587).

*Dasyprocta aguti* possesses, according to Tullberg, a limited spiral. I found the same state of affairs in a newly born specimen, where the spiral was only twisted upon itself once, the



condition being therefore much as in the half-grown *Hydrochoerus* just referred to.

Tullberg's figure of the Agouti is not quite so satisfactory as are the majority of his figures. It is so small that various details are left out. I therefore venture to supplement him by another figure of an allied species *Dasyprocta punctata* (text-fig. 119). In this specimen the colic loop is, as shown, rather larger than in *D. aguti*. It is precisely as in the Lemurs *Galago* and *Nycticebus* (see p. 578). The first part of the colon, as correctly shown by Tullberg, runs parallel with and very close to the cæcum, to which it is attached by a mesentery. There is a kind of attempt—so to speak—at its origin of an ansa paracæcalis like that of the Murines. The duodenum is attached both to the colic spiral and to the commencement of the cæcum, which bends back upon itself at its free end as shown in the figure. The great omentum is attached to the colon where it emerges from the spiral and also to the contiguous part of the spiral itself. It is not, however, attached to the whole left border of the spiral as in the Lemurs mentioned. I should mention that the cæco-colic ligament is attached along one of the two muscular bands upon the cæcum, the other being on the opposite side.

The small Barbary Mouse, *Arvicanthis pumilio*, has the simplest colon of any Rodent which I have had the opportunity of examining\*, and the conditions characterising this genus have not been dealt with by Tullberg. The colon itself is relatively short and thrown into no temporary folds. The cæcum lies on the right side of the body rather low down, and the colon ascends, shows a transverse region, and then forms the descending colon. There is only one ansa coli present, and that is just where the colon emerges from the cæcum. It is there twisted into a short spiral. This ansa paracæcalis is in principle like that of other Rodents such as *Cricetus*. But it is the only loop present in *Arvicanthis*. It is noticeable that it has the characteristically Murine form. I could find no trace, at the angles formed by the bending of the colon, between the transverse and descending regions, of even so rudimentary a persistent loop as there is in *Cricetus*.

Tullberg has described various points in the anatomy of the two species of *Otomys*, viz. *O. unisulcatus* and *O. bisulcatus*, but has not dealt with the gut except to give the proportions of the several regions in the latter of those two species. Having had the opportunity of dissecting *O. irroratus*, I am able to fill in that lacuna in our knowledge of the Rodentia. In this Rodent we find almost exactly the same characters as in *Mus*. That is, there is only one colic loop and that is situated just at the commencement of the colon where it emerges from the cæcum. This ansa coli is doubled upon itself once, and this forms an "N" which is bound down to the cæcum. There are no other ansæ along the course of the colon. The great omentum seems to be not present

\* *Mus rattus* is equally simple, and like *M. decumanus* figured by Mitchell—with perhaps even a less marked ansa coli.



at all as a free fold or as attached to the colon. This is an exaggeration of the characters to which Klaatsch has called attention in *Mus* and *Myoxus*. The splenic omentum (ligamentum recto-lienale) is attached to the colon direct as in *Mus*, and not to the mesorectum as is often the case in Mammals.

Although the loops of the colon in the Beaver have been figured by Tullberg, I do not find myself entirely in agreement with that figure. My own observations refer to the parts of the intestine to be dealt with as seen from the ventral surface—the surface exposed on dissection. I gather that the same view has been taken by Dr. Tullberg, since he represents the rectum as lying dorsally to those folds. If this be the case, the Beaver is another example of a Rodent showing some variation from specimen to specimen as is shown in the Vizcacha. The colon where it leaves the cæcum bends to the left and runs forward in close proximity to itself, being bound here by a mesentery. It then curves round and passes back again parallel to the beginning of the cæcum and large intestine, but on the opposite, *i. e.* the right, side, being here also attached closely to the gut in question by mesentery. The tube then bends upon itself and runs again parallel to itself for a little distance, being still attached by mesentery. The colon diverges to the right and forms the first of two ansæ coli like those of *Sciurus* &c. The first of these is attached by its left-hand limb to the ascending portion of the colon. This loop is slightly twisted to the left, and is indeed a rudimentary spiral like that of the Capybara &c. Immediately after the end of this loop the colon is modified into a similar loop of about equal length. Thereafter the colon runs in a broad curve to the rectum. It will be observed that the direction of the colon according to my observations is at first in the opposite direction as described by Tullberg.

The duodenum has varied attachments to the neighbouring regions of the colon and to the parietes, the latter of which I am not able to describe accurately. It is, however, important to note that the duodenum follows the curve of the first ansa coli and is attached to it by mesentery; there is also the usual ligamentum cavoduodenale.

(3) *Coils of Small Intestine*.—As a general rule the festooned coils of the small intestine are not at all permanent coils; the intestine can be passed through the fingers in a perfectly straight line without tearing or in any way distorting the mesenteron. At the same time of course the entire gut cannot be laid out in a circle or a portion of a circle owing to the shortness of its supporting mesentery. One portion can thus be freed from the rest, which in correspondence become closer and denser elsewhere. There are, however, exceptions to this general rule which I have observed among the Marsupials. In a specimen of *Pseudochirus peregrinus* it was impossible to straighten out the coils of the small intestine which were quite fixed. This characteristic,



however, appears to be individual and not to pertain to the species or genus; for in another example the small intestine was "normal." In another Marsupial, *Epyprymnus rufescens*, the small intestine, considerably shorter than that of *Pseudochirus*, was also thrown into permanent coils. Here, however, I can only report upon a single individual.

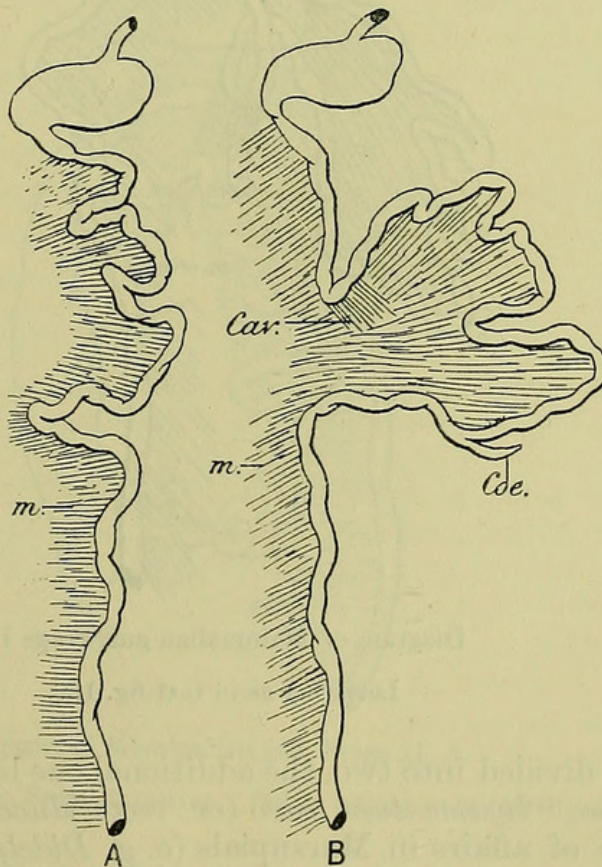
Among a considerable number of lower Mammals whose alimentary tracts I have recently studied, only *Dasypus vellerosus* (of which I have dissected a single example only) shows the same fixation of the numerous coils of the small intestine.

It is evident that this phenomenon is not a common one among the Mammalia, and it is at present doubtful how far it is characteristic, in the rare cases where it does occur, of a given species or genus.

#### General Considerations.

From the foregoing considerations it is clear that we can trace a number of stages of evolution of the intestinal part of the alimentary tract in the various groups of Mammalia which are not shown in their complete entirety in any one group.

Text-fig. 120.



**A**, Diagram of primitive Mammalian gut, Stage I.—**B**, Stage II.

Cœ. Cæcum. Cav. Lig. cavoduodenale. m. Dorsal mesentery.

In *Stage I*. the intestine is suspended upon a continuous mesentery and is not rotated upon itself to form the primary loop.



This is met with as an exception in the Marsupialia (e. g. *Antechinomys*); in the two Edentate American Anteaters, *Myrmecophaga jubata* and *Tamandua tetradactyla*; in *Centetes* (occasionally), at any rate, as representing the Insectivora; in the Elephant, so far as can be gathered from Flower's description \*, as representative of the Ungulates. In the Odontoceti (*vide* Max Weber †) this arrangement of the intestine would appear to be the rule; but not in other Whales. *Tarsius* is the only Lemurine Mammal known to form an intestine slung upon a continuous mesentery ‡.

In *Stage II.* we have an intestine showing only the single rotation upon itself without any further specialisation, so far as concerns the gut. The suspensory mesentery, however, has

Text-fig. 121.

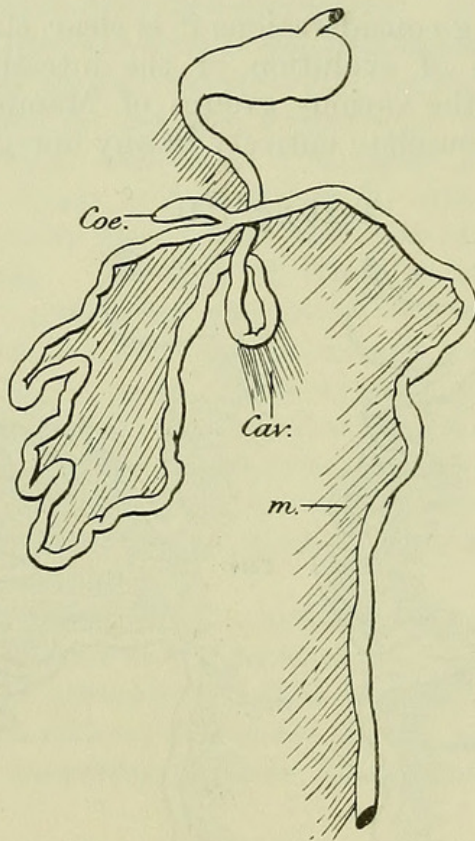


Diagram of Mammalian gut, Stage II.

Lettering as in text-fig. 120.

naturally divided into two, the additional one being what Klaatsch terms the "*ligamentum cavo-(or recto-)duodenale.*" We find this state of affairs in Marsupials (e. g. *Didelphys*, *Macropus*), in Edentates (e. g. *Dasypus*, *Orycteropus*), in Carnivora (? without exception), in Lemurs (e. g. *Microcebus*), in Primates (? without

\* Med. Times & Gazette, *loc. cit.*

† Die Säugethiere. See for a particular instance (Porpoise) Hepburn & Waterston, Trans. R. Soc. Ed. xl. pt. ii. 1902.

‡ Klaatsch, *loc. cit.*



exception \*). A slight modification of this stage is seen in many Carnivora and in the Primate *Chrysothrix*, where the intestine can be laid out flat without tearing the mesenteries; this is achieved by the reduction of the ligamentum cavoduodenale, and it is possible that the entire disappearance of this mesentery may account for such cases as *Centetes*, which therefore show an unreal primitiveness due to a reversion by degeneration.

This stage may be subdivided into two; of which one, Stage II. A, will include those forms in which the intestine is merely folded over once without further specialisation, and will include some Marsupials (e. g. *Didelphys*, *Hypsiprymnus*), Edentates (e. g. *Dasypus*), Carnivora (? all genera), Lemurs (e. g. *Microcebus*); and Stage II. B, which will be characterised by the further specialisation caused by the attachment to the colon of the omentum: this second group will contain many Marsupials (e. g. *Macropus*), Edentata (*Orycteropus*), Primates (division of Anthropoidea without exception).

Text-fig. 122.

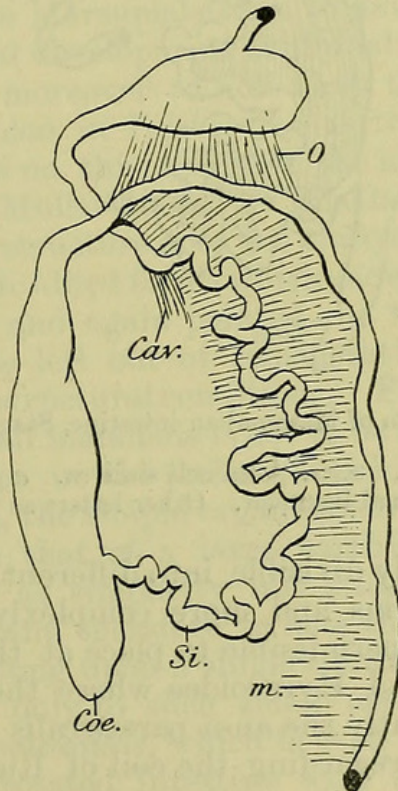


Diagram of Mammalian gut, Stage II. A.

O. Omentum. Si. Small intestine. Other letters as in text-fig. 120.

In *Stage III.* the essential difference from the two earlier stages is the formation of fixed permanent loops of the colon, termed *ansæ coli*. Combined with this is always an intestine

\* Klaatsch's figure (*loc. cit.* fig. 12, p. 671) of the young *Hapale* with an *ansa coli* absent in the adult (fig. 13, p. 672) suggests the possibility of the Primate simplicity being due to reversion.



with the usual rotation of Stage II., and there is also invariably a connection of the omentum with the colon, and furthermore, always a secondary connection of the duodenum with the colon at its commencement. This stage is represented by Lemurs (the majority), all of the Hyracoidea, Perissodactyla\* and Artiodactyla†, and, finally, Rodents.

Text-fig. 123.

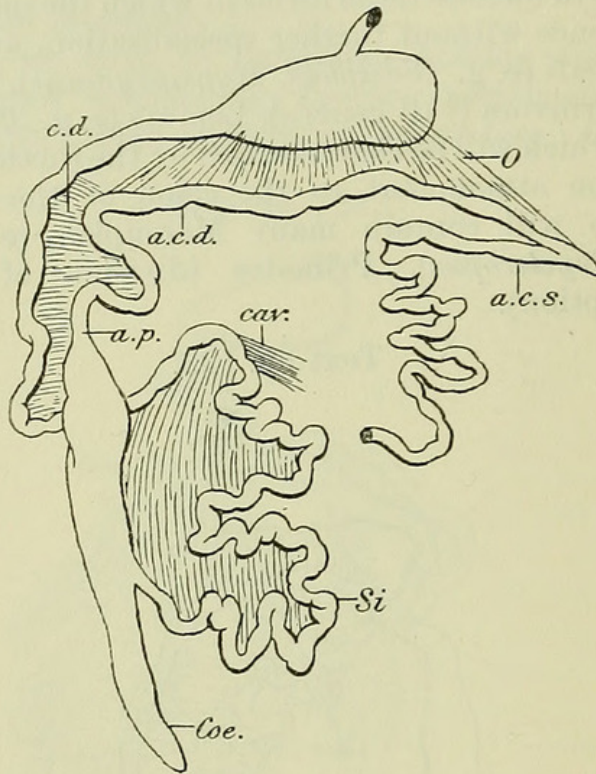


Diagram of Mammalian intestine, Stage III.

*a.c.d.* Ansa coli dextra. *a.c.s.* Ansa coli sinistra. *a.p.* Ansa paracæcalis.  
*c.d.* Colico-duodenal ligament. Other letters as in text-fig. 120.

This Stage is hardly divisible into different grades. There are, it is true, simpler forms and more complexly convoluted colons. It might perhaps be permissible to place at the base of the series the Perissodactyla and Hyracoidea where there is but one ansa coli, and that apparently the ansa paracæcalis of other types. If Klaatsch be right in regarding the coil of Ruminants and Swine as an ansa paracæcalis, this group would be added. In this case we arrive at the interesting conclusion that the colic spiral is not strictly homologous through those groups which show it. For in the Lemurs it cannot be doubted that the spiral is the ansa coli dextra. It is only the Rodentia which show the maximum of coiling of the colon, and in the more differentiated genera of that order (e. g. *Castor*) there are three ansæ coli, though not more.

\* I have not dealt above in detail with the single simple *ansa coli* of Horses, Tapir, and Rhinoceroses, since it has been so often described.

† See especially Lönnberg, Acta Ac. Upsala, 1903, K. Vet.-Ak. Handl. 1901, and some other memoirs.



But other genera, e. g. *Mus* and *Arvicanthis*, with one ansa paracæcalis, and *Sciurus* with two ansæ, dextra and sinistra, and *Aulacodus* with only the ansa coli dextra, render it impossible to make hard and fast lines of division.

It will be noticed from the above account of the several stages seen in the Mammalian gut, that the Lemurs are the only group in which every stage but one is to be seen in a well-marked fashion. This fact of itself is enough to negative any accurate classificatory results to be deduced from the series of facts brought together in the present communication, though I offer later (p. 596) some observations upon the affinities of different groups as judged by the varied modifications of the intestinal canal.

Furthermore, it will be gathered from what has been brought forward in the present communication that the Marsupials, although their intestinal tract shows in a well-developed fashion only two stages, show indications as it were of the third stage. Occasionally an ansa coli exists, while secondary connections between the duodenum and commencement of the colon are found in *Trichosurus*. Arising, as is now believed, from some early Eutherian type, the Marsupials seem to have retained the potentialities of intestinal development exhibited in the later Eutheria.

It is important moreover to note that the attachment of the omentum to the colon in *Trichosurus* is to the extreme right of the latter; for it is on this side that the attachment commences in Man (Johannes Müller quoted by Klaatsch).

Simplification of structure does not always imply an archaic position with reference to allied forms which show a less simple anatomy. It has been again and again pointed out that size is an element which is not to be left out of consideration in weighing such apparently archaic structural conditions. For example, the smooth brain of many small mammals is not to be interpreted as evidence of the lowly position in the series of such smooth-brained types. On the other hand, the simple organisation of a Naid Oligochæte as compared with that of a large earthworm, may be at least partly interpreted as simplicity not altogether due to reduced size. It is important therefore to note that the simple intestine of *Antechinomys* slung upon a single continuous mesentery is not a feature confined only to such small mammals. In comparing this form with *Arvicanthis*, which is even smaller, we find in the latter the usual rotated intestine with even a fixed colic loop. And other examples will be apparent from the foregoing pages as well as from previous writings on the subject. At the same time it is not to be forgotten that other instances may be due to simplification, and to belong therefore to a different category though apparently quite similar.

Although it is true that the specialised loops of the colon are often associated with a colon of great length, there is as it would appear no necessary connection between length and complexity, or even occurrence, of these special loops. The existence of such coils is in fact a character of given orders of mammals. Among



those orders where they occur, that is to say the Rodentia, Perissodactyla, Artiodactyla, Hyracoidea, and Lemurs, there is no relation between complexity of coils and length of gut. The small Rodent *Arvicanthis* has a short colon not longer than that of many mammals of other groups without any trace of coils. And yet it possesses one ansa, the postcæcalis. The existence of three ansæ in the Beaver does not argue a longer colon than in the Agouti, where there is only one ansa, the ansa coli dextra. The complex spiral of *Indris* is not associated with a markedly longer colon than that which bears the one loop of the genus *Hyrax*. It is therefore clear that we must seek for the origin of these fixed loops of the colon in some other way than need for packing away a large tract of gut in a limited space. And it has been already suggested that this may be found in the attachment of the omentum.

*Value of Intestinal modifications in Classification.*

Apart from certain facts given by Weber and others as distinctive of various groups of Mammals, Dr. Mitchell seems to be the only person who has attempted to discuss in detail the classificatory results to be obtained from a consideration of the varying characters of the intestinal tract. In a preliminary criticism of resemblances—an attempt to differentiate those upon which weight should be laid from those which cannot be admitted as of classificatory importance, this author has committed himself to a statement that will not receive the agreement of zoologists. "Likenesses" he writes (on p. 528) "which are due to the common possession of primitive features cannot be regarded as evidence of near relationship; that certain members of a group have retained what was once the property of all the members of that group can be no reason for placing such creatures close together in a system if that system is to be based on blood-relationship." It is, I imagine, by absolutely universal consent that *Echidna* and *Ornithorhynchus* are placed together in one order, Monotremata, and mainly by virtue of the facts that in both there is a large coracoid and a generally "primitive" shoulder-girdle: that in both the egg is large-yolked and meroblastic with a follicle of at most two layers of cells: that in both the anterior abdominal vein is either present or indicated by a large ventral mesentery: that in both the heart valve of the right auriculo-ventricular ostium has retained the partly muscular structure of that of lower types; and by other features all of which are primitive.

One can of course accede to Dr. Mitchell's assertion that the loss of a particular character in two groups is no reason for placing them in proximity, and that a new structural acquisition is evidence of relationship in proportion to the anatomical complexity of that structure; this latter is a perfectly correct restatement of Sir E. Ray Lankester's use of the Molluscan Odontophore as a test for



the inclusion of a particular type in that phylum. Dr. Mitchell's sketch of the "archecentric" condition of the mammalian gut agrees absolutely with the figures given in any text-book of Human Anatomy \* of the early human gut, and any mammalian gut.

There is in fact no doubt whatever that the primitive Mammalian gut was in all essentials a gut like that of the Reptilia, *i. e.*, a tube of no great length, and therefore with but few convolutions suspended by a continuous mesentery and with no permanent folds of any part. I leave undecided whether a cæcum or cæca are necessary adjuncts of this archetypal intestine, or whether they or it should lie about halfway down the intestinal tube.

Greater or less length is clearly of no importance inasmuch as that feature has been shown to vary in individuals (see above p. 585). Viewing the matter from this point of vantage, we ought to regard as most primitive in position any groups or group in which the alimentary tract has retained this Reptilian character throughout; which in fact are so far not one generation removed from the entire group of Lacertilia (including *Hatteria*), where no other conditions are, so far as anatomical investigation has gone, to be found.

So far as I can say from my own knowledge and from reliable statements published upon the matter, the only groups in which this primitive gut exists obviously are the Polyprotodontia (excluding the American forms), the Xenarthra (excluding Armadillos), the Proboscidea, the Odontoceti, and the Insectivora. But with regard to the latter the case of *Centetes* described above rather suggests a reversion. The Lemurs can hardly be added, since *Tarsius* is the only form which shows this straight mesentery unfolded anywhere; and as that genus is so minute in size the feature may be the result of degeneration.

Why Dr. Mitchell should remove from such an assemblage † the Insectivora, Proboscidea, and Odontoceti, and add to it the Tubulidentata and Diprotodont Marsupials, is not altogether easy to understand. His arrangement appears to me to be so far purely capricious, and to be based upon no facts. Moreover, I would point out that very nearly all zoologists would agree in regarding the groups which I have thus placed in juxtaposition as being ancient groups.

Dr. Mitchell, however, appears to me to be perfectly right in asserting that the Carnivora have not moved far from the common centre; though why this statement should be qualified by the suggestion that the reduction of the hind gut is a specialisation is not so apparent. As Dr. Lönnberg has well pointed out in the case of certain Marsupials ‡ (and others have pointed out in other

\* *Cf. e. g.* D. J. Cunningham's Text-book.

† According to him the "ancestral group" contains Marsupialia, Xenarthra, Tubulidentata, and Galeopithecidae. All Marsupials, I presume, are included.

‡ P. Z. S. 1902, vol. i. p. 12.



groups), there is a close association between the relative lengths of the regions of the gut and the food, a relation which is by no means ignored by Mitchell, though he does not quote any previous memoirs in discussing this matter.

Surely the American monkey *Chrysotrrix* (see above p. 577), with a very short straight intestine, cannot be considered to differ importantly by this character from e. g. *Hapale* with the usual three-sided Primate large intestinal loop. On the contrary, I should be disposed to assert that the short colon of the Carnivora, persisting as it does through the whole order, differing as they do widely in their food, is rather evidence of an ancient state of affairs.

Moreover, a glance at the earliest Mammalia known would seem to suggest that a carnivorous, insectivorous, or at most omnivorous way of life was the primitive mammalian mode of life, a view which is strengthened by reflections upon the origin of the group, whether from Reptilian or Amphibian like forms. Otherwise it might be pointed out that on the whole the simple form of gut was associated with a shortness of gut associated in its turn with a carnivorous habit. The Elephant however (if I rightly interpret the investigations and statements of others) seems to possess a simple gut supported upon a continuous mesentery.

This, however, is by no means saying the same thing as to assert that the five groups mentioned are to be combined into a superorder and contrasted with the remaining Mammalia which stand in various relations to them. On the contrary, it appears to be totally impossible to classify the mammals by the form of their intestine, the chief reason for this being that so many grades are seen in the same group. On the other hand, it may be confidently said that the Ungulates and Rodents are some way removed from the base of the mammalian series; for in none of them are primitive conditions to be seen. These have, it would appear, become entirely lost.

It is particularly noteworthy that the Anthropeidea (understanding by this term the "apes" and "monkeys"), as contrasted with the Lemuroidea, exhibit primitive characters\*, though not so primitive as the five groups with which we commenced this survey. There are no fixed loops to the colon, and there are the same fluctuations in the relative lengths of the small and large intestine that we find in e. g. the Marsupials. But special mesenteric connections render complex the coils of the gut, though not so numerous as we meet with in Rodents. On the other hand, the Lemurs present us with no particular likeness to the other Primates. The path pursued by these animals is really much the same as that pursued by the Rodents and the Ungulates. But this does not in my opinion imply affinity; it means no more than that there is a definite line of increasing complexity of the gut which is followed in all.

In fact, on the whole a study of the intestinal coils of Mammalia

\* Cf. however Klaatsch, p. 671, fig. 12 for "lemurine" stage in young *Hapale*.







seems to lend support to the view that existing mammals have radiated out separately in many directions from a common stem, and that no two groups are very markedly nearer to each other than any others.

This view is in accord with certain opinions expressed by Prof. Osborn. The relative positions of the various groups (excluding those of which I have not sufficient knowledge derived from memoirs or from my own observations) can be expressed in some such diagram (p. 599) as that which accompanies these remarks. The stages referred to are described on a previous page.

#### IV. *Note on the Existence of a Suprarenal Portal System in Marsupials.*

Although it is possibly true that physiologically there is no renal portal or suprarenal portal system\*, it is plain that among Reptiles, as contrasted with Mammals, there are veins entering the kidneys and the suprarenal bodies from the parietes and hind limbs forming afferent veins to those glands, and thus contrasting with efferent veins which convey the blood from the glands in question directly to the postcaval system. Whether the capillaries intervening between the afferent and efferent veins are real capillaries or sinusoids does not affect the anatomical facts just stated, though naturally of great embryological and physiological importance. Neither does my own suggestion† that the suprarenal portal system is really due to the disappearance of that section of the postcardinal vein which runs over or near to that organ on each side and the consequent opening of its (the postcardinal vein's) affluents into the substance of the gland. It is still a fact that among Reptiles the suprarenal organs send a vein or veins to the postcaval and receive a vein or veins from the adjacent parietes. And this feature, whatever may be its physiological importance or want of importance, is an anatomical feature in which the lower Vertebrata differ from the Mammalia.

This being the case, attention is directed to the accompanying drawing (text-fig. 124, B) which represents the veins in the immediate neighbourhood of the kidneys of an example of the Marsupial *Dasyurus maugai*. It will be seen that the suprarenal body of the left side of the body lies anteriorly to the left renal vein and not in contact with it. The vein from this body opens directly into the postcaval vein between the points of entrance thereto of the two renal veins, but nearest to the left renal vein. In addition, however, to this vein connected with the suprarenal body, another vein is depicted in the figure which arises by more than one veinlet from the adjacent muscles. This vein runs in a direction parallel to that of the postcaval and ends in the suprarenal body, which it enters at the end remote from that whence the suprarenal affluent of the postcaval emerges from the

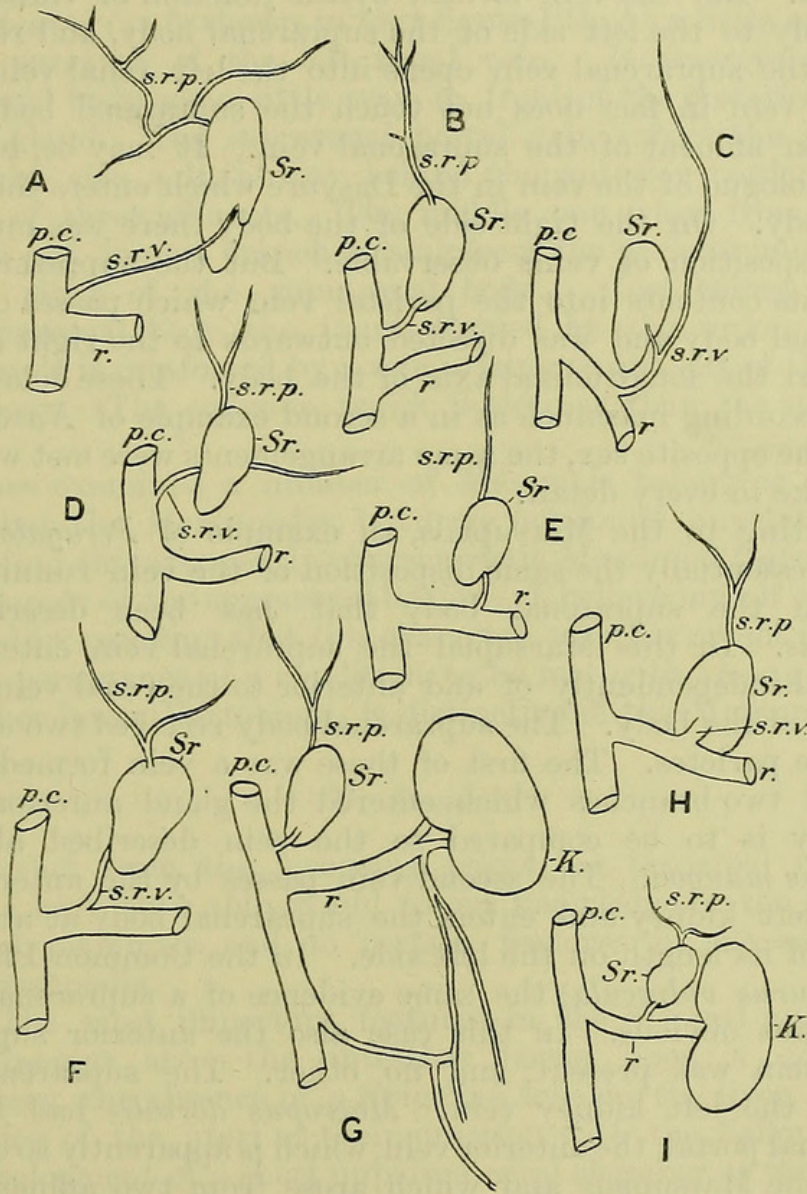
\* Cf. Woodland, P. Z. S. 1906, p. 886.

† P. Z. S. 1906, p. 24.



gland. *Dasyurus viverrinus* was exactly the same. In an example of *Macropus agilis* the same vein is present, but there are slight differences from the conditions observed and just described in *Dasyurus maugæi*. In the *Macropus* the suprarenal vein enters the left renal, and the suprarenal portal, as I venture to term the

Text-fig. 124.



Suprarenal veins in various Mammals.

- |                                 |                                   |                                      |
|---------------------------------|-----------------------------------|--------------------------------------|
| A. <i>Thylacinus</i> .          | B. <i>Dasyurus maugæi</i> .       | C. <i>Nasua rufa</i> .               |
| D. <i>Peragale lagotis</i> .    | E. <i>Trichosurus vulpecula</i> . | F. <i>Macropus dorsalis</i> .        |
| G. <i>Dasyurus viverrinus</i> . | H. <i>Bettongia ogilbyi</i> .     | I. <i>Phascologale penicillata</i> . |

p.c. Postcaval vein. K. Kidney. r. Renal vein. Sr. Suprarenal body.  
s.r.p. Suprarenal portal. s.r.v. Suprarenal vein.

vein to which attention is directed in the present paper, enters as in *Dasyurus* at the opposite end of the suprarenal body. The suprarenal vein differs from that of *D. maugæi* in that it receives a tributary from the parietes. The left suprarenal veins of



*Macropus ualabatus* were much the same, but I did not observe the parietal branch of the suprarenal vein.

This state of affairs may now be compared with that observable in the higher Mammalia. In an example of *Nasua rufa* the veins in question had the disposition shown in text-figure 124, C. There is, as in the Marsupials already dealt with, a vein arising from the parietal musculature anteriorly. It arises by two main branches. But the vein formed by the junction of these passes ultimately to the left side of the suprarenal body, and receiving from it the suprarenal vein opens into the left renal vein. The parietal vein in fact does not touch the suprarenal body; it is merely an affluent of the suprarenal vein. It may be, however, the homologue of the vein in the *Dasyurus* which enters the suprarenal body. On the right side of the body there was much the same disposition of veins observable. But the suprarenal vein poured its contents into the parietal vein which passes over the suprarenal body and was directed outwards to the right at right angles to the longitudinal axis of the body. These details were worth recording inasmuch as in a second example of *Nasua rufa*, and of the opposite sex, the same arrangements were met with and were alike in every detail.

Reverting to the Marsupials, an example of *Peragale lagotis* showed essentially the same disposition of the vein running into or from the suprarenal body that has been described in *Dasyurus*. In this Marsupial the suprarenal vein entered the postcaval independently of and anterior to the renal vein on the left side of the body. The suprarenal body received two affluents from the parietes. The first of these was a vein formed by the union of two branches which entered the gland anteriorly, and evidently is to be compared to the vein described above in *Dasyurus maugai*. The second vein passes by the anterior end of the left kidney and enters the suprarenal body at about the middle of its length on the left side. In the Common Phalanger (*Trichosurus vulpecula*) the same evidence of a suprarenal portal system was obvious. In this case also the anterior suprarenal portal vein was present, and no other. The suprarenal vein entered the left kidney vein. *Macropus dorsalis* had but one suprarenal portal, the anterior vein, which is apparently so constant among the Marsupials and which arose from two affluents. In the features described in the present communication, *Petrogale penicillata* is exactly like *Trichosurus vulpecula*. *Phascologale penicillata* is slightly different from any of the Marsupials as yet described. The suprarenal vein opens, as is so frequently the case, into the renal vein on the left side of the body. Exactly opposite to it the suprarenal portal opens into the suprarenal body. But this vein before entering the gland receives a branch running transversely and just skirting the anterior margin of the left kidney, the conditions being therefore slightly like those of *Peragale* just described, and indeed intermediate between the condition observable in that Marsupial and in those where the



one vein bifurcates anteriorly. *Bettongia ogilbyi* is like many other Marsupials; the suprarenal portal is single and anterior in position, being formed by the union of two affluents which join at an acute angle. As *Thylacinus* is a scarce type and not likely to be much dissected in the future, I venture to give a particular account of the veins connected with the suprarenal body, which I noted during the dissection of a specimen which died in the Society's Gardens in January 1906. The suprarenal vein enters the postcaval (as is shown in text-figure 124, A) a little anteriorly to the entrance of the left renal vein. It emerges from the suprarenal body some little way in front of the posterior border of the gland. The suprarenal portal vein enters the gland on the right side a little way behind the anterior border. It is formed of three affluents. The middle one arises from the diaphragm and joins a branch arising from the parietal musculature to the right of the suprarenal body. Just before entering the suprarenal body the trunk formed by the union of these two vessels is reinforced by a vein arising to the left of the suprarenal body. The common trunk is thinner than the suprarenal vein.

I have examined a number of Mammals belonging to orders other than the Marsupialia, but have not found anything at all resembling this apparently characteristic Marsupial feature in the blood-supply of the suprarenal bodies. I believe myself at present justified in asserting that this character, whether or not it be held to be a persistence of a condition to be met with among Reptiles and other lower Vertebrata, is distinctive of the Marsupialia.

#### V. *Resumé.*

I extract from the foregoing pages the principal new facts which I have been able to add to our knowledge of the intestinal tract of mammals and to certain features in the anatomy of the Marsupialia.

(1) The most important features in the visceral anatomy of *Antechinomys* are: the intestine borne upon a continuous mesentery, the absence of a Spigelian lobe in the liver, the wide dilatation of the uteri at their junction with the Fallopian tube, the development of a short unpaired cæcal chamber at the junction of the uteri.

(2) A specimen of *Phascologale macdonnellensis* showed a persistent umbilical membrane (proving an umbilical placentation in this species), which passes between the fibres of the rectus muscle divided for its passage, and is continuous with the great and splenic omentum. The umbilical membrane is also attached to small intestine. The intestinal canal is short and carried on a continuous mesentery. The liver in this species, as in *P. penicillata*, has a Spigelian lobe, also present in the genus *Sminthopsis*.

(3) In many (? in all) Marsupials the suprarenal bodies receive



a vein from the parietes as well as emit one to the renal vein or postcaval as the case may be; there is thus a rudiment of a supra-renal portal system in these animals, not found in at least many Eutherian Mammals.

(4) Though the intestinal tract of Marsupials is on the whole simple, there are traces (*Didelphys*, *Trichosurus*) of the ansæ coli and (*Trichosurus*) of the colico-duodenal ligament of more differentiated forms.

(5) A gut suspended upon a continuous mesentery is described for the first time not only in *Antechinomys*, but in *Tamandua*; on the other hand, a number of genera of Carnivora are described and the alleged continuous mesentery in *Ursus* is shown to be only apparent and due to the reduction of the ligamentum cavoduodenale. The continuous mesentery of *Centetes* is shown to be not universal in the species and is therefore probably to be looked upon as a reversion.

(6) To the numerous descriptions and figures of Rodents' alimentary tracts gathered together or published for the first time by Tullberg, a description of the colon and ansæ coli of *Otomys*, *Aulacodus*, and some other forms is added. The enormously long ansa coli dextra of the latter shows that the spiral found in certain Rodents is not necessarily to be looked upon as due to the need for packing away such a long loop. The spiral of *Hydrochaerus* is shown to be a late development since it does not occur in half-grown examples. The colon of the minute *Arvicanthis* (with one ansa only, the a. paracæcalis) shows that in this group reduction of size is not necessarily accompanied by entire simplification of the gut.

(7) The older descriptions of the spiral coil in certain Lemurs, e. g. *Nycticebus*, are shown to be correct as against more recent statements. *Microcebus* is shown to possess a simple colon without ansæ. *Galago* (2 spp.) is shown to possess a spiral like *Nycticebus* &c. And it is pointed out that all the forms with a specialised gut, i. e. with this spiral, are also specialised in the loss of the elsewhere characteristic carpal vibrissæ.

(8) Some account is given of the alimentary tract of the little known species *Theropithecus gelada* and *Semnopithecus melalophus* and the American *Chrysothrix sciureus*.

(9) The intestinal tract of *Hyrax*, contrary to some statements, has been shown to possess an ansa paracæcalis which may perhaps be compared to that of the Perissodactyla, and to possess the ligamentum colico-duodenale of more differentiated forms.

(10) As a very general rule the loops of the small intestine are loose folds not in any way fixed. Rarely, however (e. g. *Dasypus vellerosus*), I have found them to be fixed.

(11) That the colic loops vary is shown by the instance of *Lagostomus trichodactylus*, in which each of the three individuals dissected by myself or Tullberg is slightly different in the proportions of those loops, and by *Hyrax capensis*.

(12) It has been pointed out that in man the omentum is at



first attached to the right side of the transverse colon and subsequently to the left side, the intermediate space being filled up later. The two earlier stages are represented in lower mammals; in *Trichosurus* the omentum is attached to the colon only on the extreme right of the transverse bend, and in *Orycteropus* and *Hyrax* the attachment is double, to the early part of the colon and to a more distal region—the intervening tract being free of the omentum.

(13) The view, deducible from previous investigations, that four stages of advancing complexity are shown in the Mammalian gut, is strengthened by fresh facts; the Lemurs are shown to be the only group in which all but one of these four stages occur.

4. The Armour of the Extinct Reptiles of the Genus *Pareiasaurus*. By H. G. SEELEY, F.R.S., F.Z.S., King's College, London.

[Received April 29, 1908.]

(Text-figures 125–129.)

In "Further Observations on *Pareiasaurus*," Phil. Trans. B. Royal Society, 1892, I gave a short account of the dermal armour, pp. 345–6. It is limited to the dorsal region, and is figured in plate 17, and indicated by the letters *ds* in the description of the plate, p. 368. The scutes are only known in this example of *Pareiasaurus bairdi*, extracted from the rock by myself. They were originally covered with matrix. Their existence was not suspected, and it is possible that the more anterior scutes may have been partly lost in removing the intractable rock; and those seen in the British Museum specimen were preserved by great skill in chiselling. The ossifications are flat and inconspicuous, except where the lateral plates overhang the neural spines.

In the small figure of the skeleton given in the 'Story of the Earth,' 1895, text-fig. 18, p. 126, the scutes were made more evident by dark outlines. Each scute is about 2 inches wide by  $1\frac{3}{4}$  inch long. There is a median row extending down the back, which as preserved now rests upon the summits of the neural spines of the dorsal vertebræ and the interspaces between them. There are also two lateral rows, one of which flanks each side of the median row. These are arranged symmetrically in pairs, and extend transversely outward from their contact with the median row, but alternate with them by being placed at the junction between each two median scutes. The lateral scutes in *Pareiasaurus bairdi* are not flat but convexly curved as they extend outward, giving some support to the idea that this armour formed an elevated ridge on the back. In the present condition of the specimen this armour is only seen on seven consecutive later dorsal vertebræ and one or two earlier dorsals; and there is no evidence that it was present over more than twelve vertebræ.





Beddard, Frank E. 1908. "On the Anatomy of Antechinomys and some other Marsupials, with special reference to the Intestinal Tract and Mesenteries of these and other Mammals." *Proceedings of the Zoological Society of London* 1908, 561–605. <https://doi.org/10.1111/j.1469-7998.1908.tb07392.x>.

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