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VII. *On the Intestinal Tract of Birds; with Remarks on the Valuation and Nomenclature of Zoological Characters.* By P. Chalmers Mitchell, *M.A., D.Sc. Oxon., F.L.S., F.Z.S., Lecturer on Biology at the London Hospital Medical College.*

(Plates 21–23.)

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Introduction.

In 1813, in one of a series of papers on the Solvent Glands and Gizzards of Birds, Sir E. Home (15) gave a description and some measurements of the intestines in the Ostrich, Emu, Cassowary, and Rhea; and in 1814 (16) the same author described the course of the intestines and the form of the cæca in a number of birds, giving figures, in which, however, the coils were represented as freed from their blood-vessels and mesenteries. In the second edition of the 'Leçons' Cuvier (5) described the arrangement of the intestinal tract in some dozen birds and distinguished regions, as the "duodenal loop";

the "median loop," extending from the duodenum to the unpaired cæcum; the "colic loop," extending from the median loop to the insertion of the paired cæca; and the "rectum." Following Meckel, he identified the "unpaired cæcum" as the rudiment of the yolk-sac. Cuvier, however, had no great range of facts before him, and refrained from any general conclusions. Owen, in Todd's 'Cyclopædia of Anatomy and Physiology' (31), added little to the investigations of Home and Cuvier; and Macgillivray (22) did little more than to point out that the subject might yet afford useful facts for taxonomy. Thereafter the subject was apparently completely neglected until Dr. Gadow (10, 11, 12) began his extensive and extremely interesting investigations. Gadow studied and figured the loops and blood-vessels in a large number of forms, distinguished the loops of the intestine as being "open" or "closed" according to the width of the mesentery between the limbs of the fold, named the folds "right-handed" or "left-handed" according to the position of the descending limb; but, above all, described at length and based taxonomic distinctions on the mode in which the loops were folded within the cœlom.

In 1894, working in the Prosectorium of the Zoological Society, I examined the intestines of a number of birds in the method from which Gadow obtained his notable conclusions: but I found not infrequently that there were individual variations in the disposition of the loops, particularly as regarded their "right"- and "left-handedness," no doubt in connection with the writhing movements of the gut during life, and came to the conclusion that there was more to be learned from investigation of the relation of the loops to the unfolded mesentery than from consideration of the mode in which the folds were packed. The method of examination, which I have since found to be an extension of Cuvier's method, I described in 1895 (25), and, at greater length, in 1896 (26). It depends on the morphological nature of the intestinal tract of Vertebrates, which is a tube suspended in the cœlom by a fold of mesentery attached to the dorsal wall. The tube, in its course, describes an arc between two fixed points, the pyloric end of the stomach anteriorly, and the insertion of the rectum to the cloaca posteriorly. A third fixed point is given in the embryonic stage by the attachment of the yolk-sac nearly in the middle of the ventral edge of the arc, and this point is often marked in the adult by Meckel's diverticulum (see *infra*, p. 175). The intestinal tract increases considerably in length between the fixed points, and along with its mesentery, which similarly increases, it is thrown into a series of loops which are folded on one another in the various modes described by Gadow. When the intestines have been removed from the bird by section at the pylorus and cloaca and by cutting the mesentery along its dorsal attachment, the cut end of the duodenum and of the rectum may be pinned on a board to the operator's right-hand, these two points and the cut edge of the mesentery stretching between them being placed in their natural relative positions. Then, with some trouble in the more complicated cases, the various loops may be unfolded to the left and pinned out; whereupon the mesentery appears as a flat sheet, in shape roughly the segment of a circle, the cut dorsal edge of the mesentery being the sector, and the arc, which carries the intestinal tract, being irregularly distorted. The sheet of mesentery is of course double, and the blood-vessels and autonomic nervous system run between the two sheets, being situated outside the cœlom. The figures which illustrate

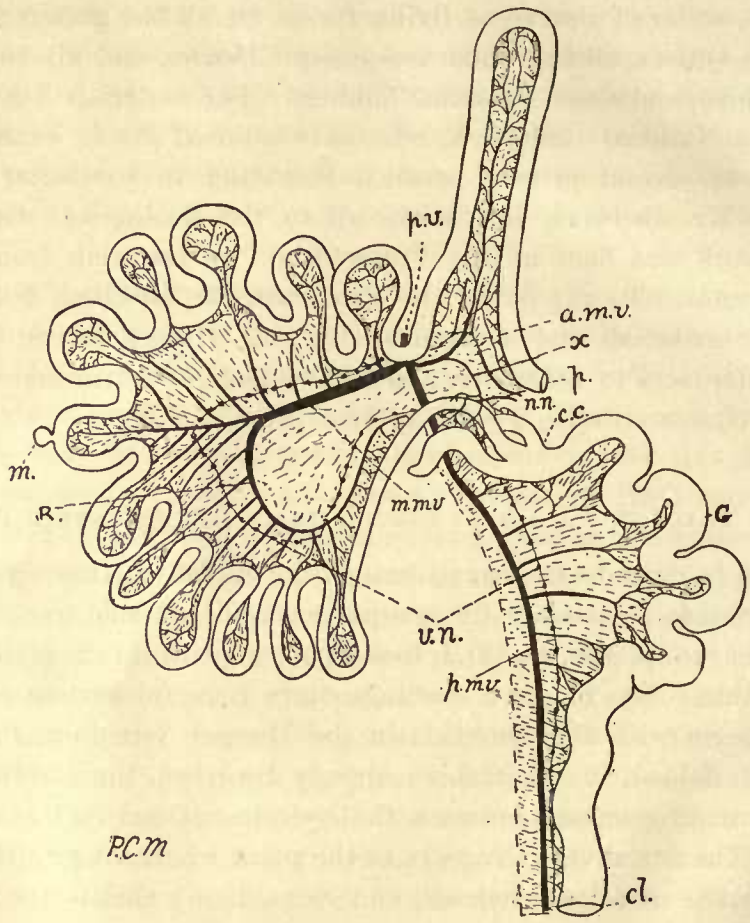
this memoir represent the intestinal tracts of various birds as seen in preparations of the kind described, and therefore illustrate the morphological conditions of the tracts. In 1896 (26) I had already a considerable material, and described and figured some of the chief modifications of the common type displayed in the groups of birds. Since then I have been able to add largely to my material. I have now examined many hundreds of birds, including a number of rare forms, and representing nearly all the important groups of birds. Taking the System given by Dr. Gadow in Bronn's 'Thier-Reich,' vol. vi. part ii. pp. 299–301, as one specially familiar to anatomists, I find that my material includes, so far of course as living forms go, all the groups of Ratites, and, of Carinates, all the Orders, all the Suborders except *Mesites*, and all the Families except Mesitidæ, Galbulidæ, and some Passerine families. For materials I am indebted to the authorities of the National Collection, who have allowed me to examine a number of spirit-specimens, to several private persons, including in particular Mr. C. Hose of Borneo through Mr. Beddard, but above all to the Zoological Society of London. Nearly all the work was done at the Prosectorium on materials from the Gardens or sent to the Prosector. To my friend the Prosector, Mr. Beddard, F.R.S., I am deeply indebted both for materials and assistance. To Prof. Howes, F.R.S., I am indebted for many valuable references to literature, and I have had the advantage of discussing the nomenclature of characters with Prof. Ray Lankester, F.R.S.

The Tract in *Palamedea cornuta* as an Archecentric Type.

It is convenient to describe the conditions of the intestinal tract in one form in some detail so as to provide a standard for comparison and to avoid unnecessary repetition. In a former paper (26. p. 138, fig. 2) I took the condition in an embryo of an Argus Pheasant, about thirty days old, as a starting-point; here, for various reasons which will appear later, I begin with the condition in the Horned Screamer, *Palamedea cornuta* (fig. 1). When unfolded, in the fashion already described, the intestinal tract is seen to present three main portions between the pyloric cut end (*p.*) and the cloacal cut extremity (*cl.*). The first division from *p.* to the point where, at *p.v.*, the cut portal vein is represented consists of a long, narrow, and closed loop; this is the duodenal loop of Cuvier: it contains the pancreas between its ascending and descending limbs, and receives the ducts of the pancreas and liver. It always in the undisturbed condition lies bent backwards towards the cloaca, ventrad of all the other loops, and is therefore the first portion of the gut to be seen when the abdomen is opened from the ventral surface in the usual fashion. Its ascending and descending limbs are held together by a narrow outgrowth of the mesentery. The mesentery, after leaving the duodenum, expands into a large, nearly circular fold, at the circumference of which, from the end of the duodenum to *c.c.*, the point of insertion of the cæca, is suspended the great portion of the intestine. About the middle of this portion is situated Meckel's Diverticulum (*m.*), which is well known to be a relic of the embryonic stalk of the yolk-sac (*cf.* 26. fig. 2). This portion I name Meckel's Tract, as it carries Meckel's diverticulum. In *Palamedea* it presents a number of minor, simple corrugations, but in more specialized forms the loops present extremely definite and well-marked types of divergence from

this simple condition. Cuvier (5) divides this median portion into an "*Anse moyenne*," extending from the duodenum to Meckel's diverticulum, and an "*Anse colique*," from the diverticulum to the insertion of the cæca. The examination of a larger number of types, however, shows that although the remains of the yolk-sac when present give a point of orientation, still there is not a natural point of division between the loops at the insertion of the yolk rudiment, which, indeed, most frequently lies at the summit of a minor loop. Moreover, the adjective "colic" rightly belongs to a lower

Fig. 1.



Intestinal Tract of *Palamedea cornuta*. From *p.* to *p.v.* is the Duodenum; from *p.v.* to *c.c.*, the insertion of the cæca, is Meckel's Tract; from *c.c.* to *cl.* is the Large Intestine, here convoluted in its anterior portion, *G* *.

p.v., portal vein; *a.m.v.*, anterior mesenteric or duodenal vein; *m.m.v.*, middle mesenteric vein; *p.m.v.*, posterior mesenteric or rectal vein; *x*, "bridging" factor of duodenal vein from cæca; *R*, recurrent factor of middle mesenteric vein; *p.*, pylorus; *m.*, Meckel's diverticulum; *cl.*, cloaca; *n.n.*, nerves entering mesentery; *v.n.*, "visceral nerve," ganglionated chain of the autonomic nervous system.

portion of the gut, as the colon of mammalian anatomy, from which the name was taken, is not the portion on which Meckel's diverticulum may be found. It is worth noting, however, that very often a change in the colour of the gut, denoting a phase in the digestive processes, begins just distal to the diverticulum. Meckel's tract, in the

* Since the large intestine is, with few exceptions, short in birds and but rarely differentiated into anything comparable to a colon, it will be simpler to refer to it in this Memoir as *rectum*.

undisturbed condition, lies very irregularly folded, or rather crumpled-up dorsad of the duodenum and ventrad of the rectum. Its posterior portion is nearly straight, an extremely common state. The rectum or third portion of the gut extends from *c.c.*, the end of Meckel's tract, to *cl.*, where it enters the cloaca. It is suspended by a long straight piece of mesentery continuous with the mesentery of Meckel's tract. In the figure, as in some of the later cases, the rectum is represented as folded over to the right so that the cut edge of the mesentery from the duodenum to the cloaca is twisted on itself at the point where the cæca are inserted. The large intestine in most birds is extremely short; its condition in *Palamedea*, where it is convoluted and might be divided into colon and rectum, is unusual. The calibre of the gut varies: the condition seen in *Palamedea* is very usual; the duodenum is wider than Meckel's tract, and the rectum is wider than either that or the duodenum. The cæca are equal in size and of moderate length, being intermediate between the short thick stumps of Passerines and the extremely long, irregularly dilated pouches of the fowl. The blood-vessels, shown in black in this and the subsequent figures, are the veins. At *p.v.* is represented the cut edge of the main portal vein on its way to break up in the liver; the large factor from the stomach and spleen is not represented, but the three characteristic intestinal factors are figured. These are the *anterior mesenteric* or *duodenal*, draining the duodenum, and at *x* receiving a small factor which runs forwards from the cæca and posterior part of Meckel's tract. The draining of these parts of the intestine by a tributary or tributaries of the duodenal vessel is seen here in a simple form, but, as will be seen later, becomes a peculiar and important structural feature. The second or *middle mesenteric factor* of the portal drains Meckel's tract; its main axis runs from Meckel's diverticulum, but a strong factor, which I call the "recurrent mesenteric," curves round from backwards following the contour of the tract. The *posterior mesenteric*, or *rectal* factor, drains the rectum; in many birds it arises from two factors which run backwards along the ventral surface of the kidneys and join opposite the junction of the rectum and cloaca, entering the rectal mesentery at that point. These three components of the portal correspond to the three main divisions of the intestines—the Duodenum, Meckel's tract, and the Rectum; they meet nearly at the same point, but, in different birds, the order of their joining to form the common portal differs; and, after giving considerable attention to the matter, as I cannot find significance in the order of their junction, I shall not refer to it in this memoir. The arteries of the mesentery are small relatively to the veins; their minor branches follow the minor branches of the veins fairly closely; the main branches arise from the dorsal aorta. The dotted chain marked *v.n.* in the figure is the part of the "autonomic nervous system" which follows the intestine. It is extremely plain in some birds, as in *Palamedea*, where it consists of a ganglionated chain following the general contour of the intestinal loops. The nature of my material has not allowed me to follow it out in the majority of my specimens. To certain general points in relation to it I shall recur later.

Valuation and Nomenclature of Characters.

In the description of the structure of an organ or anatomical part as it occurs in a large series of different forms, it becomes necessary from simple convenience to attempt some kind of valuation according to which the series of facts shall fall into definitely-named groups. When there is attempted the difficult passage from descriptive anatomy to morphology, it is necessary that the valuation and nomenclature should be in relation to the theory of descent with modification. I assume that birds were monophyletic in origin, and that the existing forms have branched out in diverging directions from the ancestral group. The members of this ancestral group, at the stage when they first might have been called birds, possessed an heritage of characters and tendencies, and these characters and tendencies have undergone modifications different in amount and nature in the different groups. The first business is to come to a decision as precise as possible as to the ground-plan, or archetype, the most ancestral condition of the structures under consideration. In the present case, I find that the condition of the gut in *Palamedea* (fig. 1) may be taken (after allowance for its length, as it is a large bird and vegetarian) as representing closely the ancestral type. The form of the gut is extremely simple; it is distinguished from the intestinal tract of reptiles chiefly by the fact that the three divisions—the duodenum, Meckel's tract, and the rectum—are sharply marked off one from the other. Meckel's diverticulum, the morphological median point of Meckel's tract, occurs nearly at the actual median point. The pair of cæca are of moderate length and are functional. The arrangement of the veins is also extremely simple. It will be seen in the systematic part of this memoir that it is not difficult to refer the more complicated types of arrangement of the tract to the condition in *Palamedea*. I propose to call such a condition "archecentric," implying that it represents a primitive, ancestral, or central condition, from which the conditions to be found in the other cases have diverged. It is obvious that the possession by two or more groups of birds of a character in its archecentric form cannot be an indication in itself that these groups are more closely related to one another than they are to groups possessing the character in another form; for if the diagnosis of archecentricity be correct, the condition has been present in all birds, and may be retained by any. For example, I have recently (28, 29) endeavoured to show that the condition in the wing known as diastataxy is archecentric; that is to say, that in the ancestral wing there was a gap in the series of quills proximad of the fourth secondary quill. If that be correct, the fact that two groups of birds possess diastataxic wings is no reason for uniting the groups.

When the ancestral condition is modified, it may be regarded as having moved outwards along some radius from the archecentric position. Such modified conditions I propose to call "apocentric." Again, it must be obvious that the mere apocentricity of a character can be no guide to the affinities of its possessor. For instance, in the work on the wing of birds, to which I have already referred, I tried to show that the condition of the wing known as eutaxic is apocentric; that is to say, that it is a modification of the archecentric condition, which in this matter is the condition termed diastataxic. Before deciding as to the value of eutaxy in a natural classification, it would be necessary

to decide whether the modification of the archecentric condition were a simple change that we might expect to occur in independent cases, or if it involved intricate and precisely combined anatomical changes that we could not expect to occur twice independently. In fact, having come to the conclusion that a character is apocentric, we must pass on to consideration of the problem whether or no the apocentricity be *uniradial* or *multiradial*. In the case of eutaxy I came to the conclusion that it was the result of a simple closing of the quill series, which might have occurred repeatedly, and probably did occur repeatedly, and that therefore it was an instance of what I call here "multiradial apocentricity." Similar and common multiradial apocentricities, from which no direct argument of kinship is to be drawn, are to be found in conditions depending on the degeneration of a structure. If, for example, the presence of basipterygoid processes be archecentric in birds, their absence is a multiradial apocentricity from which no direct argument as to affinity may be drawn.

These multiradial apocentricities lie at the root of many of the phenomena that have been grouped under the designation "Convergence." Especially in the case of manifest adaptations, organs belonging to creatures very far apart genealogically may be moulded into conditions which are extremely alike. It is of course the business of science to distinguish the dissimilarities of genetic material under the similarities which are the results of adaptation to a common purpose. Ray Lankester (20) long ago designated such parallelism of modifications as Homoplasy; and there seems little reason to doubt that a careful discrimination and elimination of the homoplastic features in so-called cases of convergence would leave a residuum plainly showing the genetic differences, and dispelling many of the hazy ideas which have been grouped round the word convergence. In the case of the alimentary canal, it is easy to set apart certain modifications as directly adaptive, and as therefore of no value when the character of an organ is being considered as an indication of the natural affinities of its possessor. For the apocentric modifications in question have been produced in different mammals as well as in different birds, and hence in birds these modifications must be multiradial and no indication of relationship. I find in the intestinal tract of birds four plain homoplasies—that is to say, four kinds of adaptation which produce multiradial apocentricity; three of these are well known, the fourth, so far as I am aware, has not yet been pointed out. That all four occur among mammals as well as among birds is a fortunate circumstance that definitely proves their multiradial character.

First Homoplastic Modification. Lengthening of the gut in graminiferous and grazing birds.—This feature has been well known for long, and is in obvious relation to the circumstance that the nutrient constituents of the food of such creatures are in a form difficult to digest and in intimate admixture with a large bulk of indigestible material. Much time and much surface are required for digestion and absorption, and these are provided for by increase in length of the gut.

Second Homoplastic Modification. Lengthening of the gut with thickening of its wall and relative decrease of its calibre in piscivorous birds.—The very long and narrow gut with stout walls is known in birds and mammals. The small calibre and thick wall are doubtless a protection against mechanical injury by sharp bones. The extreme

length is at first surprising, as we are accustomed to regard fish as being readily digestible. However, a bird does not eat fish carefully with a knife and fork, but bolts it whole. Dr. Hutchison, a recent writer on foods (17), calls attention to the large amount of waste matter in uncooked fish, amounting to fully seventy per cent.

Third Homoplastic Modification. Shortening of the gut in frugivorous birds.—The tendency of the gut in birds and mammals which live chiefly on fruit to be very short, thin-walled, and wide is well known, and is in direct relation to two simple physiological factors. The nutritious substances in fruits are in a form which renders them capable of rapid and fairly complete absorption, and the organic salts present stimulate osmosis. The ease of absorption makes a relatively large surface unnecessary, and the large calibre of the gut not only diminishes the outflow from the blood caused by the presence of organic salts, but it decreases the danger of violent purging. The vigour of peristalsis in birds is remarkable; when the duodenum of a pigeon contracts it becomes as hard and tense as a piece of cartilage.

Fourth Homoplastic Modification. Increase of length rather than of calibre in large birds.—I am not aware that the circumstance has been noticed, but it is the case that in large birds and large mammals the gut tends to be relatively longer than in small birds and small mammals. The explanation, I think, is simple. In the course of phylogenetic increase in size, the various organs increase in size correlatively with the whole, but in a mode corresponding to their functions. The first business of the intestine is to present to the food-absorbing surface sufficient to supply the needs of the whole body. As the calibre of a tube increases, its capacity increases more rapidly than its surface; it follows that to preserve the same relation of intestinal surface to intestinal capacity, the length of the gut must increase more than the calibre in the course of phylogenetic increase of size. It is interesting to notice that the cæca and the rectum, two portions of the gut of birds in which absorption is not so great, increase in large birds almost as much in calibre as in length, so that very frequently large birds display cæca and rectum which appear to be much wider than the anterior portions of the intestinal tract. It is plain, from what has been said, that no genetic significance is to be attached to such conditions, which are merely a result of the homoplastic modification due to large size of the whole creature.

There is no need to discuss here the difficult problems as to the mode of origin of homoplastic resemblances. To some extent they may be freshly epigenetic in each generation; and Gadow's (12) investigations into the lengths of the gut in chicks as compared with adults would seem to show that there is much to be learned as to the occurrence of changes of form and length in direct relation to changes of diet. They may have come about by a slow selection of strains with genetic variations in the direction of increased length or of capacity to acquire increased length at the stimulation of food; or, on neo-Lamarckian principles, they may be the summations of the effect of stimulations in a series of generations. It is enough to state that these homoplastic modifications must be allowed for or "corrected" before the drawing of conclusions as to relationship. Before the condition of an intestinal tract can be taken as affording a clue to the affinities of its possessor, it must, in imagination, be shortened, in the case

of a large bird, or a graminiferous or piscivorous bird, or lengthened in the case of a frugivorous bird. In more general terms: when we are satisfied that an apocentricity is multiradial, as is certainly the case when it is homoplastic, we must neglect it when we are dealing with the one character as a guide to affinity (fig. 2).

Fig. 2.

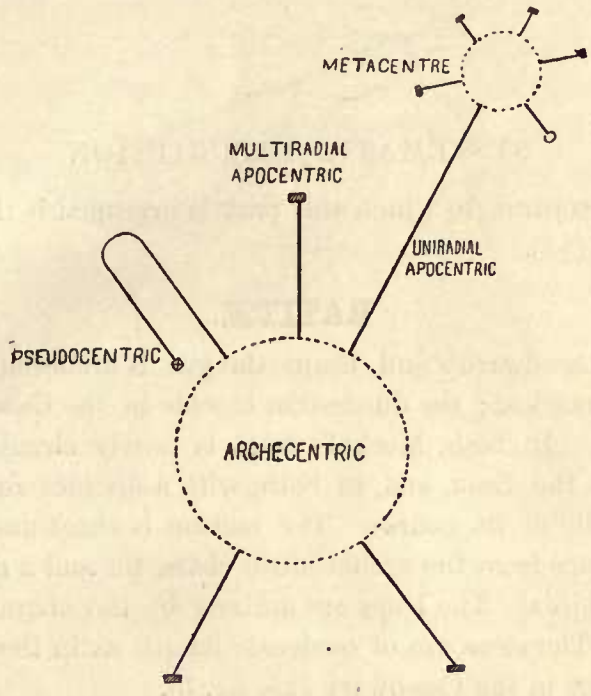


Diagram to explain Nomenclature of Characters.

A complex apocentric modification of a kind that we cannot well expect to be repeated independently, and that may be designated as uniradial, must be the most certain guide to affinity. It happens frequently that such a modification forms a new centre around which new diverging modifications are produced. Such a centre I propose to call a "Metacentre," borrowing a convenient term from physics. It is obvious that the condition of a character, archecentric so far as the whole group of birds is concerned, is metacentric with regard to the common stock of birds and reptiles, and that the transformation of an apocentric character into a metacentre is simply an event in the general process of divergent evolution. I justify the nomenclature which I am proposing largely because it brings the valuation and classification of characters into line with our conception of the general process of evolution.

Finally, there remains to distinguish a form of apocentricity extremely common and often perplexing. Such conditions are marked by an apparent simplicity that, however, reveals its secondary nature by some small and apparently meaningless complexity. Such a condition that mimics the archecentric condition but which can be distinguished from it, I propose to call "Pseudocentric."

I trust that the ideas underlying this attempt at the valuation and nomenclature of characters, so far from being novel, are merely a codification of criteria in common

employment among naturalists. I find, however, that such a codification was necessary when I tried to arrange systematically the modifications of the characters with which this memoir deals. So far as I have used them in my own work, I have found them illuminating, and I offer them in the conviction that the rigorous discipline which their use entails would prove of general utility.

SYSTEMATIC DESCRIPTION.

The Classification according to which this part is arranged is that given by Gadow in Bronn's 'Thier-Reich' (12).

RATITÆ.

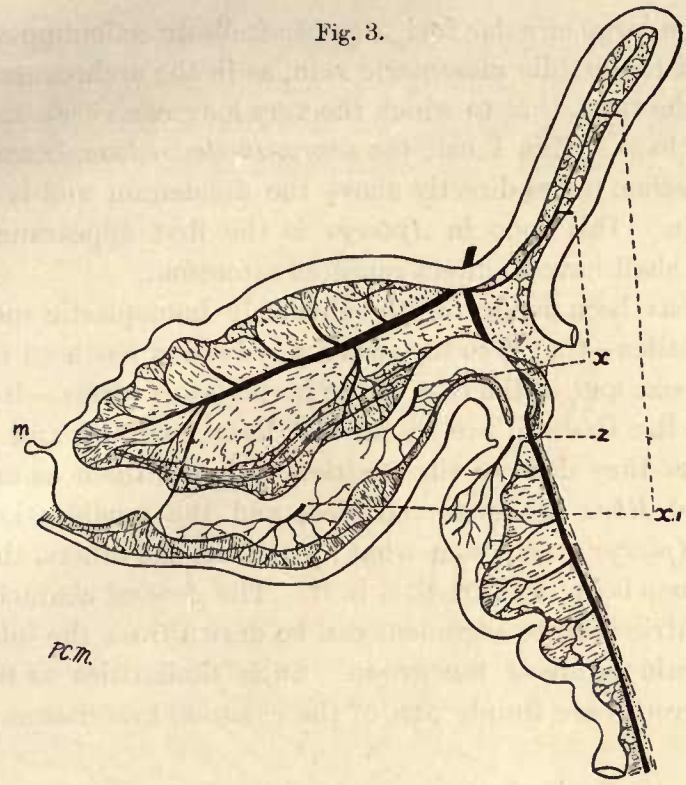
Casuarii.—In the Cassowaries and Emus the gut is archecentric in character. The three regions are well marked; the duodenum is wide in the Cassowary, but longer and narrower in the Emu. In both, Meckel's tract is nearly circular in form, with well-marked minor folds in the Emu, and, in both, with a distinct relic of Meckel's diverticulum about the middle of its course. The rectum is short and nearly straight, this being the only divergence from the archecentric character and a divergence displayed by the vast majority of birds. The loops are drained by the characteristic factors of the common portal vein. The cæca are of moderate length as in the type. I have already given a figure of the gut in the Cassowary (26. fig. 3).

Struthiones.—The Ostrich (26. fig. 4) is also markedly archecentric. The divergences from the archecentric type are very slight: the duodenum is rather longer and has a minor loop situated on its distal limb; the rectum is enormously long, being in fact at least equal in length to the first two portions together; the cæca also are extremely long. The factor of the duodenal vein from the cæca comes off rather further from the main stem of the portal vein, and instead of running forwards within the mesentery, it leaves the mesentery and in consequence must be separated when the intestine is unfolded: in this condition it forms what I call a "bridging" vein.

Rheæ.—In *Rhea americana* (fig. 3) the gut is archecentric, and indeed can be distinguished from that of *Palamedea* only in two points. Meckel's tract is somewhat elongated, Meckel's diverticulum lying at its apex, and the cæca are much longer relatively. The region of the cæca is drained by two "bridging" factors of the duodenal vein which leave the mesentery and have to be divided when the duodenum is unfolded outwards. A slight peculiarity that I have noticed in no other bird is that a factor of the splenic vein (fig. 3, *z*) drains the proximal portion of the rectum.

Apteryges.—The gut of the *Apteryx* (fig. 4), while markedly archecentric, is the most modified of those among Struthious birds. The duodenum and the rectum conform to type, save that the rectum is relatively shorter and is straight. The greater portion of

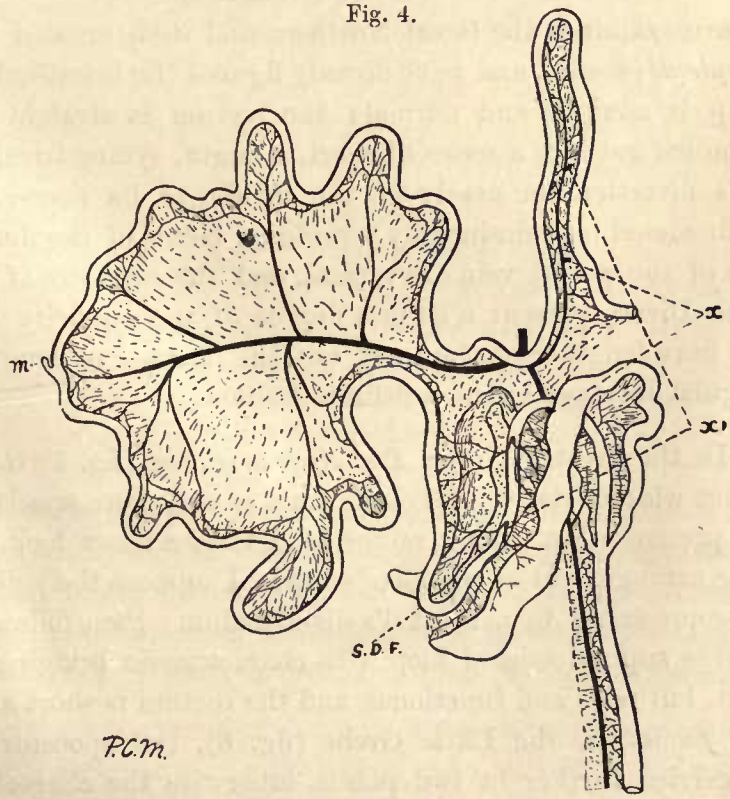
Fig. 3.



Intestinal Tract of *Rhea americana*.

x, *x'*, cut ends of "bridging" factors of duodenal vein, draining the distal portion of Meckel's tract and one cæcum; *z*, factor of the splenic vein. General description as in legend of figure 1.

Fig. 4.



Intestinal Tract of *Apteryx Mantelli*.

For explanation, see legends of figs. 1 and 3. *S.D.F.*, apex of supra-duodenal loop.

Meckel's tract forms a large circular fold with Meckel's diverticulum at its central point, opposite the origin of the middle mesenteric vein, as in the archecentric type. But the posterior portion of the tract, that to which the very long cæca are attached, is specialized into a distinct minor loop. This I call the *supra-duodenal loop*, because, in the natural condition of the intestine, it lies directly above the duodenum and is drained by factors of the duodenal vein. This loop in *Apteryx* is the first appearance of a specialized structure to which I shall have to direct repeated attention.

When correction has been made for the obviously homoplastic modifications in the intestinal tract of Ratites—that is to say, when a reduction has been made in the case of the larger forms for size and in the case of the herbivorous forms,—it is plain that while all are archecentric, the Casuarii are by far the least modified, and that in this as in many other characters they deserve the position assigned them as extremely primitive types. *Struthio* and *Rhea* are more modified, and the modification is in the same direction in each. *Apteryx* stands somewhat apart from the others, the specialization of the supra-duodenal loop being well marked in it. The general character in all, however, is so plainly archecentric that no argument can be drawn from the intestinal tract for or against the polyphyletic nature of the group. Such similarities as they present to one another or to other groups are simply part of the common inheritance of all birds.

CARINATÆ.

COLYMBIFORMES.

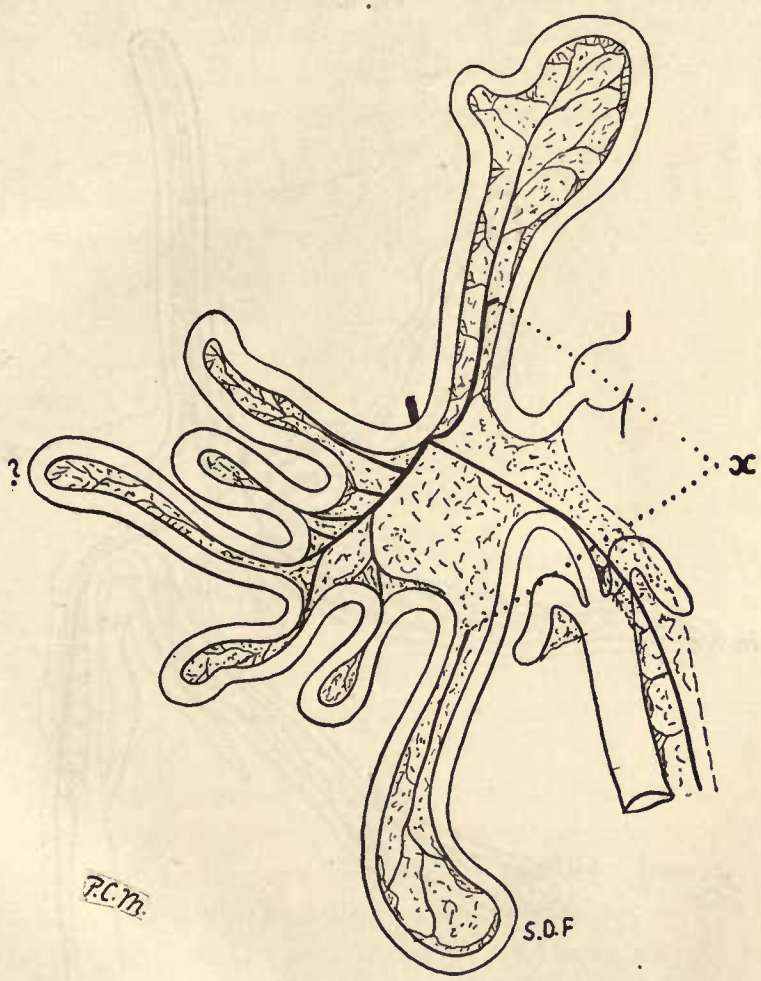
Colymbi.—I have examined the Great Northern and Red-throated Divers (*Colymbus glacialis* and *C. septentrionalis*), and have already figured the intestinal tract (26. fig. 5). The duodenal loop is straight and normal; the rectum is straight and very short. Meckel's tract is pulled out into a series of short, straight, symmetrically arranged loops with the Meckel's diverticulum nearly at the middle of its course, and with a well specialized supra-duodenal loop drained by a bridging factor of the duodenal vein. The three main factors of the portal vein are typical, and the cæca are of moderate length. It is clear that the Divers present a certain degree of apocentricity in the gut. The fish-eating habits have lengthened the tract, but the increase of length takes place not by a series of irregular loopings but in a definite fashion.

Podicipedes.—In the Crested Grebe, *Podicipes cristatus* (fig. 5) the duodenum is a large loop somewhat wider distally. Meckel's tract is still more specialized than that of the Colymbi. It presents first a long minor loop, then a short loop, then a long loop, on which, from the arrangement of the blood-vessels, I suppose the yolk-sac to have lain, although it is not represented by a Meckel's diverticulum; then follow two short loops, and then a very large supra-duodenal loop with characteristic bridging vein. The cæca are relatively short, but wide and functional, and the rectum is short and wide.

In *Tachybaptes fluviatilis*, the Little Grebe (fig. 6), the apocentricity seen in the Crested Grebe is carried further in two points, otherwise the character of the tract is

similar. Two of the minor loops of Meckel's tract are carried out to a great length, one of them bearing Meckel's diverticulum at its summit; the cæca are relatively much longer, and the supra-duodenal loop is still more highly specialized. The Podicipedes, then, present an apocentricity rather more marked than that of the Divers.

Fig. 5.



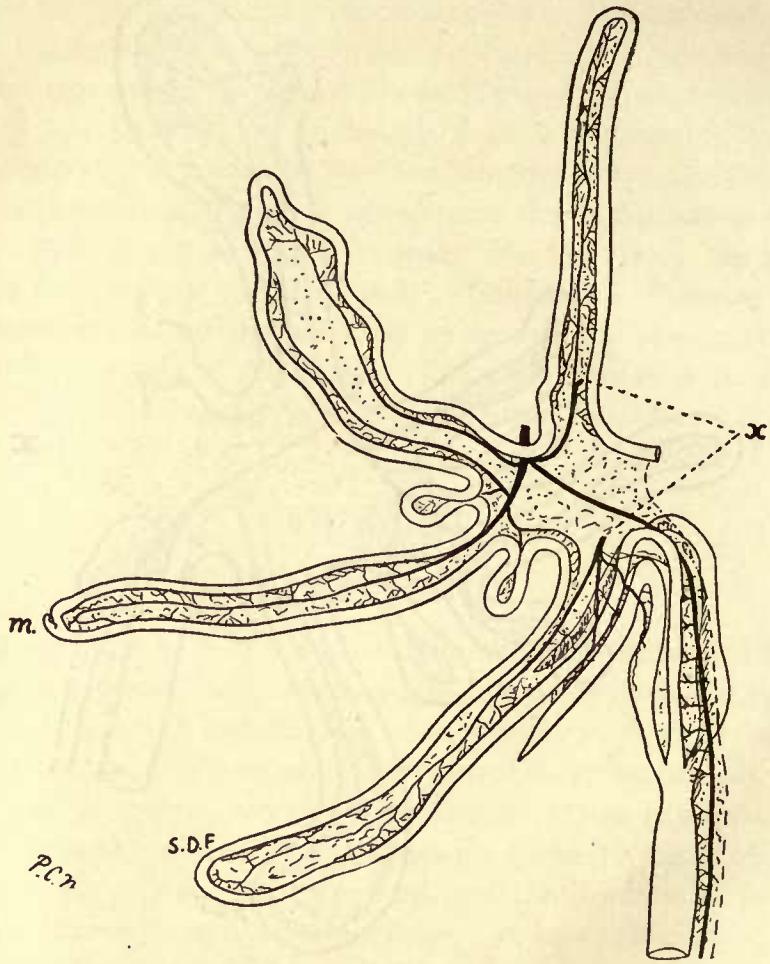
Intestinal Tract of *Podicipes cristatus*.
x, bridging factor of the duodenal vein draining *S.D.F.*, the supra-duodenal loop; ?, probable position of Meckel's diverticulum.

When allowance has been made for the size and piscivorous habits of the Colymbiform birds, it appears that while the character of the gut has moved outwards from the archecentric position chiefly in the direction of the formation of specialized straight loops (according to Gadow's nomenclature, the folding is orthocœlous), the apocentricity is not great, and is certainly not of such a uniradial character as to associate them closely with any other group.

SPHENISCIFORMES.

I have already described and figured the intestinal tract of *Eudyptes* (26. fig. 6). I now am able to add descriptions of the condition in *Spheniscus demersus* (fig. 7) and *Aptenodytes Pennanti* (fig. 8). In all three the intestine is extremely long and of

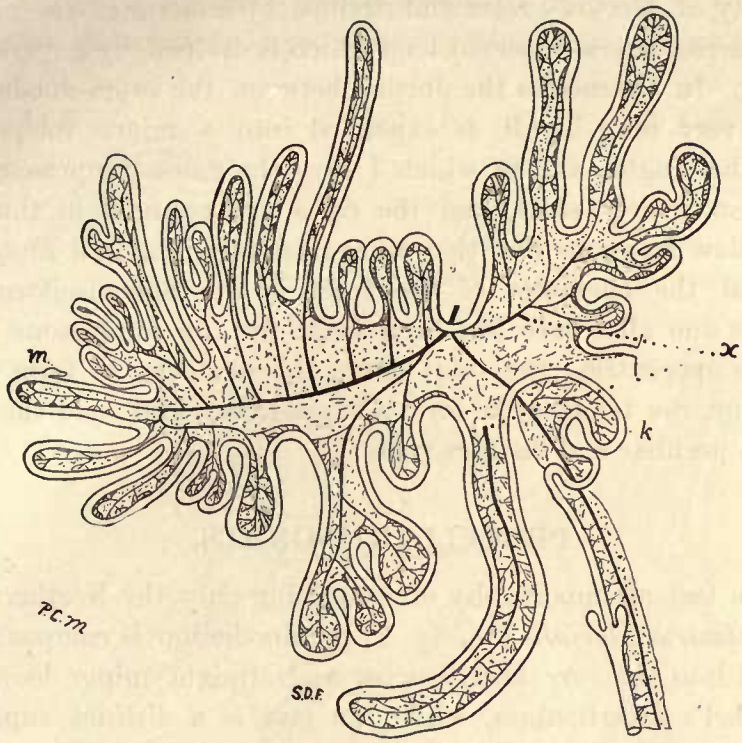
Fig. 6.



Intestinal Tract of *Tachybaptes fluviatilis*. Lettering as before.

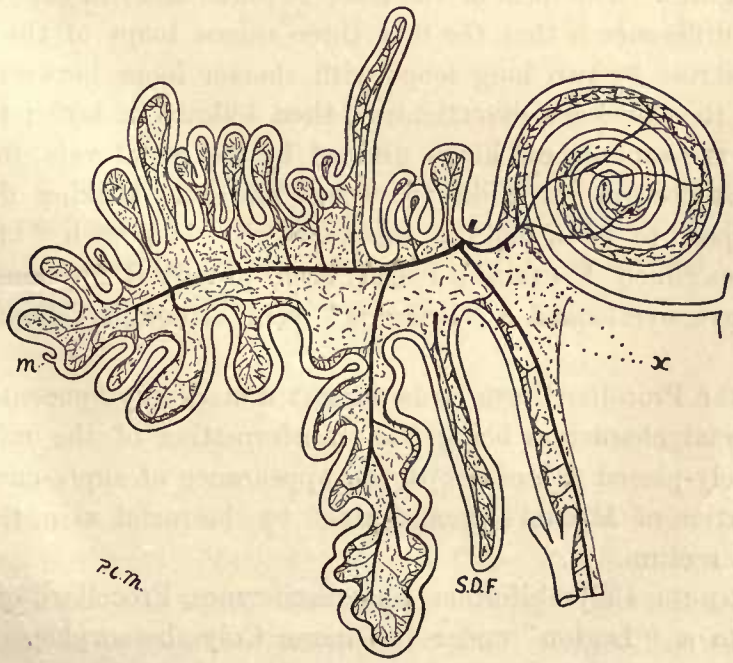
slender calibre with firm walls; in the figures the actual length is somewhat underestimated, so that the "correction" for piscivorous diet has been made partially. The three portions of the tract are well marked and are each drained by a characteristic factor of the portal vein. The duodenum is extremely long; it is thrown into a complicated set of minor loops resembling the condition in the fish-eating Eagles, in *Eudyptes* and *Spheniscus*; in *Aptenodytes* it forms a loosely rolled spiral, a mode of packing increased length that is not at all uncommon among birds and that must be regarded as a multiradial apocentricity. Meckel's tract in all three is moderately specialized; Meckel's diverticulum lies nearly at the middle of its course, but there is a strong tendency for the numerous minor loops to be extended in length or expanded

Fig. 7.



Intestinal Tract of *Spheniscus demersus*.
k, supra-cæcal kink; other lettering as before.

Fig. 8.



Intestinal Tract of *Aptenodytes Pennanti*. Lettering as before.

into minor systems. Of these, two are well-marked in all: a very large loop towards the distal extremity of Meckel's tract and drained by a factor of the middle mesenteric vein, and a long narrow supra-duodenal loop which is drained by a "bridging" factor of the duodenal vein. In *Spheniscus* the portion between the supra-duodenal loop and the rectum, which is very long in all, is expanded into a minor fold, an arrangement characteristic of the Eagles, and to which I give the name "supra-cæcal kink." The rectum in all is extremely short, and the cæca are vestigial in those that I have examined, but Gadow mentions that they were relatively long in a *Eudyptes*.

It is plain that the character of the tract in the Sphenisciformes is markedly apocentric. When due allowance has been made for the piscivorous lengthening, the form still remains apocentric: the short cæca, the tendency to form minor loops, the supra-duodenal loop, the tendency to form a supra-cæcal kink, and the extremely short rectum make up a peculiar and distinct type.

PROCELLARIIFORMES.

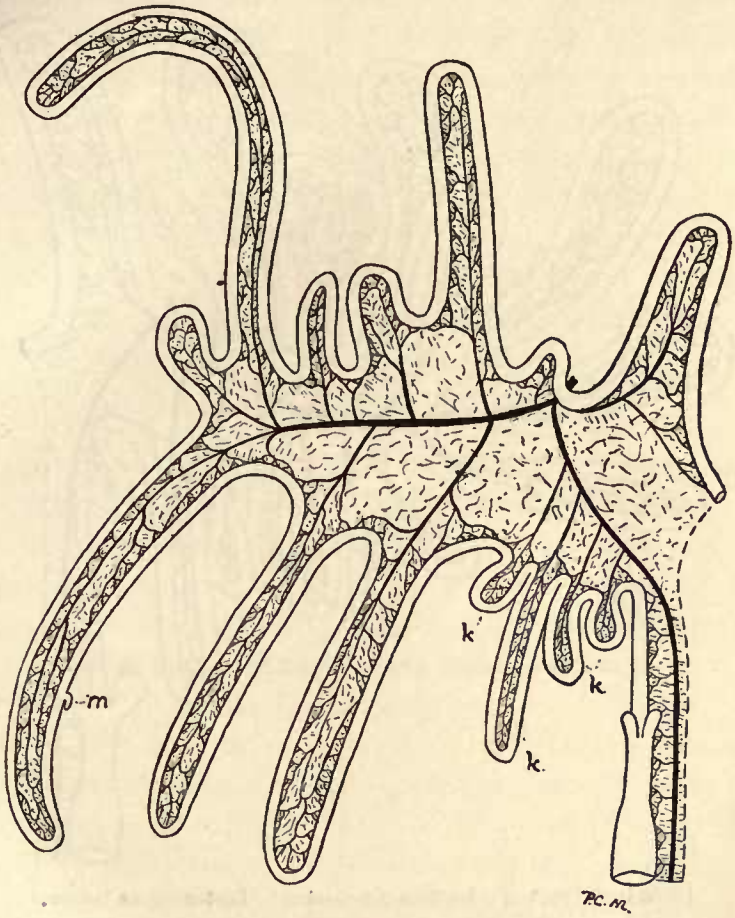
Of these I have had an opportunity of examining only the Northern Petrel and the Albatross. In *Fulmarus glacialis* (26. fig. 7) the duodenum is compound, and Meckel's tract is expanded into six very long, narrow and straight minor loops, the fourth of which bears Meckel's diverticulum, while the last is a distinct supra-duodenal loop drained by a "bridging" vein. The terminal portion of Meckel's tract is long, thrown into supra-cæcal kinks as in *Spheniscus* and the Eagles, and is drained by the posterior mesenteric vein. The cæca are vestigial, and the rectum is extremely short. In the Albatross, *Diomedea exulans* (fig. 9), the duodenum is simple, and Meckel's tract is drawn out into a series of extremely long narrow loops (the length of these is underestimated in the figure). The form of the tract is much alike in the Albatross and the Petrel; the chief difference is that the first three minor loops of the Petrel are represented in the Albatross by two long loops with shorter loops between them. A very long loop bearing the Meckel's diverticulum then follows in both; the lower portion of Meckel's tract, the supra-cæcal kinks drained by the rectal vein, the vestigial cæca, and the very short rectum are alike in each. The only striking difference is that there does not appear to be a definite supra-duodenal loop with "bridging" vein in *Diomedea*. The specimen I examined had been preserved for long in spirit, and possibly I may have overlooked a "bridging" vein, although I examined the region minutely for it.

It is plain that the Procellariiform birds present a markedly apocentric type of intestinal tract, the special characters being the transformation of the middle loop into a number of definitely-placed minor loops, the appearance of supra-cæcal kinks on the large posterior portion of Meckel's tract, drained by the rectal vein, the vestigial cæca, and the very short rectum.

Gadow (12) unites the Colymbiformes, Sphenisciformes, Procellariiformes, and extinct Ichthyornithes into a "Legion" under the name Colymbomorphæ. Concerning the intestinal tract of the extinct forms we have no information. The others have all moved out from the archecentric condition. Their apocentricity is first a relatively increased

length in association with the nature of their food, and certainly multiradial; second, Meckel's tract in all, while remaining nearly symmetrical, tends to be drawn out into a series of long, narrow, and straight loops, a feature which may give some clue to affinity;

Fig. 9.



Intestinal Tract of *Diomedea exulans*. Lettering as before.

third, the rectum in all is very short. The Colymbiformes are least modified; the Penguins and Petrels are more modified, the two latter showing degeneration of the cæca and certain peculiarities in the posterior portion of Meckel's tract, peculiarities repeated in Steganopodes and Falconiformes.

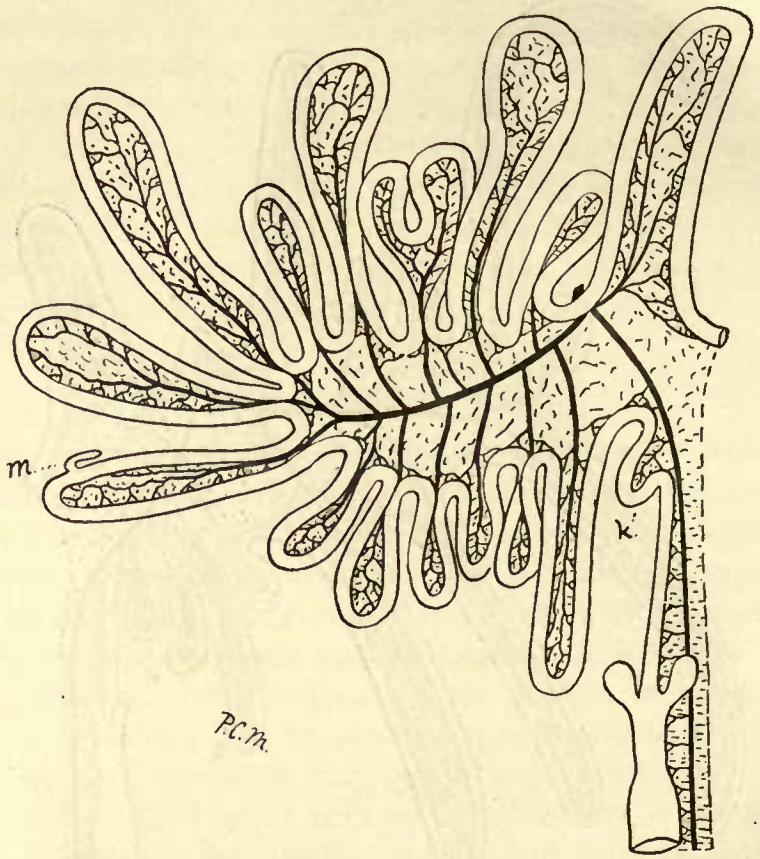
CICONIIFORMES.

STEGANOPODES.

(1) PHAETHONTIDÆ.—*Phaethon* (fig. 10) displays a simple form of alimentary tract. The duodenal loop is simple; Meckel's tract is thrown into a series of narrow, minor loops, some of which are slightly complicated by folding. Meckel's diverticulum occurs on one of the minor loops rather more near the distal end of the tract. The posterior portion has no special supra-duodenal loop, and ends in a portion drained by the rectal or

posterior mesenteric vein and exhibiting a short supra-cæcal kink. The cæca are reduced, but not to the same extent as in other Steganopodes except the Pelicans. The rectum is extremely short. The three factors of the portal vein are of diagrammatic simplicity.

Fig. 10.

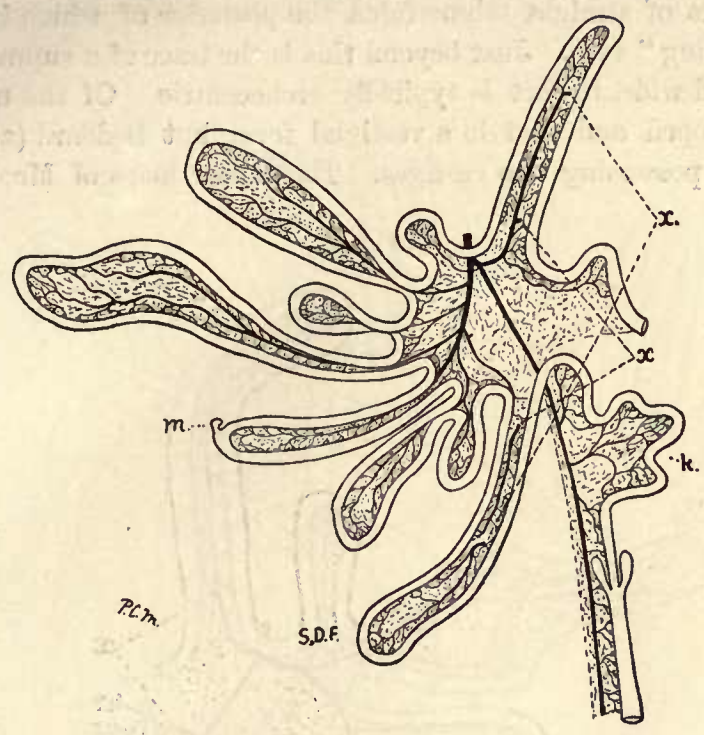


Intestinal Tract of *Phaethon flavirostris*. Lettering as before.

(2) Sulidæ.—In *Sula bassana* (fig. 11) the apocentricity of *Phaethon* is carried further. The general arrangement is similar, but the duodenum is longer and is compound; certain of the minor loops of Meckel's tract are longer, especially the last, that forming a characteristic supra-duodenal loop with bridging vein; and the kink on the posterior part of Meckel's tract, that drained by the rectal vein, is larger.

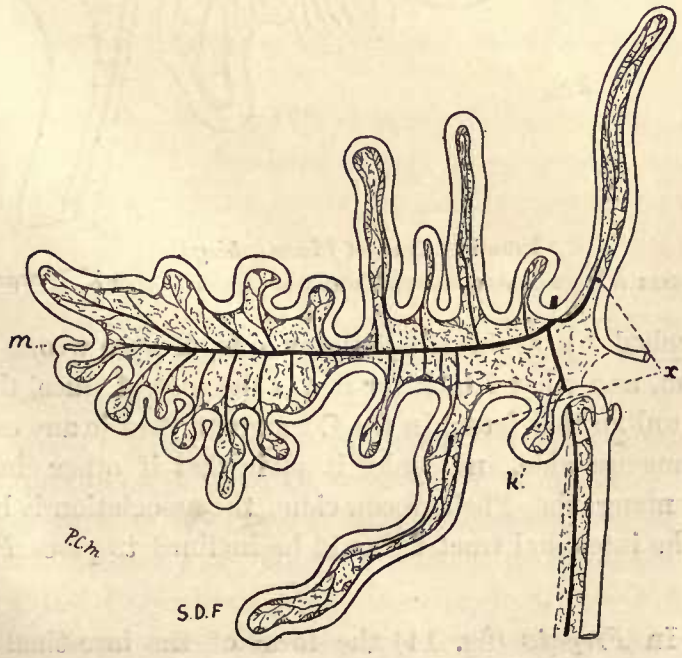
(3) Phalacrocoracidæ.—In *Phalacrocorax carbo* (fig. 12) the duodenum is very long and narrow; Meckel's tract is extremely elongated, in which respect it resembles the condition found in *Platalea* and *Phœnicopterus*, and is symmetrically disposed about the middle mesenteric vein, which in the archecentric fashion runs from a large Meckel's diverticulum. The supra-duodenal loop is long; there is a large supra-cæcal kink supplied by the rectal vein. The cæca are vestigial, and the rectum is relatively longer that in *Phaethon* and *Sula*. In *Plotus-anhinga* (fig. 13) the form of the tract presents marked differences. The duodenum is similar. The anterior portion of Meckel's tract is relatively much shorter, and consists of a single narrow loop, followed by one very

Fig. 11.



Intestinal Tract of *Sula bassana*. Lettering as before.

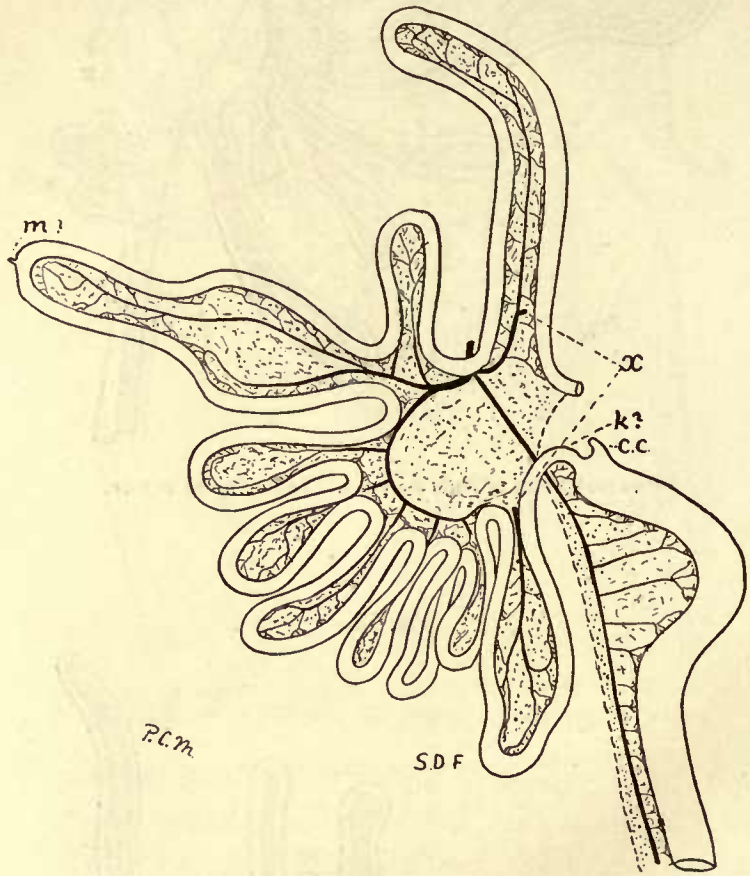
Fig. 12.



Intestinal Tract of *Phalacrocorax carbo*. Lettering as before.

long loop, at the end of which lay what I took to have been a Meckel's diverticulum. Then follows a very long posterior portion, relatively longer than in the diagram, and thrown into a series of straight minor folds, the posterior of which is a supra-duodenal loop with a "bridging" vein. Just beyond this is the trace of a supra-cæcal kink. The rectum is long and wide, in fact is typically archecentric. Of the usual pair of cæca, only one was developed, and that in a vestigial form, but Beddard (2) states that individuals vary, some possessing two vestiges. The minor loops of Meckel's tract show a

Fig. 13.



Intestinal Tract of *Plotus anhinga*.

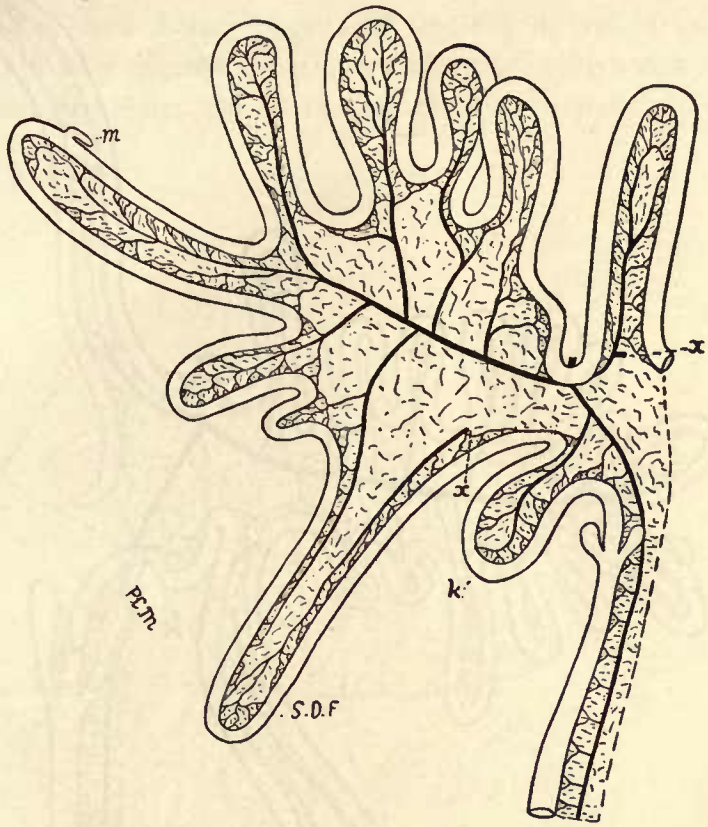
C.C., single colic cæcum; *k* ?, possible supra-cæcal kink; *m* ?, possible position of Meckel's diverticulum.

tendency to be bunched up as in the Pelicans. If I were wrong in my placing of Meckel's diverticulum, and what I took for it was the merest trace, the character of the gut would not be so unlike that found in the Cormorant; but in any event the differences between the two forms are wide, and make it plain that if other characters justify the inclusion of *Plotus* among the Phalacrocoracidæ, the association is by no means close. On the evidence of the intestinal tract I should be inclined to place *Plotus* in a separate family.

(4) Fregatidæ.—In *Fregata* (fig. 14) the form of the intestinal tract is very like that displayed by *Phaethon*. The chief differences are that in *Fregata* the whole tract is

relatively somewhat shorter, the minor expansions of Meckel's tract are less numerous, that bearing Meckel's diverticulum being longer; there is a supra-duodenal loop; the cæca are less developed and the rectum is longer.

Fig. 14.



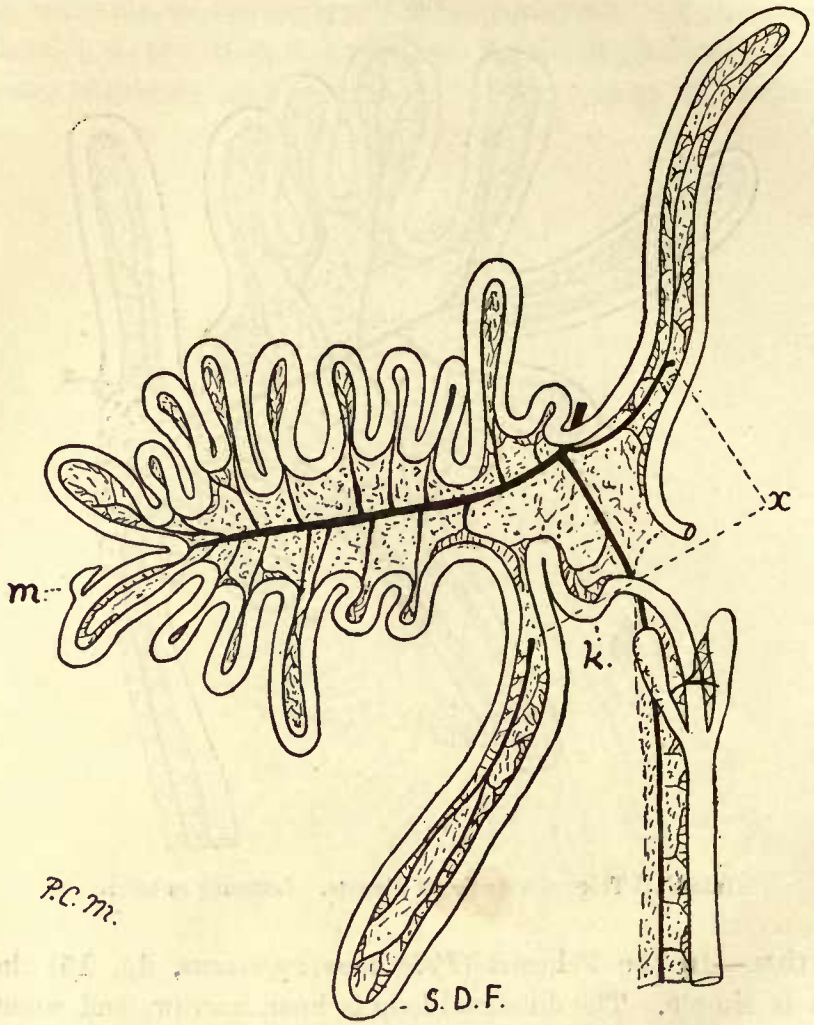
Intestinal Tract of a species of *Fregata*. Lettering as before.

(5) PELECANIDÆ.—In the Pelicans (*Pelecanus rufescens*, fig. 15) the form of the intestinal tract is simple. The duodenal loop is long, narrow, and somewhat twisted; Meckel's tract is nearly symmetrical round the middle mesenteric vein which runs from the position of a large Meckel's diverticulum. There is a well-formed supra-duodenal loop, a supra-cæcal kink drained by the rectal vein, and the cæca are relatively longer than in other Steganopodes. The minor loops of Meckel's tract tend to be bunched up towards the mesenteric vein, a feature that cannot well be represented in a diagram showing the unfolded condition.

The Steganopodes are typically piscivorous, although some of them also take any kind of floating carrion, and in all of them allowance must be made for the piscivorous length of gut. Their apocentricity, apart from such homoplasy, consists, as in the Colymbomorphæ, of a general tendency for Meckel's tract to be expanded into a series of short straight loops. In the Colymbomorphæ, however, these loops frequently increase in length and become reduced in number; in the Steganopodes the tendency is rather for the minor loops to increase in number, and for Meckel's tract to be either bunched up

tightly or much elongated as a whole. These two forms of modification of the middle loop point towards the condition found in many of the Ibididæ such as *Platalea*, and in

Fig. 15.



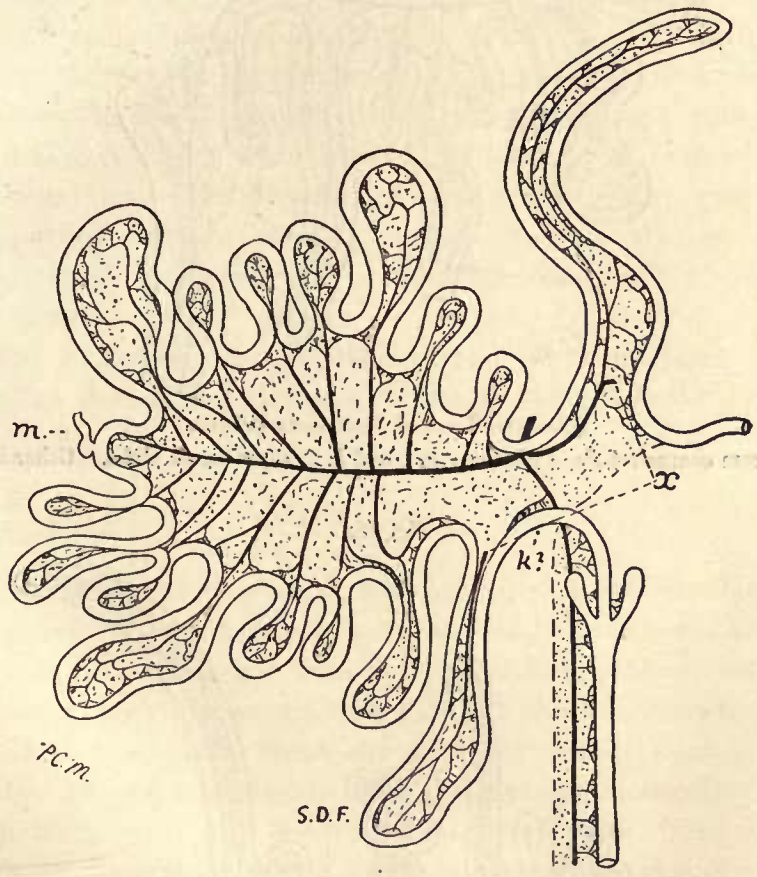
Intestinal Tract of *Pelecanus rufescens*. Lettering as before.

the Flamingoes, where Meckel's tract, in the unfolded condition not unlike that of the Pelican, is in life twisted irregularly into a spiral. I find, then, in the apocentricity of the Steganopod Meckel's tract an underlying resemblance to that of the Colymbomorphæ, as if a metacentric position had been common to all these, but from this metacentre the two sets have diverged in different directions. The reduction of the cæca, the shortening of the rectum, and the formation of minor loops above the cæca, but drained by the posterior mesenteric vein, are common, but not invariable, in the whole set.

ARDEÆ.

(1) SCOPIDÆ.—In *Scopus umbretta* (fig. 16) the duodenum is long and slightly twisted. Meckel's tract is nearly symmetrical, a large Meckel's diverticulum being near the centre of its periphery, and is expanded into a number of wide, irregular, but in the main straight minor loops, the last of these being longer and forming a typical supra-duodenal loop. The rectum is straight, of moderate length, and the pair of cæca are reduced. The veins are typical. A small area supplied by the rectal vein corresponds to the supra-cæcal kink.

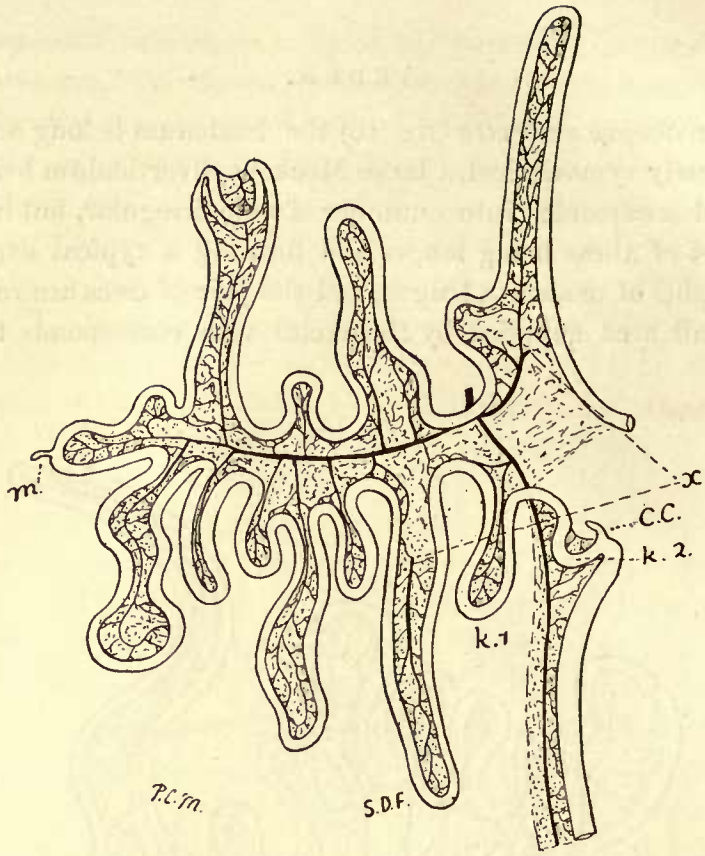
Fig. 16.



Intestinal Tract of *Scopus umbretta*. Lettering as before.

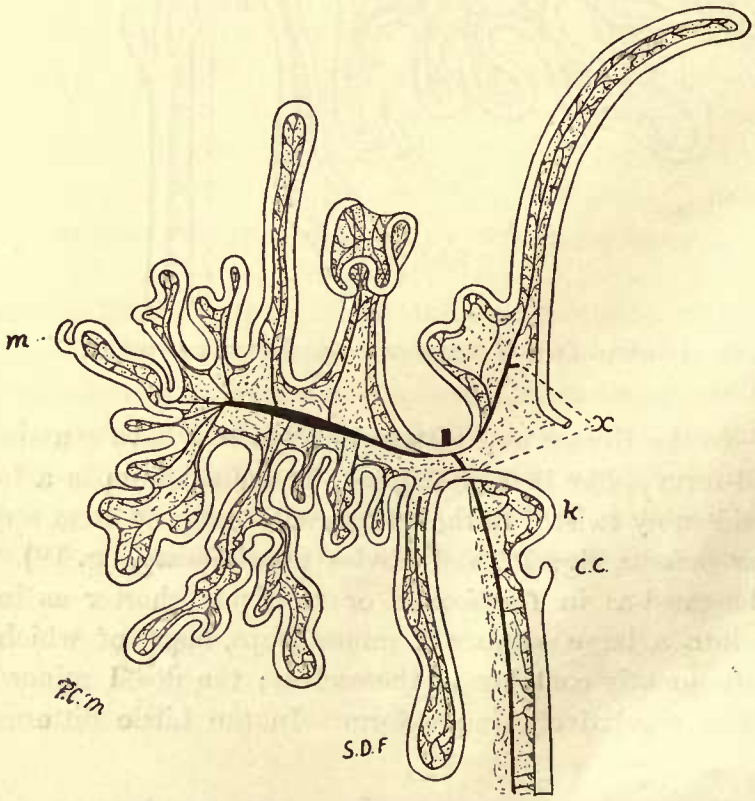
(2) ARDEIDÆ.—In the Herons and Bitterns, of which I have examined a number of species, the ground-form is like that in *Scopus*. The duodenum is a long narrow loop, nearly always considerably twisted to the left, usually more so than appears in the two figures (*Nycticorax griseus*, fig. 17, and *Ardea candidissima*, fig. 18). Meckel's tract may be rather elongated as in *Nycticorax*, or relatively shorter as in *Ardea*. It is always drawn out into a large number of minor loops, many of which are irregularly folded, and not infrequently complex in themselves; the distal minor loops in *Ardea* (fig. 18) show this in a relatively simple form. In the Little Bittern and some other

Fig. 17.



Intestinal Tract of *Nycticorax griseus.*
C.C., single colic cæcum characteristic of Herons; *k.* 1 and *k.* 2, supra-cæcal kinks. Other lettering as before.

Fig. 18.



Intestinal Tract of *Ardea candidissima.* Lettering as before.

Herons the complexity of the minor loops is very great. The penultimate loop of Meckel's tract is always a typical supra-duodenal loop with "bridging" vein, and then follows a supra-cæcal kink. It is typical of the Ardeidæ, as is well known, that one of the two colic cæca be absent, and I have found no exception to this, but Beddard has recorded such a case. The rectum itself is straight, but not very short.

A considerable part of the apocentricity of the intestinal tract in the Ardeæ must be attributed to the fact that they are relatively large birds with a diet consisting chiefly of fish, in consequence of which the gut is very long and narrow. Underlying this is a general resemblance to the ground-form of the Steganopod and Colymbomorph gut, shown in the symmetry of Meckel's tract around the middle mesenteric vein, the persistence of a large Meckel's diverticulum opposite the end of this vein, and the formation of a kink immediately above the colic cæca but supplied by the rectal vein. The special Ardeine features are the elongation of the duodenum as a narrow fold curving to the left; the throwing out of Meckel's tract into minor loops, which, straight in the simpler forms and always folded over simply ("orthocœly" of Gadow), tend to become complicated in themselves. The persistence of only one of the colic cæca is a most peculiar feature, normally absent only in *Scopus*. But the absence occurs not infrequently as an individual abnormality in some other birds, and I shall make further reference to such cases.

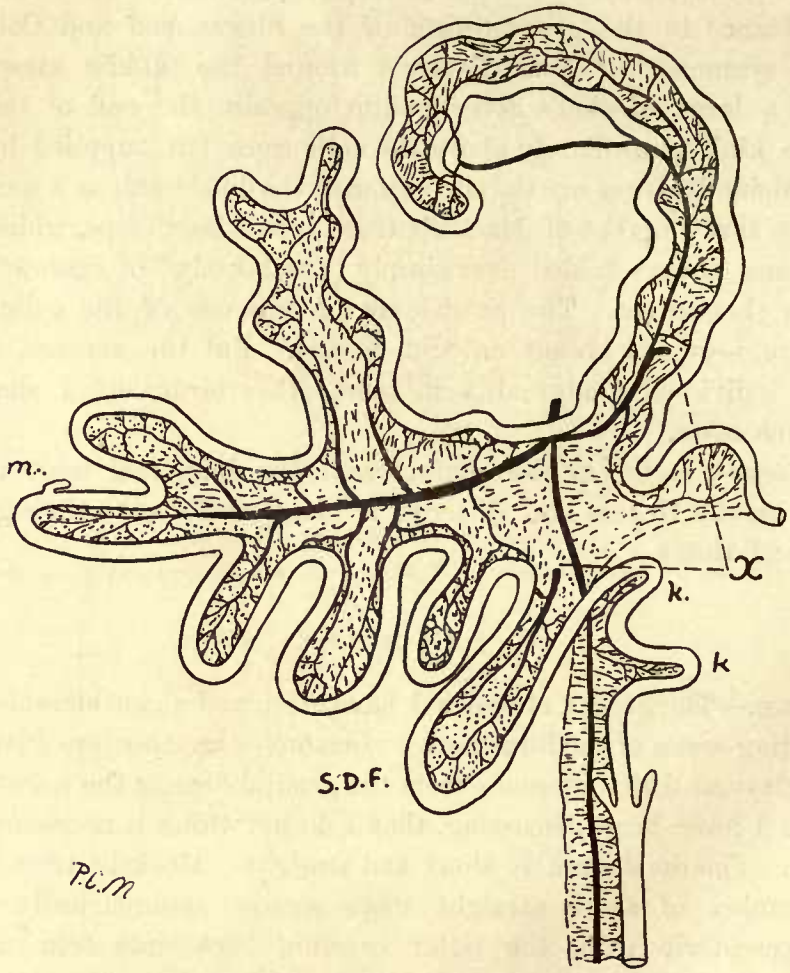
Although *Scopus*, so far as the character of the intestinal tract takes us, is more archecentric than the Herons and Bitterns, it plainly belongs to their group rather than to the Storks and Ibises.

Ciconiæ.

(1) Ciconiidæ.—The Storks, of which I have examined a considerable number, present a most interesting series of modifications. *Anastomus oscitans* (see Plate 21), the Indian Open-bill, displays so little difference from the ground-form of the intestinal tract among the set of birds I have been discussing, that I do not think it necessary to figure it in a separate block. The duodenum is short and straight; Meckel's tract is thrown into a very large number of short straight loops nearly symmetrically disposed around the middle mesenteric vein, the latter running backwards from a large Meckel's diverticulum. There is a very large and complicated supra-duodenal loop, more complicated than in any of the other Storks I have examined, but drained by the usual bridging vein. Above the reduced cæca lies a short kink drained by the rectal vein, and the rectum is straight and of moderate length. In *Pseudotantalus ibis* (fig. 19) the typical Ciconiine apocentricity begins to appear, and this is of the definite type that I call uniradial and am inclined to regard as a sure sign of affinity. The duodenum is enormously long, but the bending which appeared in Herons is here transformed to a spiral twist, represented in the figure as partially uncoiled, with the result that the vein is out of the mesentery. The first minor loop of Meckel's tract is very large and is in itself slightly twisted, and, in the unfolded state, partly rolled in the duodenal spiral. The remaining portion of Meckel's tract consists of a few simple folds, symmetrical

about the middle mesenteric vein, which runs from a Meckel's diverticulum. The distal portion of Meckel's tract forms first a distinct but short supra-duodenal loop, and then a double kink drained by the rectal vein. The cæca are reduced and the rectum is straight and short. *Dissura episcopus*, *Leptoptilus crumeniferus*, *L. argala*, and *Ciconia alba* are practically identical with this condition. In *Ciconia nigra*, which I have already figured (26. fig. 9), the condition is similar, except that the duodenal loop and the first

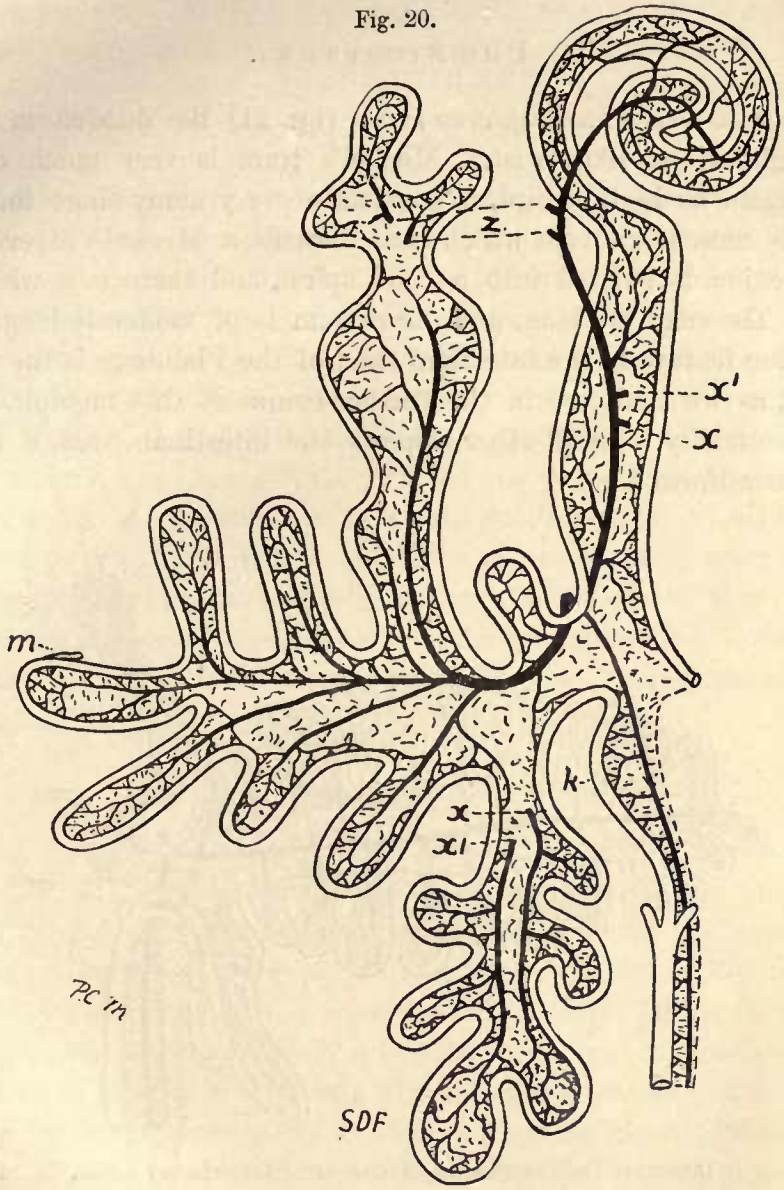
Fig. 19.



Intestinal Tract of *Pseudotantalus ibis*. Lettering as before.

loop of Meckel's tract form more perfect spirals, which in the unfolded condition are rolled together. In *Mycteria americana* (fig. 20) a similar condition exists, but the duodenal spiral and the spiral on the first loop of Meckel's tract are still longer and more complex, and are more intimately rolled together, with the result that certain factors of the duodenal vein run across draining the loop with which the duodenum is associated. These are represented in the figure as divided and the spirals are partly untwisted. Among the Storks, then, we see the interesting state of affairs that the character of the gut, starting from a metacentric position common to a large group of birds, develops along a special radius forming a uniradial line of apocentricity.

Fig. 20.



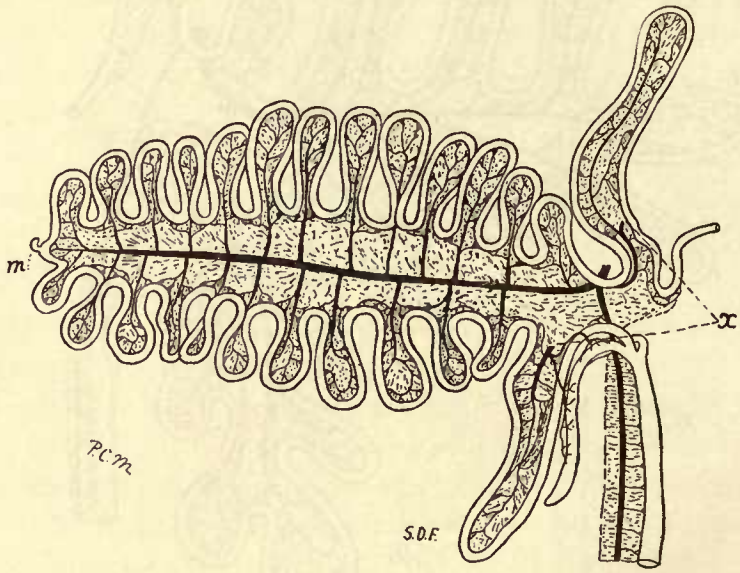
Intestinal Tract of *Mycteria americana*.
z, cut ends of veins from first loop of Meckel's Tract to duodenal vein.

(2) Ibididæ.—I have already figured the intestinal tract of *Platalea leucorodia* (26. fig. 8). It is more archecentric than that found in other Ciconiiform birds. The duodenum is a long narrow loop bent round to the left as in the Herons, but showing no trace of spiral formation. Meckel's tract consists of an elongated system of short loops, symmetrically disposed round the middle mesenteric vein, which runs from a Meckel's diverticulum. This region of the gut is slightly twisted into a spiral in the unfolded condition. The last loop of Meckel's tract forms a simple supra-duodenal fold; the cæca are short, and the rectum is straight but considerably reduced. *Platalea* is certainly low down in the Ciconiiform scale, but none the less it displays the features of the group in a simple form, and is quite different in the character of the gut from *Numenius* (Plate 22), a low Charadriiform bird with which it has been compared.

PHŒNICOPTERI.

PHŒNICOPTERIDÆ.—In *Phœnicopterus ruber* (fig. 21) the duodenum is a simple loop, but with a slight Heron-like twist. Meckel's tract is very much elongated as in *Platalea*, and, again as in that bird, it consists of very many short loops symmetrical about the middle mesenteric vein which runs towards a Meckel's diverticulum. As in *Platalea* this region is twisted into a rude spiral, and there is a well-formed supra-duodenal loop. The cæca are long, and the rectum is of moderate length but straight. The only Anserine feature in the intestinal tract of the Flamingo is the presence of long cæca; and this, as we shall see in the further course of this memoir, is an obviously multiradial apocentricity. In all other respects the intestinal tract of the Flamingo is that of a low Ciconiiform bird.

Fig. 21.



Intestinal Tract of *Phœnicopterus ruber*. Lettering as before.

It is unnecessary to do more than sum up in a few words the conditions of the gut found among the Ciconiiform birds. The ground-form is closely similar to that of the Colymbomorphæ, pointing towards the existence of a common metacentre for all these birds. From this metacentre the groups of Ciconiiformes have diverged in different directions and to different amounts. The Steganopods show a tendency to the bunching up of the loops of Meckel's tract on the axis given by the middle mesenteric vein. The Herons display a tendency to the individual elaboration of the minor loops of Meckel's tract. The Ciconiine birds show the most definitely uniradial apocentricity, consisting of an elaboration and intimate connection between the duodenum and the first loop of Meckel's tract, with a reduction of the posterior portion of Meckel's tract, except the supra-duodenal loop. The Ibididæ, or at least *Platalea*, show a primitive elaboration of Meckel's tract as a whole, and this tendency is carried further in the Flamingoes.

ANSERIFORMES.

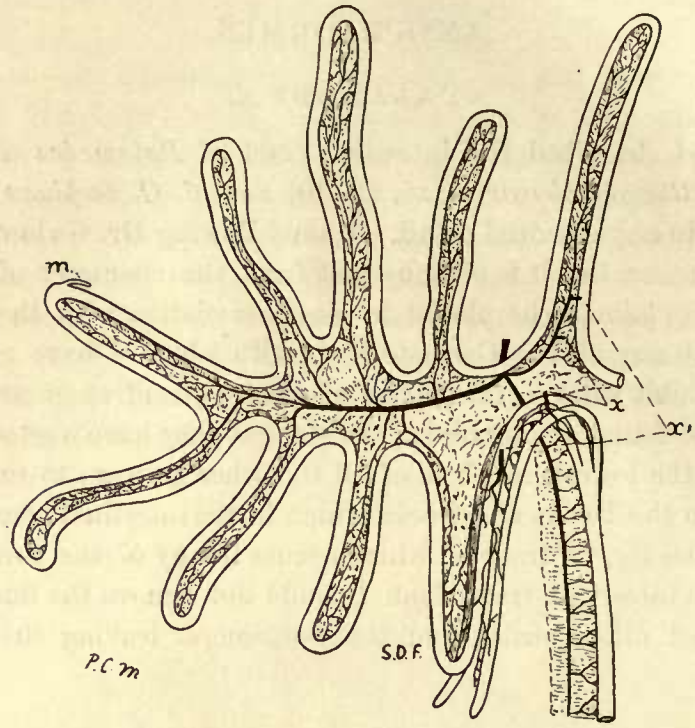
Palamedeæ.

Palamedeidæ.—I described the intestinal tract of *Palamedea* above (fig. 1). The intestinal tracts of *Chauna chavaria* (26. fig. 10) and of *C. derbiana* do not differ from that of *Palamedea* in any essential detail. I am following Dr. Gadow's classification for convenience of reference, but it is obvious that from the character of the intestines the Palamedeæ have no claim to be placed in close association with the other Anseriform birds, or indeed with any of the Carinate birds with which I have as yet been dealing. The Palamedeæ exhibit what I take to be the most primitive or archecentric type of intestinal tract to be found among birds. In the gut they have a general resemblance to the Ratites, and to the lowest members of all the other groups; to such they bear more resemblance than to the Ducks and Geese, which in the intestinal tract exhibit a definite or uniradial apocentricity, no trace of which occurs in any of the three Screamers. On the character of the intestinal tract alone I would not remove the Screamers from other birds, but rather all other birds from the Screamers, leaving them in central and primitive isolation.

Anseres.

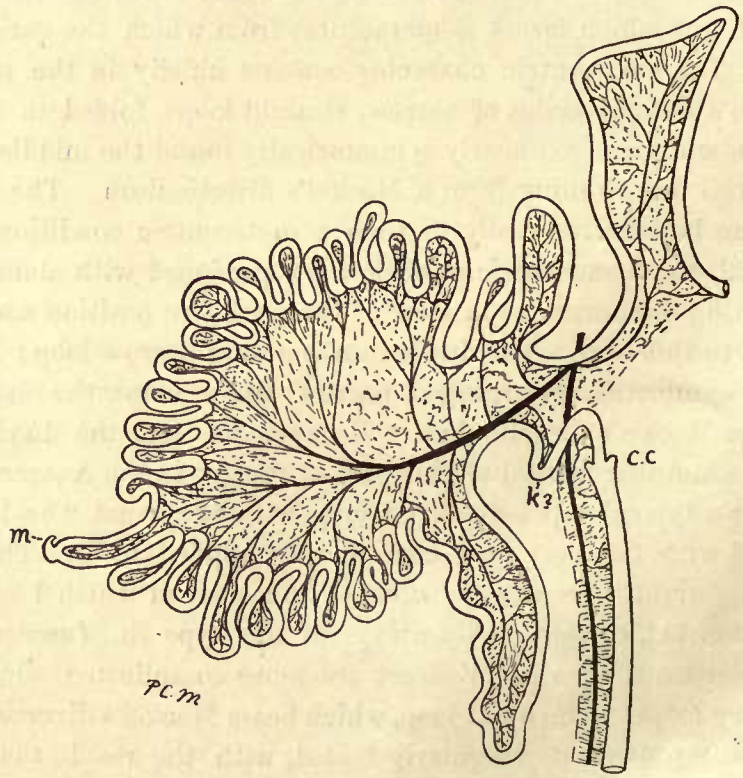
Anseridæ.—I have shown that in the Carinates I have up to this point discussed, with the exception of the Palamedeæ, there is strong evidence for the existence of the apocentric type of gut which forms a metacentre from which the various groups have diverged further. The metacentric character consists chiefly in the transformation of Meckel's tract into a definite series of narrow, straight loops, folded in the mode Gadow terms orthocœlous, and arranged nearly symmetrically round the middle mesenteric vein, which forms an axial line running from a Meckel's diverticulum. The form of the gut in the Anseridæ can be referred easily to such a metacentric condition. In *Anseranas melanoleuca* (fig. 22) this metacentric condition is reproduced with almost diagrammatic fidelity, an interesting circumstance in view of the primitive position among the Anseres generally assigned to this bird. The duodenum is a long narrow loop; Meckel's tract is thrown into very symmetrically-arranged narrow minor loops, the most peripheral of which bears a large Meckel's diverticulum. Between this and the duodenum there are three minor loops, a number typical of this part of the gut in the Anseres. The last loop of Meckel's tract is a typical supra-duodenal loop with the usual "bridging" vein from the duodenum, and with the very long cæca closely applied to it. The rectum is not very short but is straight. In *Cygnus atratus*, the tract of which I have figured in a former paper (26. fig. 11), certain modifications of the type in *Anseranas* are present. The first three minor loops of Meckel's tract are more complicated, showing a tendency to give off secondary loops. The axial loop, which bears Meckel's diverticulum, is greatly elongated and usually somewhat irregularly folded, with the result that the main vein leaves the mesentery, being shorter than the loop itself. The minor loop, just posterior

Fig. 22.



Intestinal Tract of *Anseranas melanoleuca*. Lettering as before.

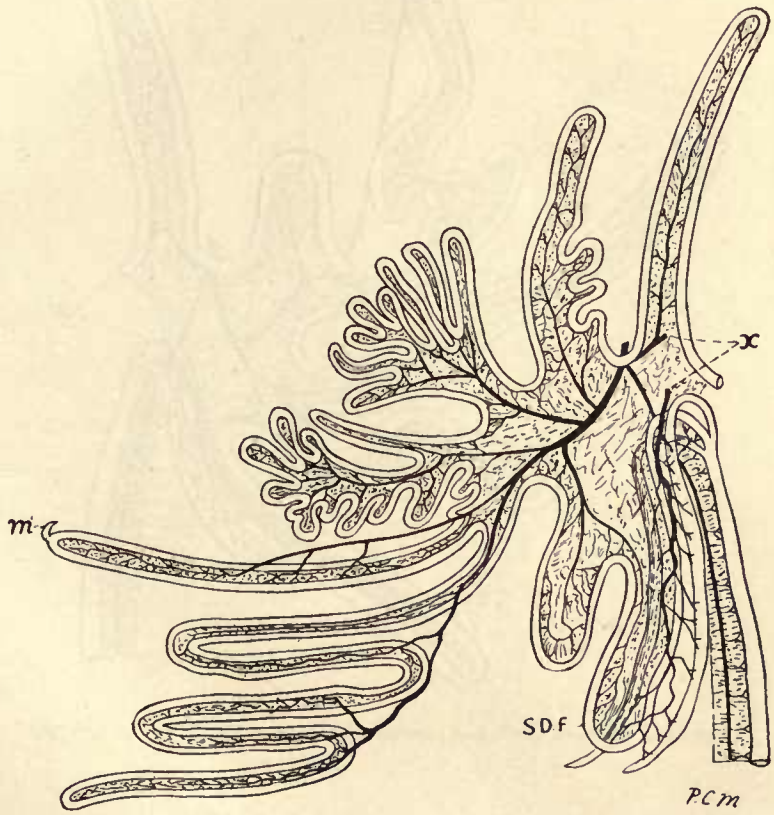
Fig. 23.



Intestinal Tract of *Mergus albellus*. Lettering as before.

to this, is usually elongated and may be similarly twisted. The supra-duodenal loop, the cæca, and the rectum are as in *Anseranas*. The vast majority of Ducks and Geese that I have examined, however different their size and habits, faithfully reproduce this type. The diagram given for *Cygnus atratus*, with the most trifling alterations, might serve for *Anas*, *Anser*, *Æx*, *Chaulelasmus*, *Bernicla*, *Dendrocygna*, *Fuligula*, *Nesonetta*, *Tadorna*, and doubtless, so constant is the type, for many others. *Mergus albellus*, the Smew, presents an interesting variation (fig. 23). The duodenum is unusually wide; Meckel's tract is thrown into a large number of very short loops at the periphery of an almost circular mesenteric fold, but Meckel's diverticulum lies at the apex of a somewhat longer fold lying in the axis of the system. There is a supra-duodenal loop, but it is not

Fig. 24.

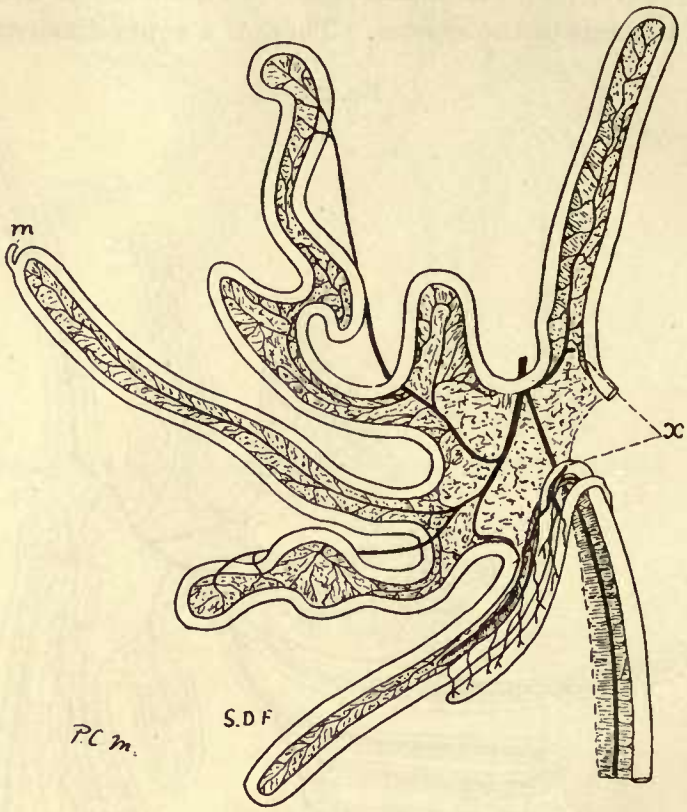


Intestinal Tract of *Spatula clypeata*. Lettering as before.

drained by a "bridging" vein. The colic cæca are paired, but practically non-existent, and Beddard (2. p. 459) mentions an instance where one of the two was absolutely non-existent. At first sight this intestinal tract appears more archecentric than that of any of the other Anseriform birds except the Palamedeæ, but I do not doubt that it is an instance of what I term pseudocentric simplicity. The cæca are obviously degenerate, and in other Mergansers they are longer; and examination of the first part of Meckel's tract shows that it might have been derived by a fusion of the three first minor loops, these having been more complicated than in *Cygnus*, and more as they are in *Spatula* (fig. 24). There is a short supra-cæcal kink, but it is not supplied by the rectal vein. *Spatula clypeata* (fig. 24) shows a form of gut which is simply a further elaboration of

the *Cygnus* type. The modifications are confined to Meckel's tract. The three most anterior minor loops of that region are complicated by an elaborate series of minor folds; the axial loop bearing Meckel's diverticulum is as in *Cygnus*, but the loop next posterior to that is enormously long and folded on itself, the vein having left the mesentery and running a much shorter course than the loop itself. In *Nettopus coromandelianus* (fig. 25) the gut is relatively shorter, and an apocentric simplification

Fig. 25.



Intestinal Tract of *Nettopus coromandelianus*. Lettering as before.

has taken place. The three proximal loops of Meckel's tract are represented by one short and then a very long loop, and the loop next distad of the axial loop is contorted. In these modified loops the veins leave the mesentery, a condition comparatively rare among birds, but very common in the Anseres.

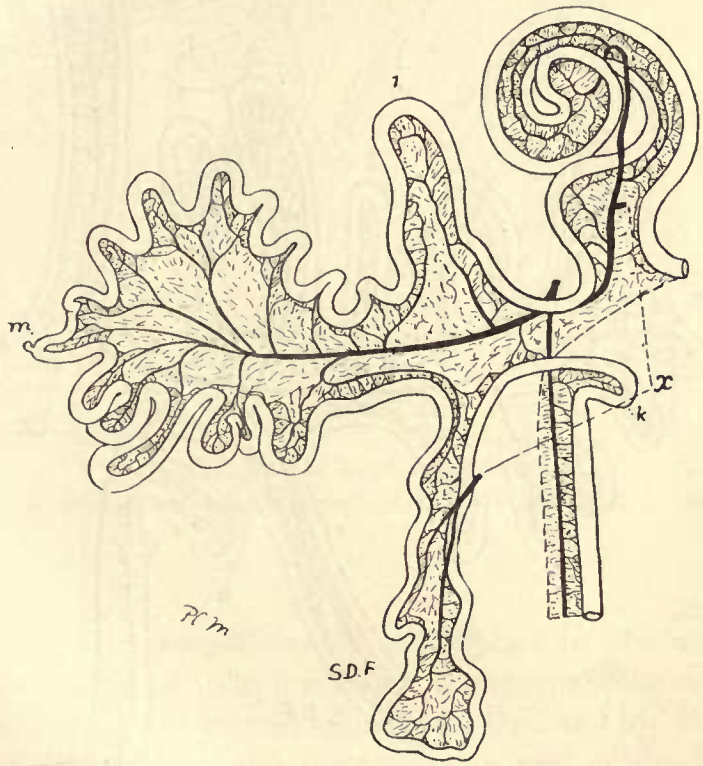
Considering them from the point of view of the intestinal tract, it is plain that the other Anseriformes must be removed from the Palamedeæ. The latter are archecentric. The former start from a metacentric position common to the Colymbomorphæ and the Ciconiiformes, but have diverged apocentrically from that position, forming a specially Anserine metacentre (Plate 22).

FALCONIFORMES.

CATHARTÆ.

CATHARTIDÆ.—Of these I have been able to examine only *Cathartes aura* (fig. 26). The duodenum is long and is coiled into an irregular spiral. Meckel's tract presents first one very wide loop and then a nearly circular expansion symmetrical about a Meckel's diverticulum and thrown into short irregular folds. Then follows a very large but

Fig. 26.



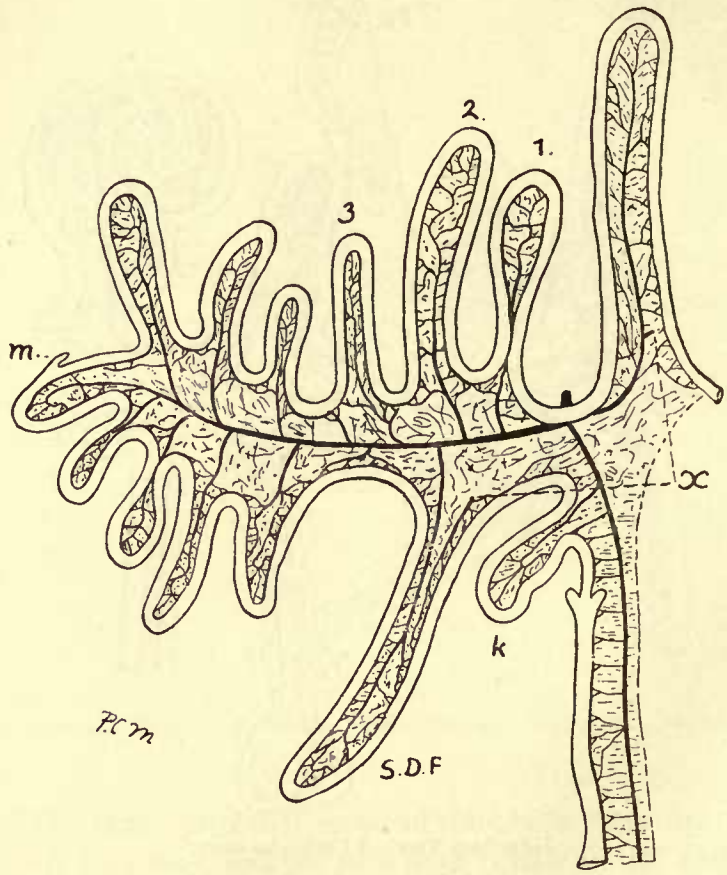
Intestinal Tract of *Cathartes aura*.
Lettering as before.

typical supra-duodenal loop with "bridging" vein. The cæca are totally absent, but immediately above their normal position lies the kink supplied by the rectal vein. I have already shown that this peculiar little loop is a recurring feature among the Carinates we have been considering. It occurs without exception in all the Falconiform birds.

Accipitres.

Gypogeranidæ.—In *Serpentarius reptilivorus* (fig. 27) the duodenum is simple. Meckel's tract presents first three narrow minor folds, and then expands into a nearly circular portion like that in *Cathartes*, the axis being given by the middle mesenteric vein which runs from a Meckel's diverticulum. Then follows a long supra-duodenal loop, drained partially by a "bridging" vein. Posterior to this is a typical supra-cæcal kink, and then a pair of reduced cæca. The rectum is of moderate length and straight.

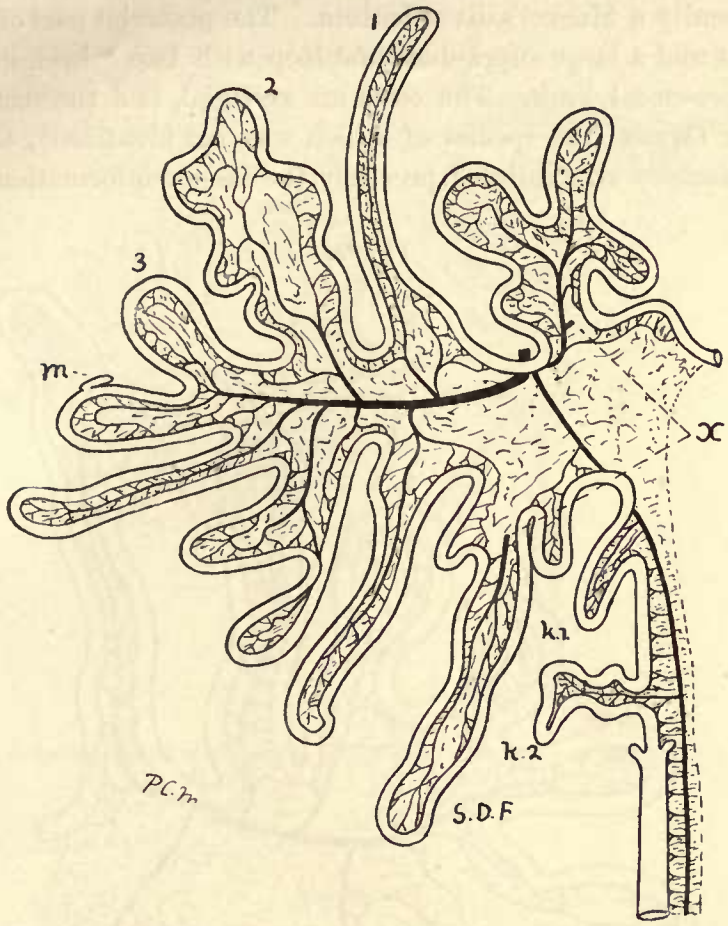
Fig. 27.



Intestinal Tract of *Serpentarius reptilivorus*. Lettering as before.

Vulturidæ.—*Neophron percnopterus* (fig. 28) and other Vultures which I have examined are closely similar. The duodenum is an irregularly expanded loop. Meckel's tract presents three distinct minor loops (numbered 1, 2, and 3 in the figure), which reappear constantly in Falconiform birds; then follows an axial loop bearing Meckel's diverticulum, and then several long, rather irregular loops, the last of which is a typical supra-duodenal loop with "bridging" vein. The cæca are vestigial, and above them lie two supra-cæcal kinks drained by the rectal vein. The rectum is short and straight.

Fig. 28.



Intestinal Tract of *Neophron percnopterus.*
1, 2, 3, three anterior loops of Meckel's Tract. Other lettering as before.

FALCONIDÆ.

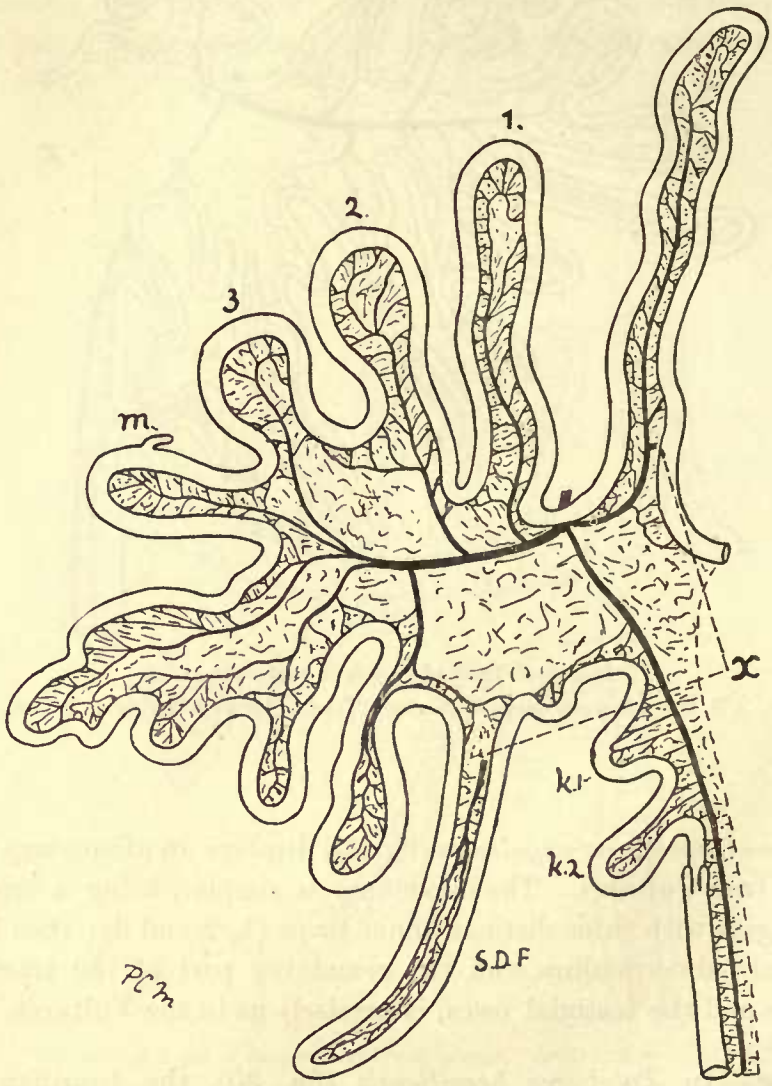
(1) *Gypaëtinæ.*—*Gypohierax angolensis* (fig. 29) displays an alimentary tract extremely like that of the true Vultures. The duodenum is simpler, being a long, narrow loop. Meckel's tract begins with three distinct minor loops (1, 2, and 3); then follows an axial loop, with Meckel's diverticulum, and the remaining part of the tract, including the supra-cæcal kinks and the vestigial cæca, is precisely as in the Vultures.

(2) *Polyborinæ.*—In *Polyborus brasiliensis* (fig. 30), the Brazilian Caracara, the duodenum forms a long, narrow loop, which is wound into a spiral. Meckel's tract consists of a set of small loops arranged very symmetrically, the axial loop as usual bearing a Meckel's diverticulum. There is a well-formed but single supra-cæcal kink in the normal position, and anterior to that a supra-duodenal loop. The cæca are vestigial, and the rectum is short and straight.

(3) *Accipitrinæ.*—In *Circus cineraceus* (fig. 31) is to be found what may be regarded as a central condition for the Falconidæ. The duodenum is a large, very wide loop.

Meckel's tract exhibits first three distinct minor loops, and then is prolonged axially, bearing at its extremity a Meckel's diverticulum. The posterior part of the tract has one or two minor loops and a large supra-duodenal loop with two "bridging" veins. Then comes a large supra-cæcal kink. The cæca are vestigial, and the rectum is short and straight. Another *Circus* (the species of which was not identified), *Circaëtus gallicus*, and *Helotarsus ecaudatus* all exhibited precisely the same conformation.

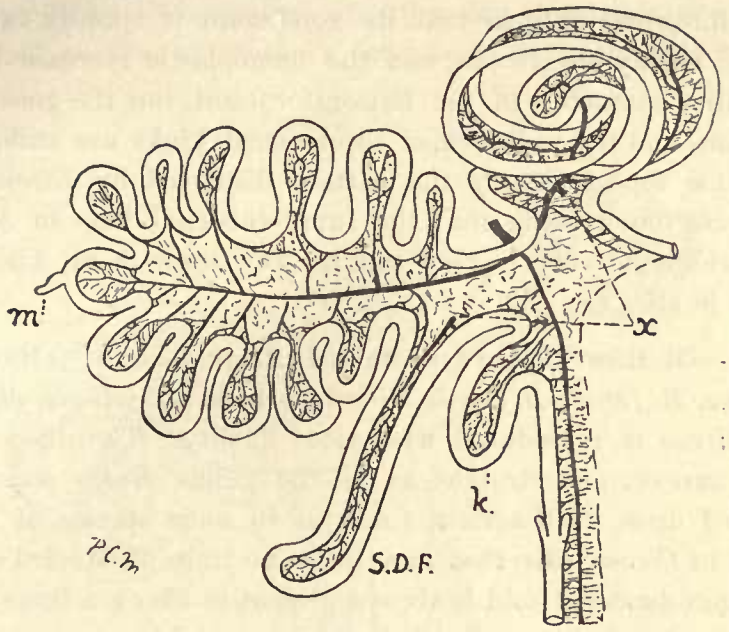
Fig. 29.



Intestinal Tract of *Gypohierax angolensis*. Lettering as before.

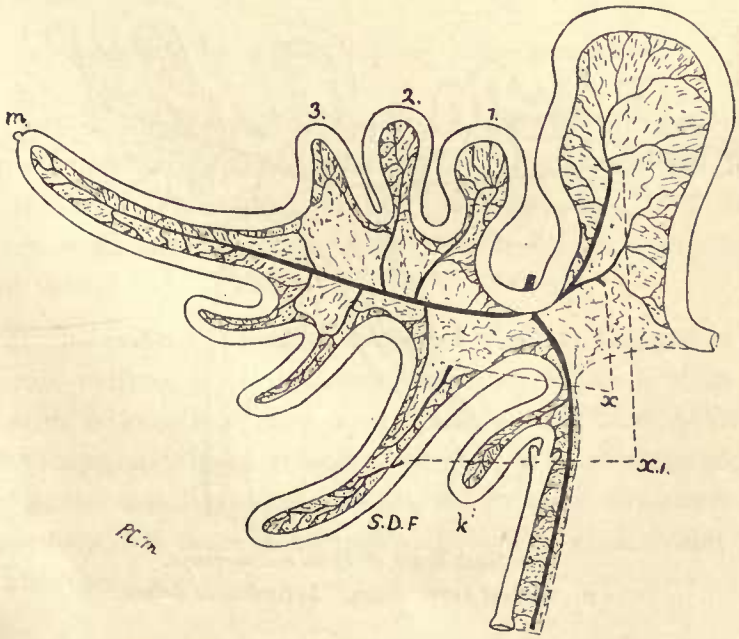
(4) *Aquilinæ*.—I have examined *Aquila audax*, *A. chrysaëtus*, *A. Verreauxi*, *Morphnus guianensis*, *Spizaëtus coronatus*, and *Haliaëtus albicilla* and *H. leucogaster*. I have already described the conformation of the gut in the White-tailed Sea-Eagle (26. fig. 12). The duodenum is very long, being thrown into a complicated system of secondary folds. Meckel's tract, also, is much elongated and its greater part is composed of a series of short irregular loops suspended at the periphery of an oval stretch of mesentery, the apex

Fig. 30.



Intestinal Tract of *Polyborus brasiliensis*. Lettering as before.

Fig. 31.



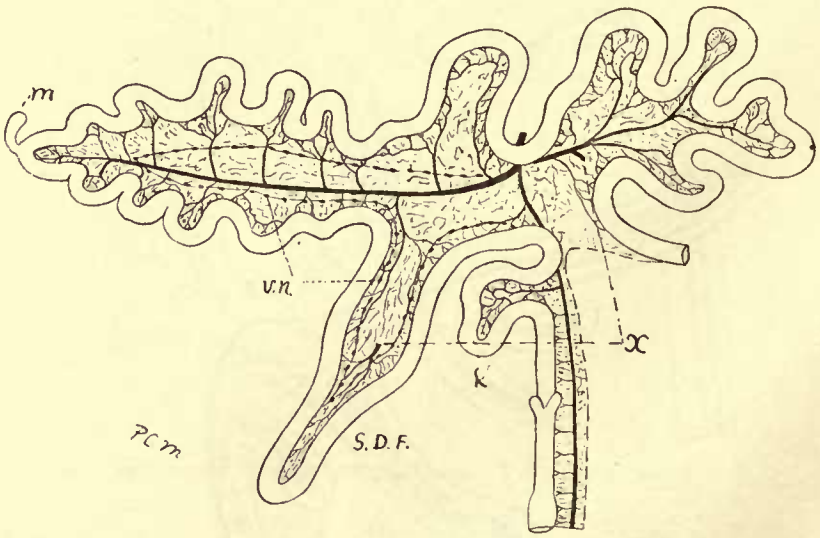
Intestinal Tract of *Circus cineraceus*. Lettering as before.

of the system carrying a Meckel's diverticulum. There is a well-formed supra-duodenal loop, which is spirally twisted, and a large supra-cæcal kink has a similar arrangement. The cæca are vestigial, and the rectum is short and straight. *Haliaëtus leucogaster* differs from the foregoing only in that its duodenum is spirally twisted. These two birds are large and chiefly piscivorous, and the homoplastic increase in gut-length has obscured the peculiar characters of the Falconiform gut, but the general symmetry, the peculiar duodenums, and the well-formed supra-cæcal kinks are sufficiently distinctive. The other Aquilinæ repeat exactly the pattern displayed by *Circus*, the only slight modification I have found being that the supra-duodenal loop in *Spizaëtus*, although drained by a "bridging" vein, is very small. The supra-cæcal kink is very large in most and distinct in all.

(5) *Buteoninæ.*—Of these I have examined *Astur tachiro*, *Asturina magnirostris*, *Buteo erythronotus*, *B. ferox*, *B. jacal*, *Milvus govinda*, *M. ictinus*, *M. migrans*. In all the pattern of *Circus* is reproduced with close fidelity. The duodenum is irregular, sometimes long, narrow, and straight as in the genus *Buteo*, sometimes irregularly expanded, or folded upon itself several times as in some species of *Milvus*. Meckel's tract is always as in *Circus*, save that in a *Buteo* no trace of Meckel's diverticulum was retained. The supra-duodenal fold is always present as also is a large supra-cæcal kink. The cæca are vestigial and the rectum is short and straight.

(6) *Falconinæ.*—I have examined *Falco concolor*, *F. Feldeggi*, *F. lanarius*, *F. melanogenys*, *F. peregrinus*, and *Microhierax melanoleucus*. The Falconinæ certainly exhibit

Fig. 32.

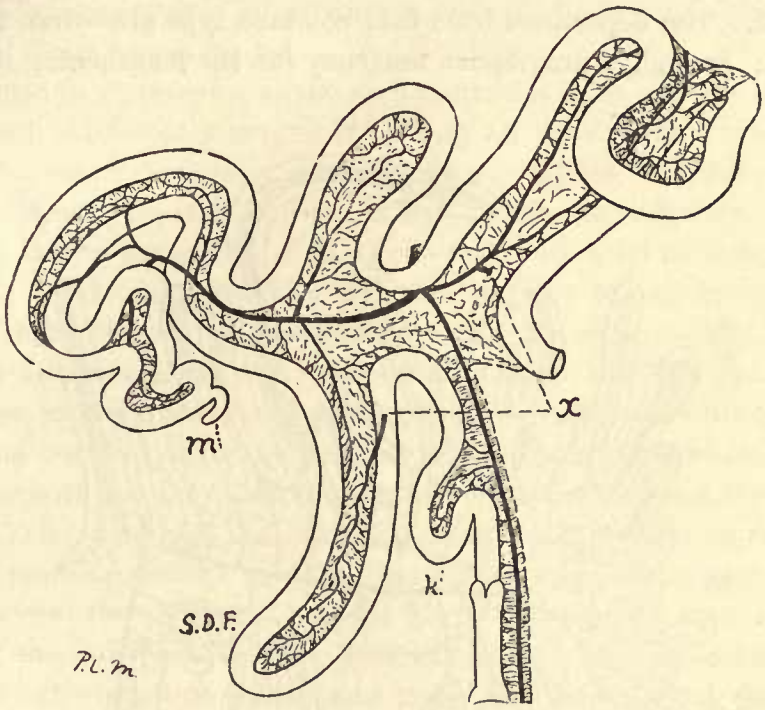


Intestinal Tract of *Falco melanogenys*.
v.n., visceral nerve-chain. Lettering as before.

the most specialized or apocentric form of gut among the Falconidæ. The duodenum is always a large irregular loop, sometimes with minor folds (fig. 32), sometimes bent on itself (fig. 33). Meckel's tract is always very much elongated in the axial line, and

invariably bears at its apex an unusually large Meckel's diverticulum. In many Falcons the first portion of Meckel's tract displays the three minor loops which recur among Falconiform birds. In *Falco melanogenys* (fig. 32) and *F. Feldeggi* (fig. 33) two of these have disappeared, probably in connection with the very great elongation of the tract as a whole. The apical portion of Meckel's tract may be irregularly twisted as in the

Fig. 33.



Intestinal Tract of *Falco Feldeggi*. Lettering as before.

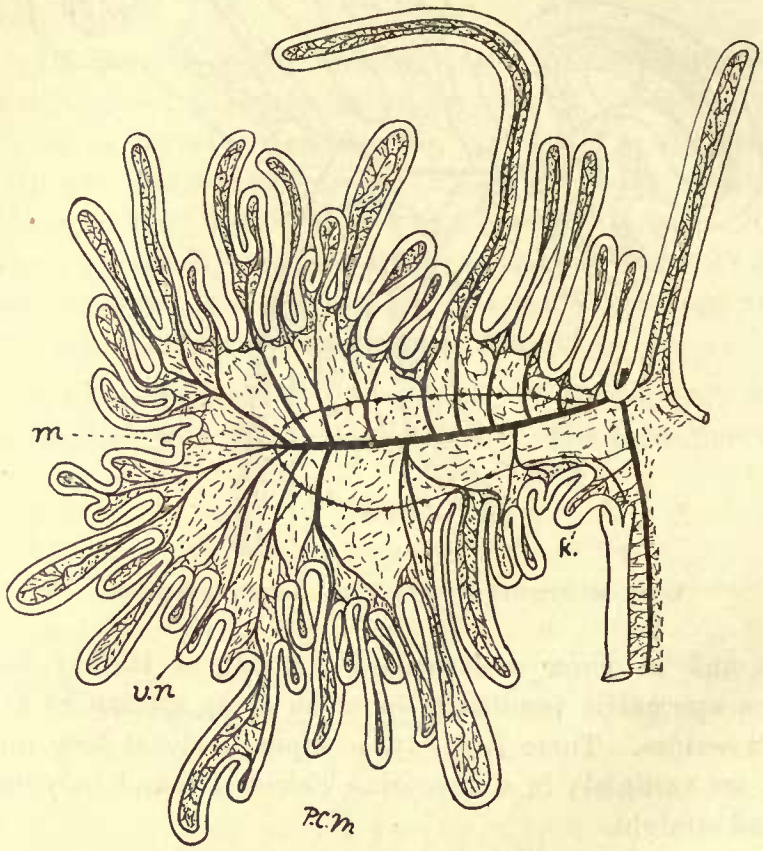
Peregrine Falcon and in *Falco melanogenys* (fig. 32), or it may be coiled into an irregular spiral, an apocentric peculiarity found in many specialized types, for instance in Pigeons and Passerines. There is always a supra-duodenal loop and a supra-cæcal kink. The cæca are vestigial; in a Peregrine Falcon I found only one present. The rectum is short and straight.

PANDIONIDÆ.—In the Osprey, *Pandion haliaëtus* (fig. 34), the gut is enormously long, and is of very narrow calibre, a modification obviously in association with piscivorous habit. The duodenum is long and narrow. Meckel's tract is thrown into a very large number of narrow loops, arranged round a nearly circular mesenteric expanse, the diverticulum being in the usual place at the central point of the curved system. There is no supra-duodenal loop, but there is a small supra-cæcal kink. The cæca are vestigial and the rectum is short and straight.

The Falconiformes are on the average rather large birds with diet in the main carnivorous, with some exceptions which are piscivorous, and a few which live on insects. Except in the piscivorous cases, there is little correction to be made for diet.

The carnivorous forms are on the average the larger, and the carnivorous shortening of the gut is in consequence disguised by the relative increase in length associated with size. The general features of the group are a tendency for the duodenum to be irregular, enlarged, very long, or spirally twisted; for Meckel's tract to exhibit three definite minor loops anterior to a median loop bearing a Meckel's diverticulum, and, posteriorly to that, first one or two irregular loops and then a supra-duodenal loop and at least one supra-cæcal kink drained by the rectal vein; the cæca are always vestigial and the rectum short and straight. The departures from this common type are—first, the irregularities in the fish-eaters; second, a progressive tendency for the lengthening of Meckel's tract

Fig. 34.



Intestinal Tract of *Pandion haliaëtus*. Lettering as before.

in the axial line with consequent obliteration of one or more of the other minor loops, and, in the most apocentric cases, with a spiral folding of the tract; third, *Serpentarius* shows distad of the first three loops of Meckel's tract a circular expansion of the mesentery bearing a number of minor loops, and this condition leads naturally to the condition in *Cathartes*, where the circular expansion involves the second and third of the definite loops on the proximal side of Meckel's tract. Attempts have been made to show a more intimate relation between the Cathartæ and some of the Ciconiiform birds than between these and other Falconiformes; there is no ground for such a conclusion in the structure of the intestinal tract. Still less ground is there for attempting to place in intimate

relation any of the Falconiformes with *Cariama*. The latter bird, as will appear later, is definitely a member of the Gruiform assemblage, and for relations between the Gruiform birds and the Falconiform birds it is necessary, so far as the characters of the intestinal tract take us, to go back to the archecentric type underlying all birds.

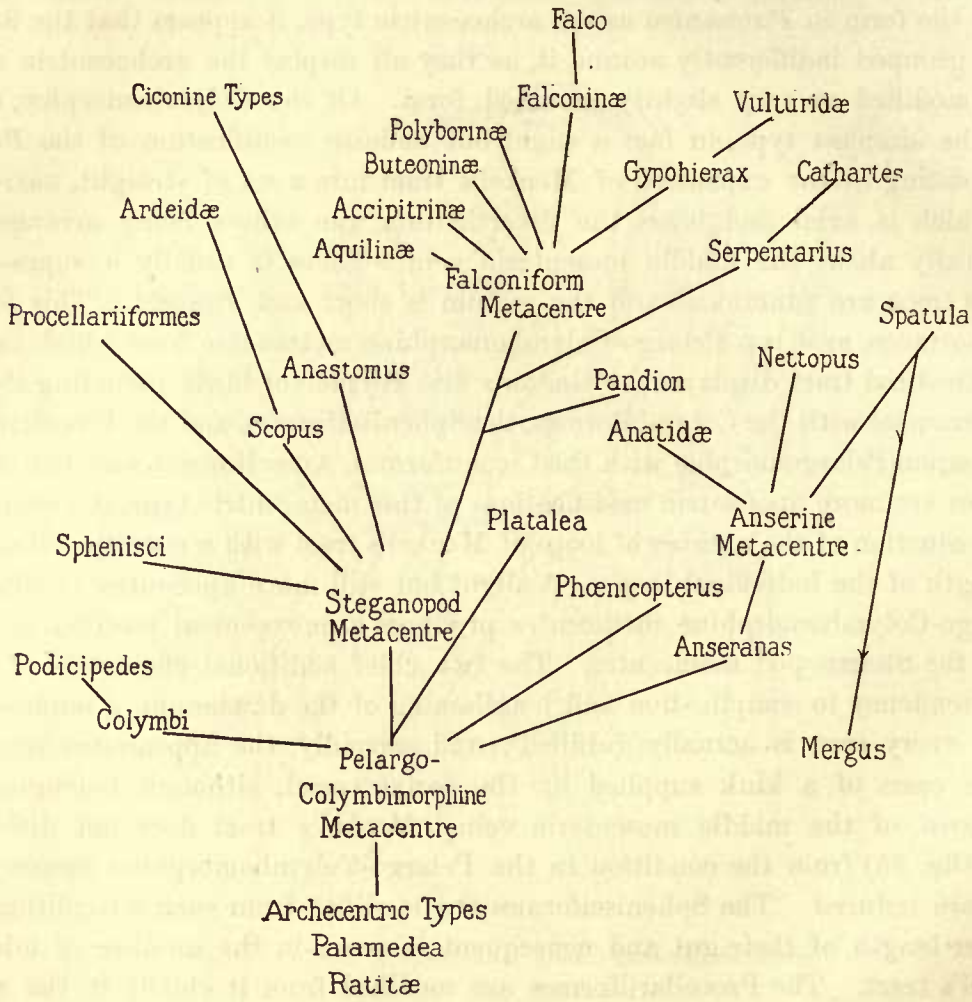
Summary of the Pelargo-Colymbomorphine Brigade. (Plate 21.)

At this point it is convenient to attempt a *résumé* of the conclusions to which study of the Intestinal Tract has so far led.

Taking the form in *Palamedea* as the archecentric type, it appears that the Struthious birds are grouped indifferently around it, as they all display the archecentric character in an unmodified or very slightly modified form. Of the Colymbomorphæ, *Colymbus* exhibits the simplest type, in fact a slight but definite modification of the *Palamedea* form, consisting in the expansion of Meckel's tract into a set of straight, narrow loops, one of which is axial and bears the diverticulum, the others being arranged nearly symmetrically about the middle mesenteric vein. There is usually a supra-duodenal loop; the cæca are functional and the rectum is short and straight. This form is of great importance, as it is a Pelargo-Colymbomorphine metacentre from which radiate the type of intestinal tract displayed by Gadow's first Brigade of birds, including the Legion Colymbomorphæ with the Colymbiformes, the Sphenisciformes, and the Procellariiformes, and the Legion Pelargomorphæ with the Ciconiiformes, Anseriformes, and Falconiformes. The Grebes are more apocentric modifications of this metacentric type, the change being chiefly a reduction of the number of loops of Meckel's tract with a corresponding increase in the length of the individual loops. A slight but still more apocentric modification of the Pelargo-Colymbomorphine metacentre produces a new central position, which may be called the Steganopod metacentre. The two chief additional characters of this are, firstly, a tendency to complication and lengthening of the duodenum, a tendency which in nearly every case is actually fulfilled; and secondly, the appearance immediately above the cæca of a kink supplied by the rectal vessel, although belonging to the drainage-area of the middle mesenteric vein. Meckel's tract does not differ fundamentally (fig. 35) from the condition in the Pelargo-Colymbomorphine metacentre, but the cæca are reduced. The Sphenisciformes are modified from such a condition only by the greater length of their gut and consequent increase in the number of minor loops on Meckel's tract. The Procellariiformes are modified from it chiefly in the reduction of the number of loops on Meckel's tract and the great increase in length of the individual loops, the axial of which may be spirally twisted in the most apocentric forms, *e. g.*, the Oceanitidæ. Of the Ciconiiformes, the Steganopods retain their metacentric position. The Ardeæ start from that position (*Scopus*), but in the Ardeidæ the minor loops of Meckel's tract become very complicated and one of the two cæca is lost. The Ciconii start from the Steganopod metacentre with forms like *Anastomus*, but they rapidly reach a more apocentric condition, the chief peculiarity of which is the spiral twisting not only of the duodenum but of the first minor loop of Meckel's tract, and the twisting of these two spirals together, so that sometimes the blood-vessels are in

common. *Platalea* is less apocentric than the Steganopod metacentre. In it Meckel's tract differs from that in the Pelargo-Colymbomorphine metacentre only in that it is elongated, thrown into many short folds, and spirally twisted as a whole. *Phœnicopterus* is like *Platalea*, but it is still more archecentric, inasmuch as its cæca are functional. The Falconiformes have developed from the Steganopod metacentre so as to display a central type of their own, characterized by an elongation of Meckel's tract, in the line of the axial loop, the latter bearing the diverticulum, and the settling down of the gut

Fig. 35.



Evolution of Intestinal Tract in the Pelargo-Colymbomorphine Brigade.
(*For* Colymbimorphine *read* Colymbomorphine.)

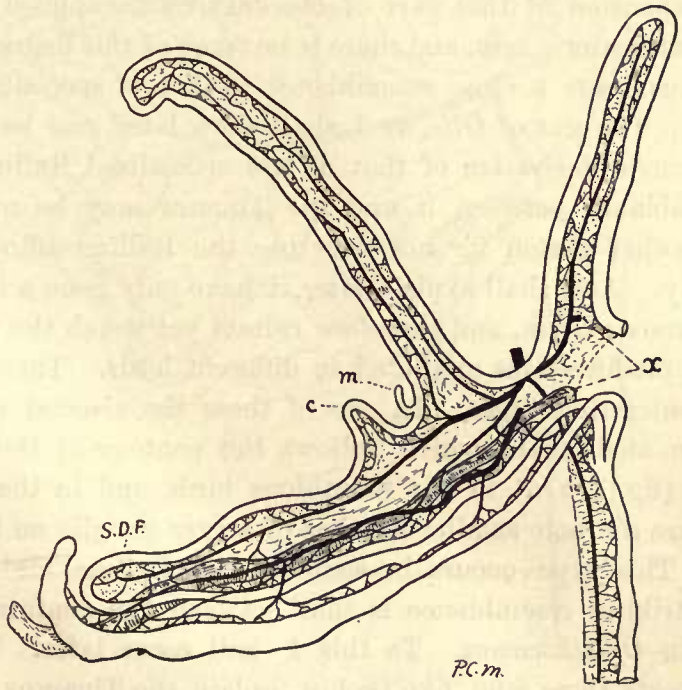
between this and the duodenum into three definitely formed loops. From this the higher Falconidæ move apocentrically, the axial loop of Meckel's tract increasing in length at the expense of the others and being twisted into a spiral. *Gypohierax*, with its irregular minor loops on Meckel's tract and its two supra-cæcal kinks, leads to the Vulturidæ. *Serpentarius* with its spherically expanded Meckel's tract arises somewhat outside the Falconiform metacentre, and may well lead to the more apocentric Cathartæ, which have

completely lost the cæca. *Pandion* stands by itself; its gut is so extremely long that none of the usual minor loops except the supra-cæcal kink can be identified. *Haliaëtus* is a simple modification of the Falconiform metacentre, the irregularity being due to increase in length. For the Anseridæ it is necessary to go back to the Pelargo-Colymbomorphine metacentre. *Anseranas* is practically in that position unmodified, save that the cæca are still longer, a condition common to all the Anseridæ except some of the Mergansers. The *Cygnus* type, with its three definite and contorted minor loops on the anterior portion of Meckel's tract and its very long axial loop with peculiar blood-vessels, gives an Anserine metacentre from which *Nettopus* and *Spatula* have diverged still further. *Mergus* is probably a pseudocentric modification of the *Spatula* type.

TINAMIFORMES.

Crypturidæ.—Of these I have been able to examine the intestinal tract of several specimens of *Rhynchotus rufescens* and *Nothura maculosa*. The conformation is practically identical in these two forms. The duodenum is a long narrow loop; Meckel's tract (*Rhynchotus rufescens*, fig. 36) is divided into two nearly equal parts, the large

Fig. 36.



Intestinal Tract of *Rhynchotus rufescens*.
c, compare loop similarly marked in Gruiformes, figs. 41, 42, 43, &c. Other lettering as before.

Meckel's diverticulum lying between the two. The first portion is one very long narrow loop; the second portion is an equally long and narrow supra-duodenal loop drained by a branch of the middle mesenteric vein as well as by the usual "bridging" factor from the duodenal vein. Meckel's diverticulum was very large in two specimens of *Rhynchotus*, small in a third, and very small in *Nothura*. The small minor loop just distad of it

represented in figure 36 was present in two specimens of *Rhynchotus*, absent in another, and present in *Nothura*. The cæca were long in all, and Beddard (2) has notified the presence of long cæca in the other genera and species, and of very peculiar cæca in *Calodromas*. The rectum is short and straight.

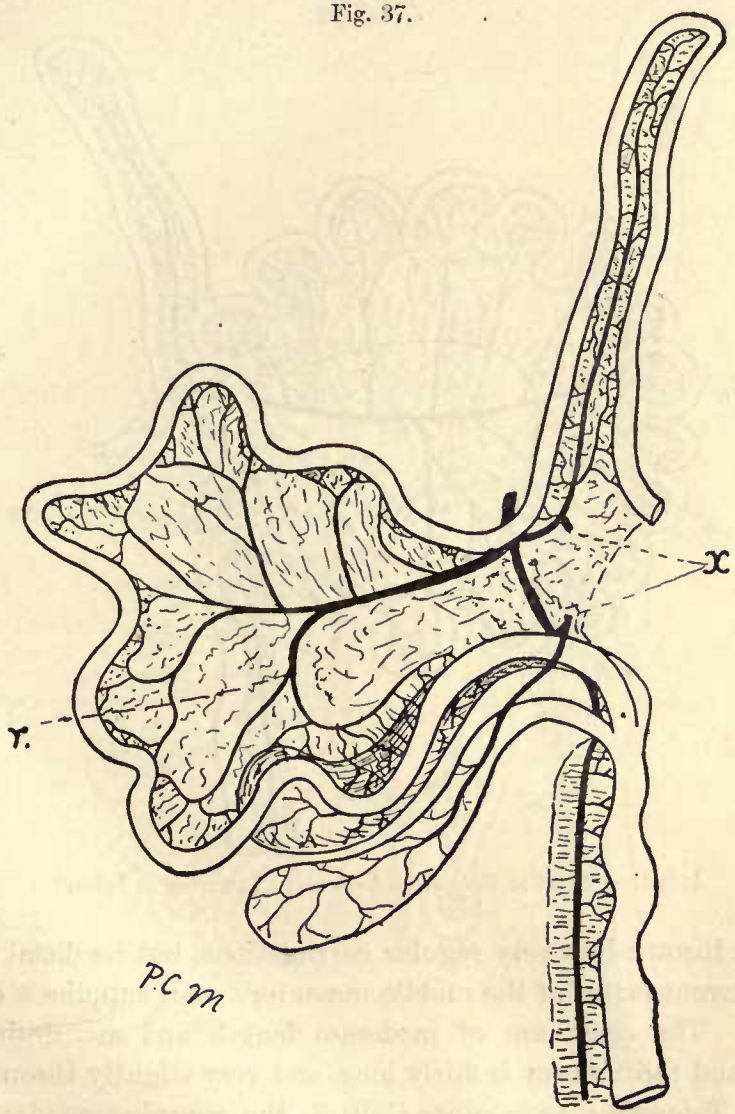
The figure may be taken as representing the morphological character of the Tract in the Tinamus, as there is little correction to be made for habits, and as the conformation is practically identical in relatively large forms such as *Rhynchotus*, and relatively small forms such as *Nothura*. It is clear, then, that the type of the intestinal tract in the Tinamiformes is markedly apocentric, and differs from the archecentric type of *Palamedea* and of the *Struthious* birds in that the rectum is straight, and more notably in that Meckel's tract is expanded into two long, straight, and narrow loops, one anterior, the other posterior to the rudiment of the yolk-sac, both being orthocœlous. Naturally, as the Ratites have intestinal tracts of archecentric conformation, it is as possible that the Tinamiform gut may be derived from the Ratite gut as from that of any other archecentric form. But so far as the character of the intestinal tract goes, there is no reason to associate the Tinamus specially with the Ratites. Nor is there any reason to associate the Tinamus in this matter with the Galliformes, for in these the gut shows a fundamental archecentricity underlying a tendency to apocentric development in the direction of expansion of that part of Meckel's tract supplied by the recurrent branch of the middle mesenteric vein, and there is no trace of this feature in the Tinamus. The gut of the Tinamus bears a close resemblance to that of specialized Ralline forms such as *Otis* (fig. 45). The gut of *Otis*, as I shall show later, can be regarded without difficulty as an apocentric derivative of that of less specialized Ralline forms, and for this reason the resemblance between it and the Tinamu may be merely superficial. There is, however, another reason for not rejecting the Ralline affinities of the Tinamiform gut too readily. As I shall explain later, I have only gone a little way in study of the autonomic nervous system, and therefore cannot yet weigh the value of evidence to be drawn from the modifications exhibited in different birds. There are, however, at least two strongly contrasting types. In one of these the visceral nerve of Meckel's tract forms a ganglionated chain which follows the contour of the gut. This type occurs in *Palamedea* (fig. 1, *v.n.*), in the Struthious birds, and in the Galliformes. In the other type there are a much smaller number of larger ganglia on the visceral nerve (*Otis*, fig. 45, *v.n.*). This type occurs in some of the Ralline birds and in at least *Nothura*. Another striking resemblance is that between the conformation of the gut in the Tinamus and in *Opisthocomus*. To this I shall recur later. The conformation of the gut, then, supports those who, like Gadow, isolate the Tinamus as Tinamiformes, but at the same time suggests possible relationships with Gruiform birds and with *Opisthocomus*.

GALLIFORMES.

Mesites.—I have no information regarding this group. Naturally knowledge of the conformation of the alimentary tract is much to be desired in the case of a bird the affinities of which are doubtful.

TURNICES.—In the Turnices (I have not seen *Pedionomus*) the duodenum (*Turnix Dussumieri*, fig. 37) is a long, narrow loop; Meckel's tract is suspended at the periphery of a nearly circular mesenteric expansion and bears no trace of the diverticulum. There is no specially formed supra-duodenal loop, but the very large cæca (which are dilated towards their extremities) are drained partly by a bridging vein from the duodenal vein. The rectum is relatively long and very slightly expanded into folds.

Fig. 37.



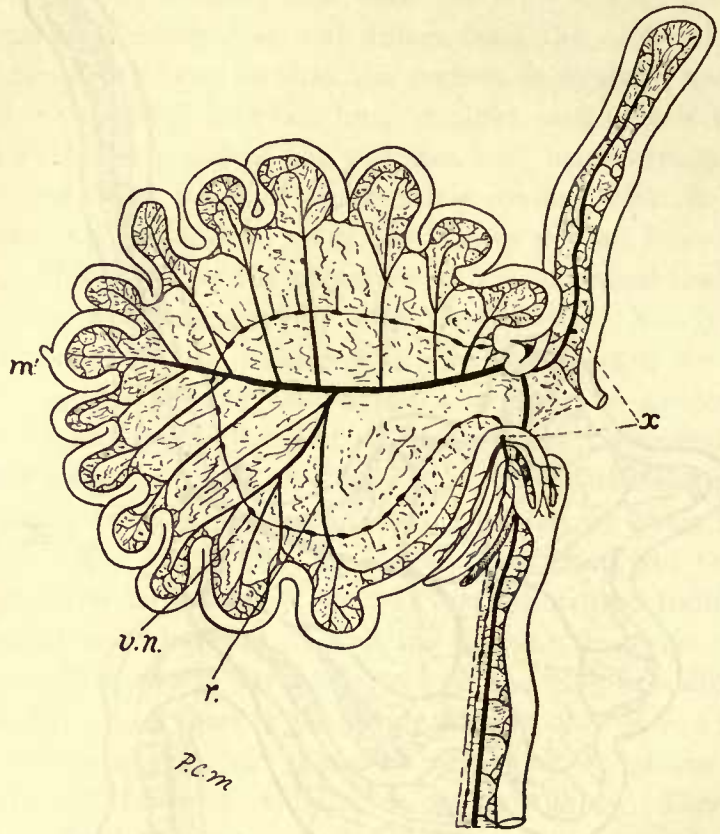
Intestinal Tract of *Turnix Dussumieri*.
r., recurrent factor of middle mesenteric vein. Other lettering as before.

This intestinal tract is markedly archecentric. The simple character and the arrangement of the blood-vessels are closely similar to the condition of *Palamedea*. The chief modifications are absence of the Meckel's diverticulum, the increased length of the cæca, and the relatively shorter rectum. So far as the character of the gut indicates systematic position, there is no reason either to retain *Turnix* among the Galliformes or to remove it from that assemblage. It is simply an archecentric form.

Galli.

Megapodidæ.—In *Talegallus Lathami* (fig. 38) the duodenum is a straight, narrow loop of moderate length. Meckel's tract is swung at the periphery of an expanse of the mesentery, and forms almost a complete circle of which the middle mesenteric vein, running from the Meckel's diverticulum, forms a diameter; for the greater part of its

Fig. 38.



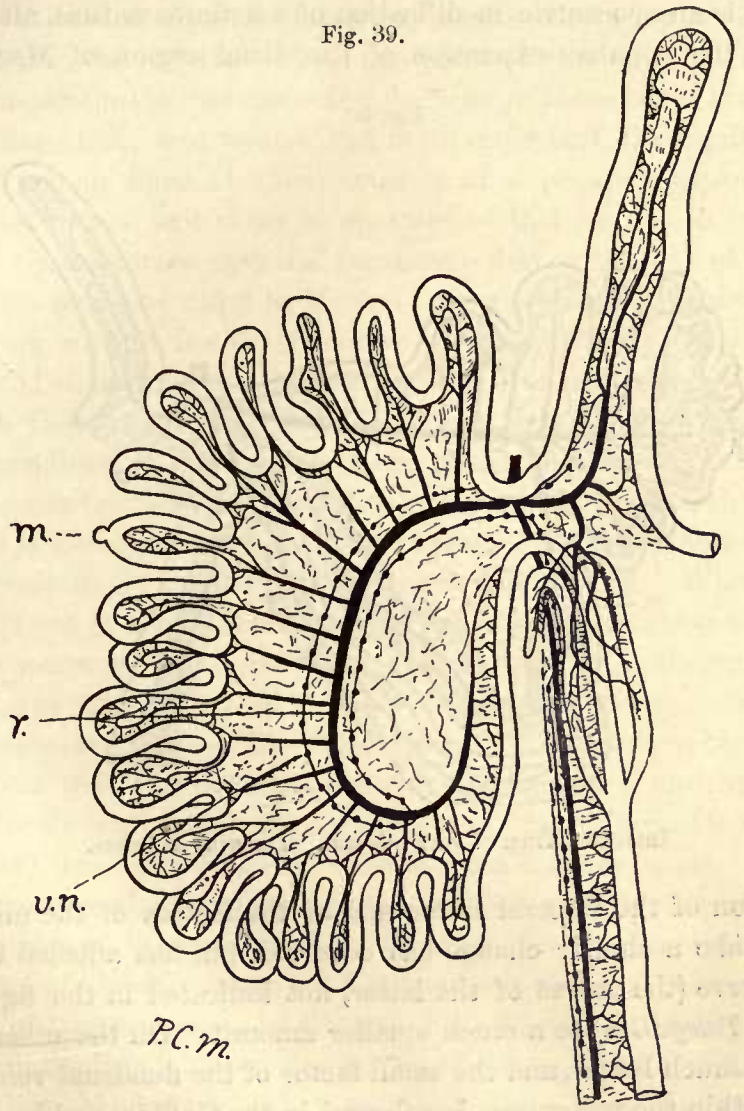
Intestinal Tract of *Talegallus Lathami*. Lettering as before.

course this tract is thrown into very regular corrugations, but its distal portion is nearly straight. The recurrent factor of the middle mesenteric vein supplies a considerable part of Meckel's tract. The cæca are of moderate length and are drained partly by a "bridging" vein, and the rectum is fairly long and very slightly thrown into folds. A striking feature in *Talegallus*, as in other Galli, is the conspicuous visceral nerve (*v.n.*), which in this bird is a ganglionated chain following the sweep of Meckel's tract.

Cracidæ.—In *Crax Daubentoni* (fig. 39) the only notable difference from *Talegallus* in the formation of the gut relates to Meckel's tract. This area is much elongated distally, with the result that the recurrent factor of the middle mesenteric vein (*r.*) which supplies the distal portion of the tract is much enlarged, and appears to be the direct continuation of the middle mesenteric. That vein, however, in the embryo runs out as usual to the diverticulum as I figured in the case of *Argus giganteus* (26. fig. 2), and its real termination in the adult is one of the minor branches of the main blood-channel.

In association with the growth of the posterior portion of Meckel's tract, the visceral ganglionated chain forms a curious elongated loop, which, on comparison of figs. 38 and 39, will be seen to be obviously connected with the distal growth of the tract. In two other species of *Crax* and in two species of *Penelope* the conformation of the gut with its blood-vessels and nerve was identical in all main points with the condition just described.

Fig. 39.



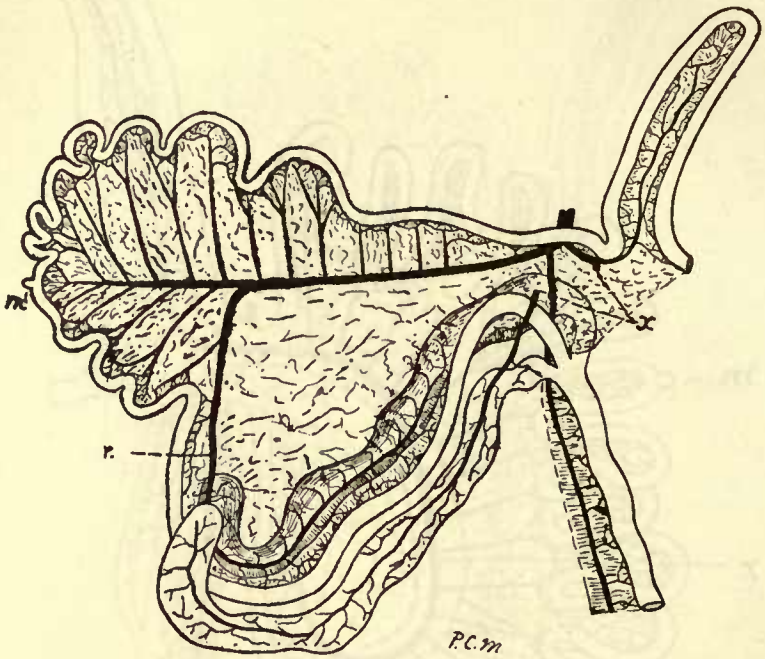
Intestinal Tract of *Crax Daubentoni*. Lettering as before.

GALLIDÆ.—I have examined a considerable number of these, including species of *Argus*, *Caccabis*, *Callipepla*, *Coturnix*, *Francolinus*, *Gallus*, *Lophophorus*, *Pavo*, *Phasianus*, *Perdix*, and *Tetrao*, and in all the conformation closely resembles that shown in the figure of *Pavo cristatus* (fig. 40). Meckel's tract is more elongated in the axial line than in the Cracidæ, and the middle mesenteric vein runs obviously from the remains of the diverticulum. There is a similar distal prolongation of the tract drained by a large recurrent vein, and to the straight distal portion of this the very

large cæca are closely applied, and are drained partly by the recurrent vein and partly by a "bridging" vein. The rectum is relatively short and straight.

In the Galli generally the only homoplastic cause of apocentricity that has to be allowed for is the increased length in the larger forms, and this is not sufficiently great to distort the morphological pattern of the intestinal coils. In all, the general character is markedly archecentric; in the Megapodidæ the archecentricity is most definite. In the Cracidæ there is an apocentric modification of a definite nature, although not great, and consisting in the peculiar expansion of the distal region of Meckel's tract with

Fig. 40.



Intestinal Tract of *Pavo cristatus*. Lettering as before.

coincident alteration of the visceral nerve and of the factors of the middle mesenteric vein. In the Gallidæ a similar change has occurred, but has affected the blood-vessels and the visceral nerve (the course of the latter, not indicated in the figure, very closely resembles that in *Talegallus*) to a much smaller amount. On the other hand, the cæca in the Gallidæ are much larger, and the small factor of the duodenal vein, which in *Crax* runs from them within the mesentery, is enlarged in the Gallidæ and has broken through the mesentery. It is plain that, so far as the conformation of the intestine indicates, the Galli are all closely allied, but there is a distinct basis for their division into Megapodidæ, Cracidæ, and Gallidæ.

Opisthocomi.

I have already described and figured the intestinal tract of *Opisthocomus cristatus* (27. fig. 1). The duodenal loop is short and wide. Meckel's tract is thrown into three well-marked narrow loops, the second of which is rather wider and has a tendency to be twisted into a very slight spiral. In a chick and in two adults I found no trace of

Meckel's diverticulum, but towards the extremity of this loop the place of attachment of the yolk-sac was marked by a strong remnant of a ventral mesentery. In a third adult this mesentery ran to a very small vestige of Meckel's diverticulum. The most distal loop of Meckel's tract was wide, and closely applied to it were the pair of large cæca, drained partly by a "bridging" factor of the duodenal vein. The rectum is unusually long, retaining the archecentric condition of being thrown into minor folds.

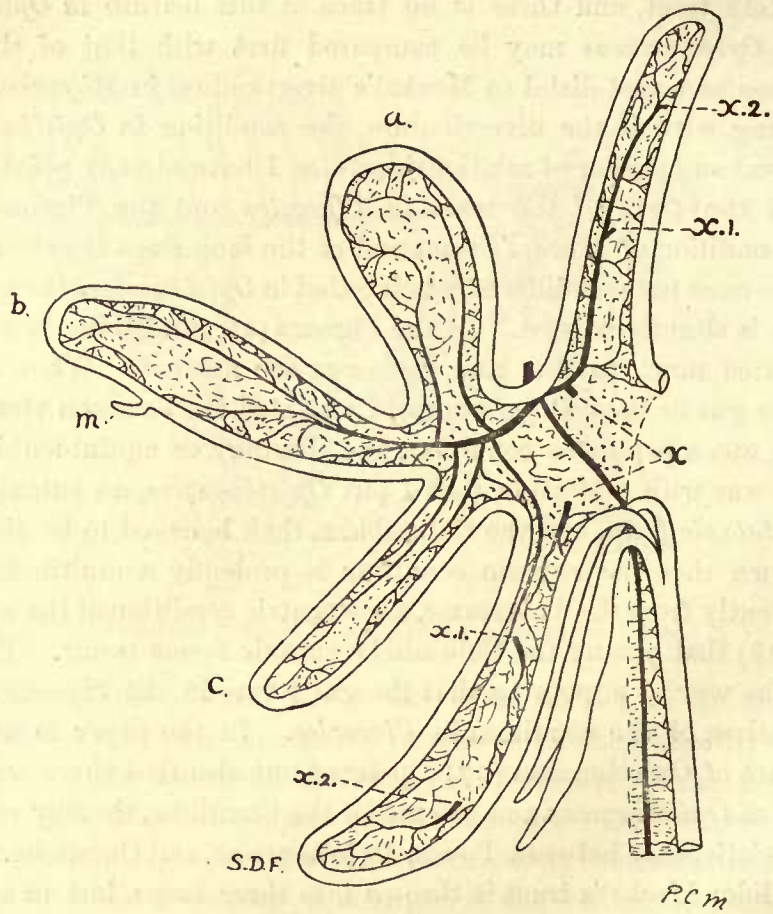
It is plain that the condition of the intestinal tract in this group is markedly apocentric, except with regard to the rectum. From this point of view the Opisthocomi do not find a natural place among the Galliformes—first, because in these latter the general condition of the gut is archecentric; and second, and more important, the small degree of apocentricity displayed among some of them consists of a peculiar expansion of the distal portion of Meckel's tract, and there is no trace of this feature in *Opisthocomus*. The apocentricity of *Opisthocomus* may be compared first with that of the Tinamus. If the very small loop seen just distal to Meckel's diverticulum in *Rhynchotus* (fig. 36) were prolonged, carrying with it the diverticulum, the condition in *Opisthocomus* would be reached. A second suggestion of relationship is, as I have already pointed out, given by comparison with the form of the tract in *Pterocles* and the Pigeons. In *Pterocles* (26. fig. 18) the condition of Meckel's tract and of the long cæca is extremely like that in *Opisthocomus*, the most notable difference being that in *Opisthocomus* the axial loop bearing the diverticulum is slightly twisted. In the Pigeons (26. fig. 19) the twisting of the axial loop may be carried much further and the cæca are reduced. When I first made this comparison of the gut in these three groups, I accepted the common view that eutaxy or quintocubitalism was a primitive condition, and diastaxy or aquintocubitalism a derived condition, and it was with hesitation that I put *Opisthocomus*, an eutaxic form, between *Pterocles*, a *diastataxic* form, and the Columbidæ, then believed to be diastataxic. Since then I have shown that the eutaxic condition is probably a multiradial apocentricity derived independently from the diastataxic, archecentric condition of the wing. Moreover, I have shown (28) that among the Columbidæ eutaxic forms occur. There is therefore no difficulty in the way of supposing that the gut forms in the Pigeons and in *Opisthocomus* are derivatives of the condition in *Pterocles*. In the paper in which I described the intestinal tract of *Opisthocomus* (27) I pointed out also that there were resemblances between the gut of *Opisthocomus* and the gut of the Cuculidæ, thereby recalling Garrod's (13) suggested relationship between Fowls, *Opisthocomus*, and Cuculidæ. It is true that among the Cuculidæ Meckel's tract is thrown into three loops, but an examination of a larger number of Cuculidæ has shown me that important differences distinguish the three loops in *Opisthocomus* and the loops in Cuculidæ.

Taking the Galliformes as a whole, it appears that the form of the gut in the Turnices is archecentric; in the Galli it is still archecentric, but with a tendency to a special mode of apocentricity; in the Opisthocomi it is markedly apocentric, and the apocentricity is quite different in kind from that found among the Galli, but with marked resemblances to the condition in *Pterocles* and the Pigeons.

GRUIFORMES.

Rallidæ.—In *Ocydromus australis* (fig. 41) what I find to be the typical Ralline conformation of the intestinal tract is presented. The duodenum is a straight, narrow loop of moderate length. Meckel's tract is drawn out into a definite number of loops, all of which are fairly straight. The first of these, marked "*a*" in the figures, succeeds the duodenum; the second ("*b*" in the figures) is axial and bears on its distal side a large Meckel's diverticulum. The third, marked "*c*," like the others is a narrow loop belonging to the drainage of the middle mesenteric vein; and the fourth is a well-marked supra-duodenal loop drained by more than one bridging factor of the duodenal vein. The

Fig. 41.



Intestinal Tract of *Ocydromus australis*.
a, *b*, *c*, the three loops of Meckel's Tract characteristic of the Gruiformes. Other lettering as before.

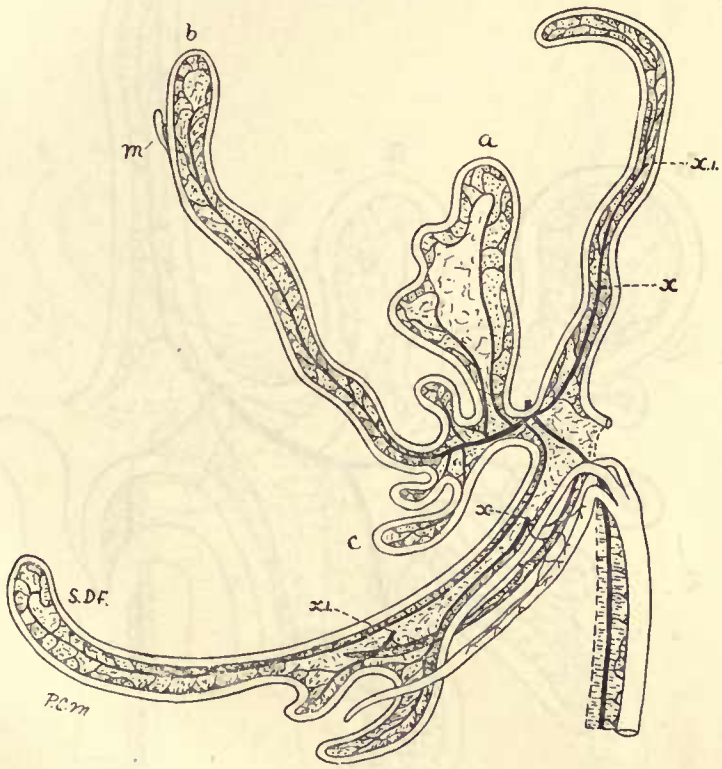
long cæca are closely attached to this last loop of Meckel's tract. The rectum is straight and of moderate length. This conformation is found in all the members of the Rallidæ that I have examined, e. g., *Aramides ypecaha*, *Crex pratensis*, *Gallinula phœnicura*, *Ionornis martinicus*, *Porphyrio cæruleus*, and *P. poliocephalus*. I *described* this condition of the gut correctly in a former paper, but in the drawing of *Crex* (26. fig. 13) the third minor loop has been omitted by an unfortunate mistake, so that the description does not

tally with the figure. The differences which occur among the Rallidæ are insignificant; in some, there are two "bridging" veins, in some, one; the Meckel's diverticulum, which is always large, may be extremely large, the size of this structure being a characteristic feature of the group; the third subsidiary loop of Meckel's tract occasionally is relatively smaller than the other loops.

GRUIDÆ.

(1) *Gruinæ.*—In *Grus virgo* (fig. 42) and other species of *Grus*, and species of *Anthropoides* and *Balearica* are practically identical, the large size has brought with it a relatively great increase of length, but the fundamental identity of the conformation of the gut with that exhibited by the Rails is obvious. The duodenum is similar,

Fig. 42.



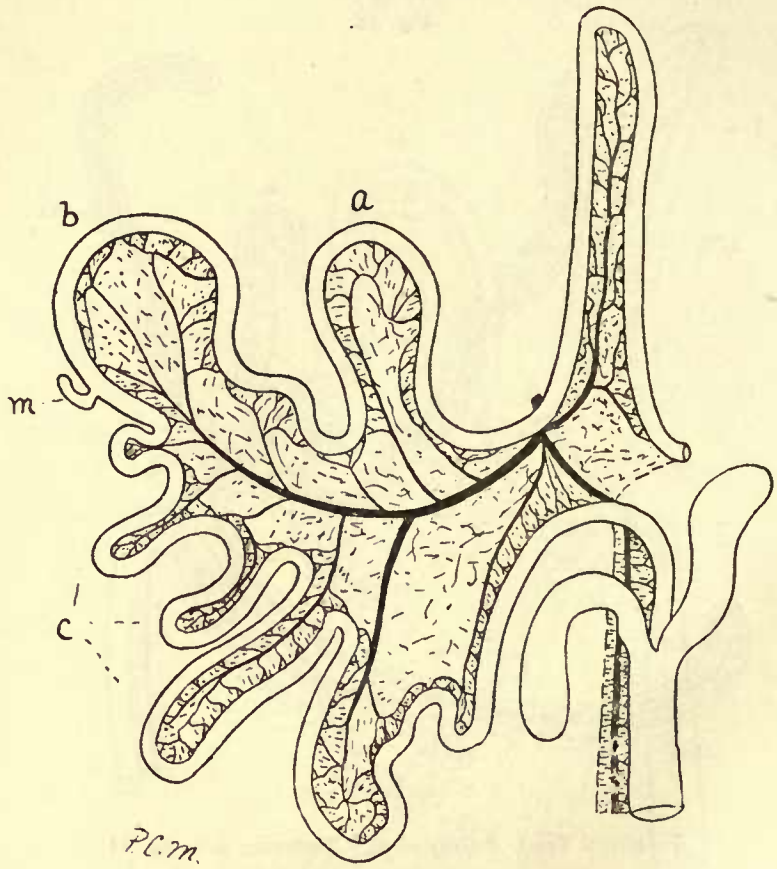
Intestinal Tract of *Grus virgo*. Lettering as in fig. 41.

although, on account of its great length, it is partly bent. Meckel's tract displays the same four loops: "*a*" being widened out; "*b*," the axial loop being very long but carrying a Meckel's diverticulum in the characteristic position, on the distal limb of the loop; "*c*" being small but compound; and the supra-duodenal loop to which the long cæca are attached being much enlarged. It is plain that we have here a simple modification of the Ralline pattern, the modification being due to the relatively greater length of gut that occurs in larger birds.

(2) *Araminæ.*—The very interesting form *Aramus scolopaceus* (fig. 43) displays a conformation of the intestinal tract which differs only in minor respects from that in the

Rails and Cranes. The duodenum is normal; Meckel's tract displays the loops which I have marked "*a*" and "*b*" precisely as in the Rails, and "*b*" the axial loop bears a large diverticulum on its distal limb. The posterior portion of the tract differs: in place of "*c*," the third loop, and of the normal supra-duodenal loop, there are a set of irregular small loops. The cæca are short but wide and in the natural condition contain fæcal matter. The rectum is short, wide, and straight. I am disposed to think that the type in *Aramus* is more archecentric than the types displayed by the Cranes and Rails. Although the axial loop with the diverticulum on its lower limb is characteristically Ralline, the general conformation of Meckel's tract is much more like the

Fig. 43.

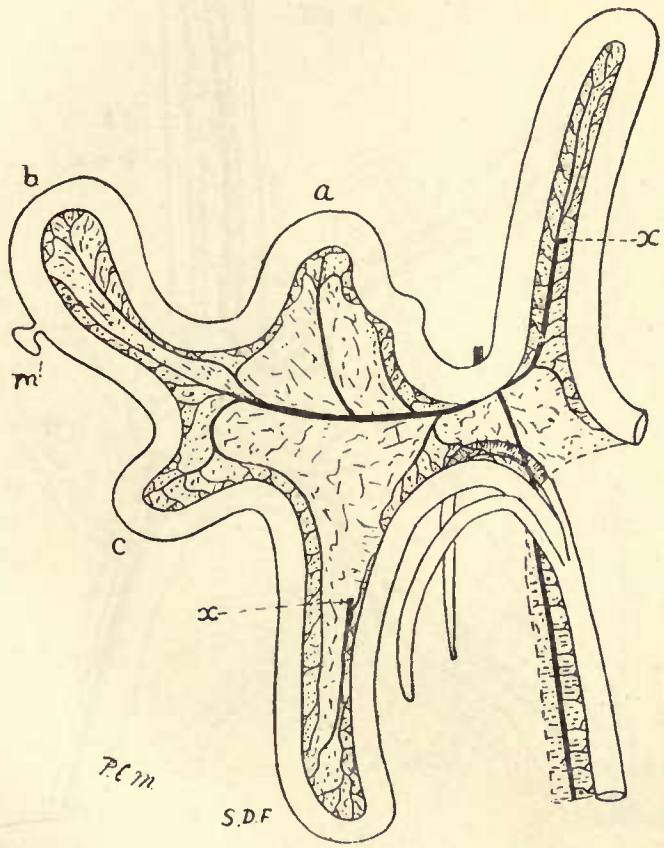


Intestinal Tract of *Aramus scolopaceus*. Lettering as in fig. 41.

archecentric condition, and this similarity is increased by the moderate length of the cæca and the absence of a specialized supra-duodenal loop. I think it is more probable that the long cæca of the Cranes and Rails are an apocentric modification than that the relatively shorter cæca of *Aramus* are pseudocentric degenerations, for, as I hope to show later, in the vast majority of cases where the cæca are obviously degenerate, the "bridging" factor or factors from the duodenal vein, which originally drained them, persist to drain a specialized supra-duodenal loop, and there is no trace of this in *Aramus*.

(3) *Psophiinæ.*—As the position of *Psophia* is one concerning which there has been no little difference of opinion, it is interesting to find that the conformation of the gut in *Psophia crepitans* (fig. 44) is typically Ralline. As will be seen, it conforms in every way to the character typical of the Rallidæ. As it is probable that the differences between the type in the Cranes and that in the Rails is due merely to the larger size of the former, there is no reason to be drawn from the character of the gut for placing *Psophia* preferentially either with the Cranes or with the Rails. It displays the ground-form common to both sets. *Psophia obscura* is simplified in the direction of Cariama and the Bustard; the loops on either side of the axial loop, *i.e.* "*a*" and "*c*," have practically disappeared, so that the conformation in *Otis* is closely imitated.

Fig. 44.



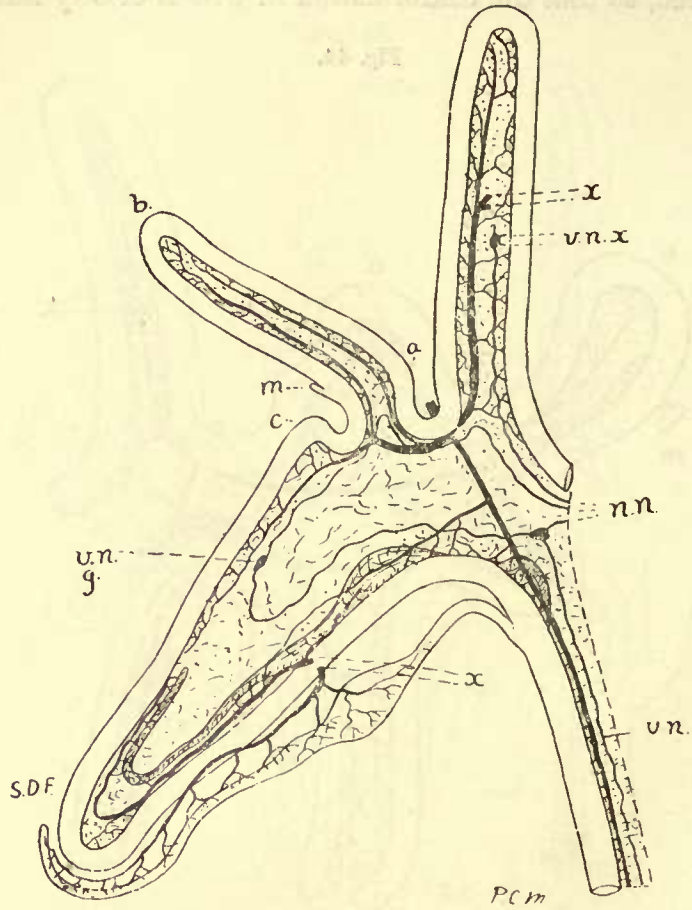
Intestinal Tract of *Psophia crepitans.* Lettering as in fig. 41.

Dicholophidæ.—I have already described and figured the intestinal tract in *Cariama cristata* (26. fig. 14), and the condition in Burmeister's Cariama (*Chunga Burmeisteri*) is practically identical. The duodenum is a long narrow loop. Meckel's tract displays the Ralline loops "*a*" and "*b*"; but the two are merged proximally, "*b*" displaying a Meckel's diverticulum on the distal limb. There is no trace of loop "*c*"; but there is a large supra-duodenal loop drained partly by a "bridging" vein, and having the long cæca closely applied to it. The rectum is straight but of fair length. It is plain that the intestinal tract of the Dicholophidæ presents an apocentric character of a definite nature, but which may be regarded as a simple derivative of the type shown in

the Rallidæ and Gruidæ, the loops of Meckel's tract being long and straight, the first and second being partly fused and the third having disappeared.

Otididæ.—I have had the opportunity of examining only *Otis tarda*, the Great Bustard. In it (fig. 45) the duodenum is a long narrow loop. Meckel's tract is thrown only into two loops, of which the second is a very large supra-duodenal loop drained by a pair of large bridging vessels, and has long and peculiar cæca closely applied to it. The proximal loop I take to be the axial loop seen in the Rallidæ; it bears upon it, low

Fig. 45.



Intestinal Tract of *Otis tarda*.

n.n., nerves entering mesentery; *v.n.x.*, ganglion in duodenum from which nerves pass to cæca and supra-duodenal loop; *v.n.g.*, large ganglion of visceral nerve; *v.n.*, branch of visceral nerve in rectum.

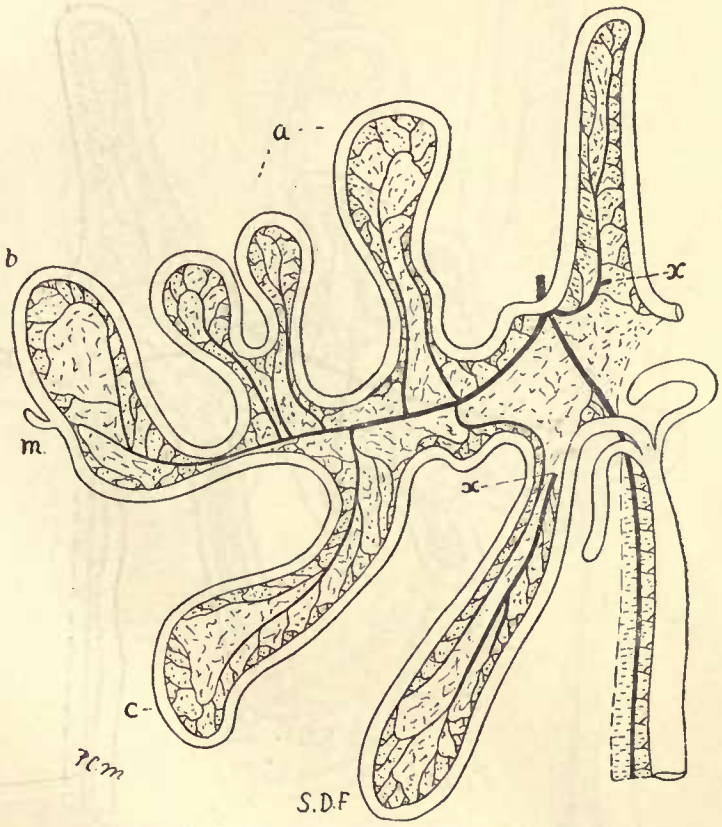
down on its distal limb, a Meckel's diverticulum. A pair of very small but quite definite folds, marked "*a*" and "*c*" in the figure, I take to represent the similarly designated large loops in the Rallidæ and Gruidæ.

The intestinal tract of *Otis* is certainly markedly apocentric. The loops are all very definite and the supra-duodenal loop in particular is highly specialized, being closely applied to the duodenum, over which it lies in the unfolded condition, and from which it receives not only a pair of bridging veins, but two branches of the autonomic visceral

nerve coming from a special ganglion in the duodenal loop (fig. 45, *v.n.x.*). The peculiar cæca which have been described by Beddard (2. p. 332) are specialized not only in their great length but in their internal structure. The general character of the gut, however, especially if I am correct in my interpretation of the small folds marked "*a*" and "*c*," is obviously Ralline. The resemblance between the guts of *Otis* and of the Tinamus is certainly striking, the only notable difference being that in the Tinamu the cæca are less specialized and that Meckel's diverticulum lies distad of the great loop of Meckel's tract rather than actually on it. I regard the closeness of the resemblance as not definitely morphological.

RHINOCHETIDÆ.—In *Rhinochetus jubatus*, the Kagu (fig. 46), the duodenum is

Fig. 46.



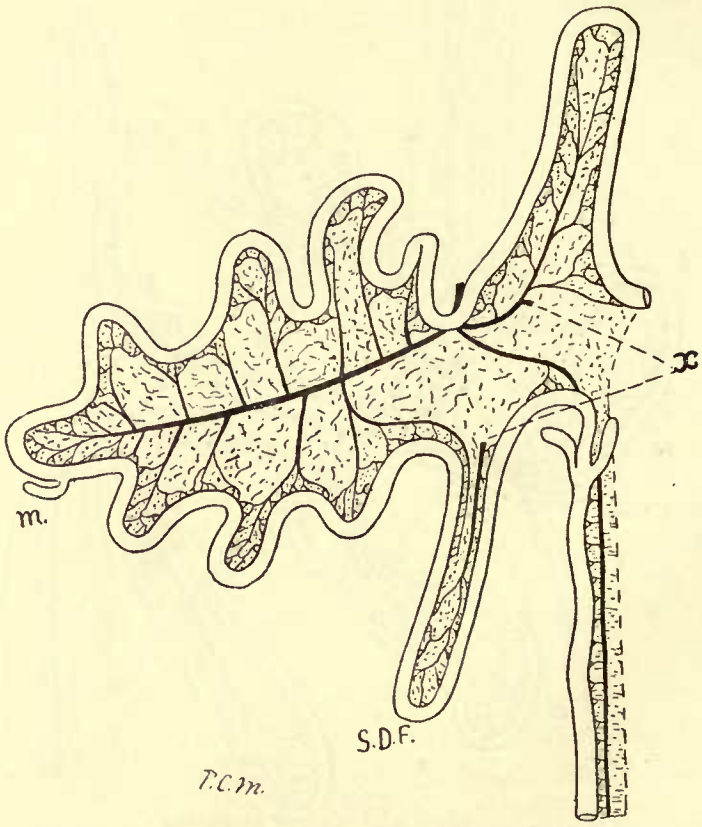
Intestinal Tract of *Rhinochetus jubatus*. Lettering as in fig. 41.

a simple, short, and narrow loop. Meckel's tract shows first a pair of minor loops, the second of which is double, then an axial loop with a large diverticulum about the middle of its distal limb, then a large simple loop marked "*c*," then a long narrow supra-duodenal loop with a bridging vein. The cæca are rather short, and the rectum is straight, wide, and of moderate length. The intestinal tract of this bird certainly differs considerably from that of other members of the Gruiform assemblage. The most important differences are the presence of an additional loop on Meckel's tract, the circumstance that the whole of that tract, with the exception of the supra-duodenal

loop, displays in the unfolded condition a slightly spiral twist, and the shortening of the cæca, a character shared with *Eurypyga*. The resemblance to the Ralline type, however, is fairly strong. Meckel's tract is produced into a set of minor loops, of which two represent "*a*," while "*b*," with the diverticulum midway on the distal limb, and "*c*" are normal, and the last is a supra-duodenal loop simplified in correspondence with the reduction of the cæca. *Rhinochetus* has been compared with *Scopus*, but the character of the tract does not support this comparison. In *Rhinochetus* there is no trace of the twisted duodenum, the diverticulum is in the Gruiform position, and Meckel's tract is thrown into definite minor loops.

EURYPYGIDÆ.—*Eurypyga helias* (fig. 47) departs still more from the other Gruiformes.

Fig. 47.



Intestinal Tract of *Eurypyga helias*. Lettering as before.

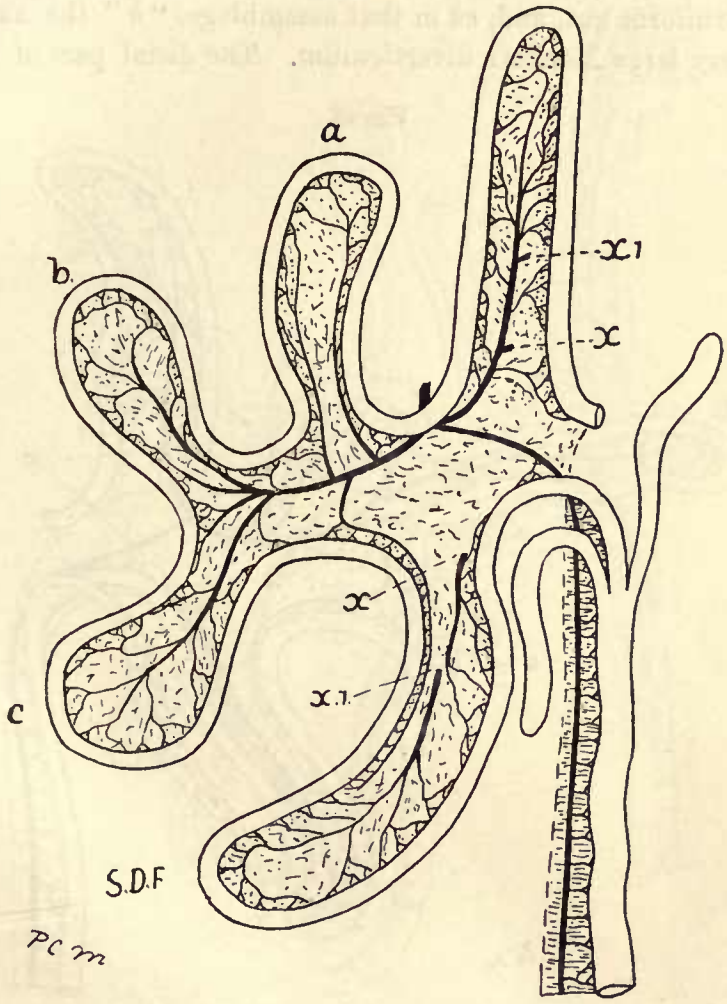
The duodenum resembles that of the other forms, but Meckel's tract is much more archecentric, the greater part of it consisting of an irregularly folded gut swung at the periphery of an oval expanse of mesentery. The large diverticulum, however, is not at the apex of the tract, but in the typical Gruiform position on the distal limb of the axial loop. The distal portion of Meckel's tract is a definite supra-duodenal loop with bridging vein. The cæca are vestigial, and the rectum is long and nearly straight.

HELIORNITHIDÆ.—In *Heliornis fulica* (fig. 48) the typical Ralline or Gruiform characters again appear. The duodenum is simple and narrow. Meckel's tract displays

the three loops "*a*," "*b*," and "*c*" very definitely drawn out. In *H. surinamensis*, the conformation is similar, although the loops are not so independent. In neither is there a diverticulum present. The posterior portion of Meckel's tract is a definite supra-duodenal loop drained by two "bridging" vessels. The cæca are of moderate length, and the rectum is as in the others.

It is plain that what I term a metacentral condition underlies the conformation of the alimentary tract in the Gruiform assemblage. This metacentre possesses a simple duodenum; Meckel's tract is produced into four straight loops, of which "*b*," the axial

Fig. 48.



Intestinal Tract of *Heliornis fulica*. Lettering as in fig. 41.

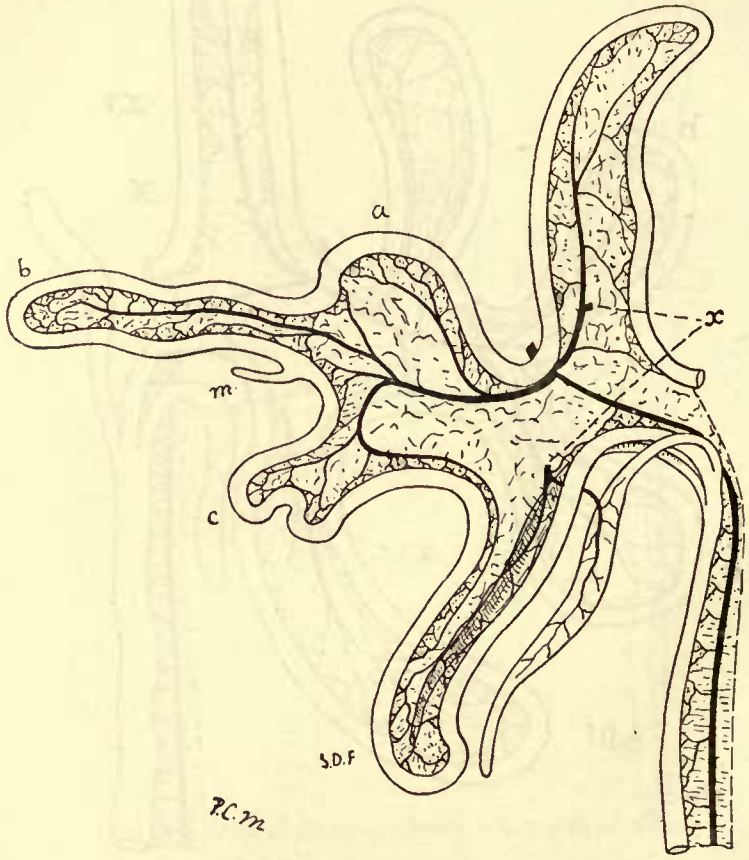
loop, carries the diverticulum on its distal limb, and of which the last is a large supra-duodenal loop drained by bridging vessels and with the long cæca closely attached to it. The Rallidæ and Gruidæ display this metacentral character without modification of any important kind. The Dicholophidæ and the Otididæ have moved apocentrically from it by reduction of loops "*a*" and "*c*" and greater specialization of the supra-duodenal loop. *Heliornis* is metacentral. *Rhinochetus* and *Eurypyga* are slightly modified, the apparent archecentricity of the latter being possibly pseudocentric.

CHARADRIIFORMES.

Limicolæ.

Charadriidæ.—I have already described and figured the conformation of the intestinal tract in the Curlew (*Numenius arquata*, 26. fig. 15). The duodenum is straight and narrow. Meckel's tract is more archecentric than in the Gruiformes, inasmuch as the minor loops are not well separated from the general course of the gut. None the less, such minor loops exist, and markedly recall the common Gruiform type, although the condition is less apocentric. There are three main loops corresponding to "*a*," "*b*," and "*c*" of the Gruiform gut, and, as in that assemblage, "*b*" the axial loop bears on its distal limb a very large Meckel's diverticulum. The distal part of the Tract consists

Fig. 49.

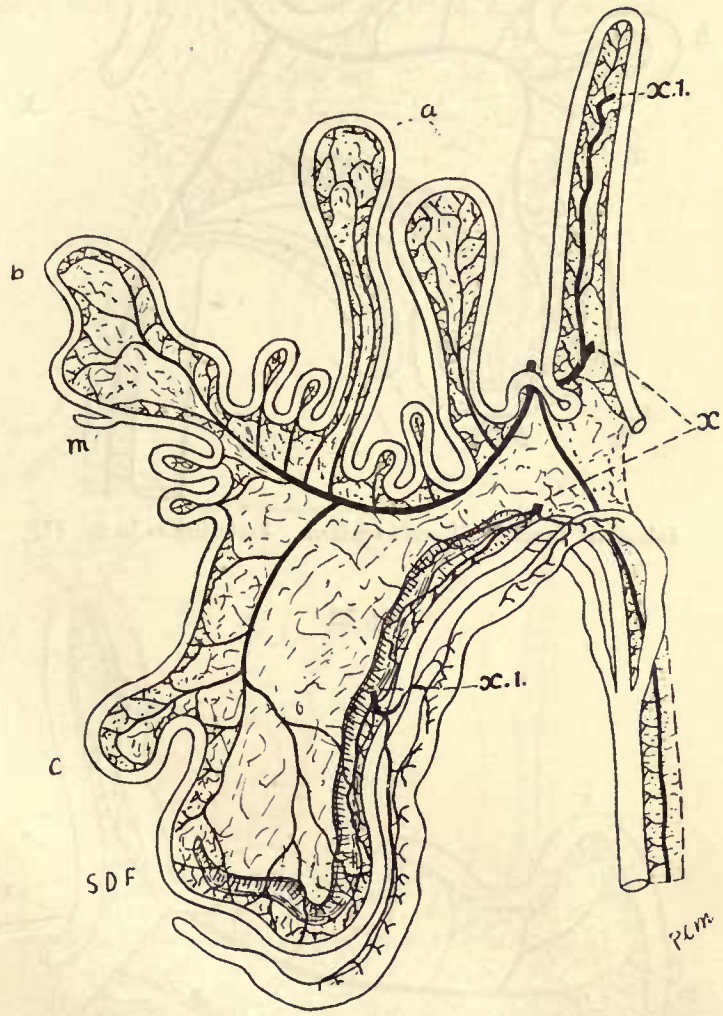


Intestinal Tract of *Tringa alpina*. Lettering as in fig. 41.

of a supra-duodenal loop not well separated from the general outline of the Tract, but drained by a "bridging" vein, and having closely attached to it the pair of long cæca. The rectum is rather short and straight. The condition in *Himantopus* is similar to this but still more archecentric—that is to say, the loops are still less marked off from the general sweep of Meckel's tract. *Vanellus vulg aris* and *V. cayennensis* are like *Numenius*. In *Tringa alpina* (fig. 49) a simple modification of the *Numenius* condition is presented. Loop "*b*" of Meckel's tract has grown out axially, leaving the large diverticulum at its

base, and the supra-duodenal loop is better separated. In *Recurvirostra avocetta* a still more apocentric modification in the same direction is reached. The axial loop has grown outwards to more than twice the length attained in *Tringa*, and is folded irregularly as a flat ribbon, partly rolled on itself and partly spirally twisted. The cæca remain long, and the other parts of the gut are as in *Tringa*. A still greater apocentric divergence of precisely the same kind occurs in *Scolopax rusticola* (Plate 22). I have already figured the very remarkable conformation assumed by its gut (26. fig. 16). The

Fig. 50.

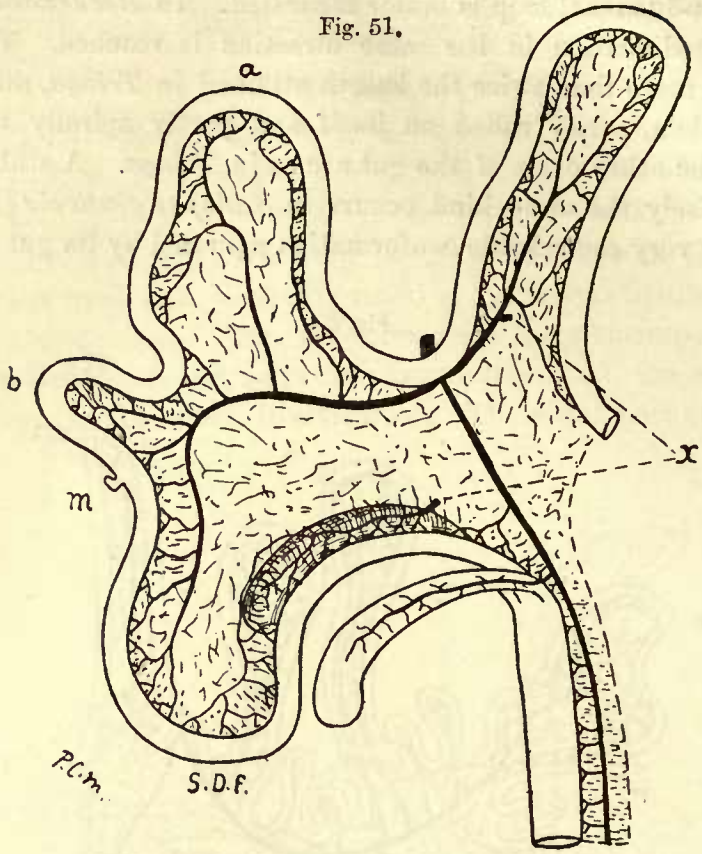


Intestinal Tract of *Chionis alba*. Lettering as in fig. 41.

change is simply that the axial loop has grown still longer than in *Recurvirostra*, and the rolling-up and spiral twist is still better marked. The cæca have degenerated, and have left isolated a small supra-duodenal loop with a bridging vein.

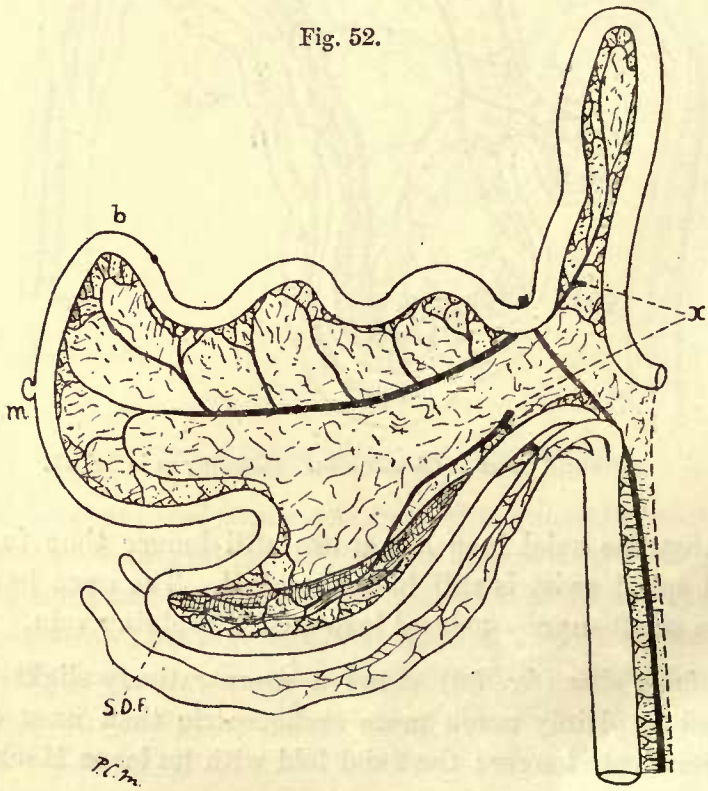
CHIONIDÆ.—*Chionis alba* (fig. 50) shows a comparatively slight modification of the *Numenius* type, and is plainly much more archecentric than most of the Charadriidæ. Meckel's tract is relatively longer; the axial fold with its large Meckel's diverticulum is

Fig. 51.



Intestinal Tract of *Glareola ocularis*. Lettering as in fig. 41.

Fig. 52.

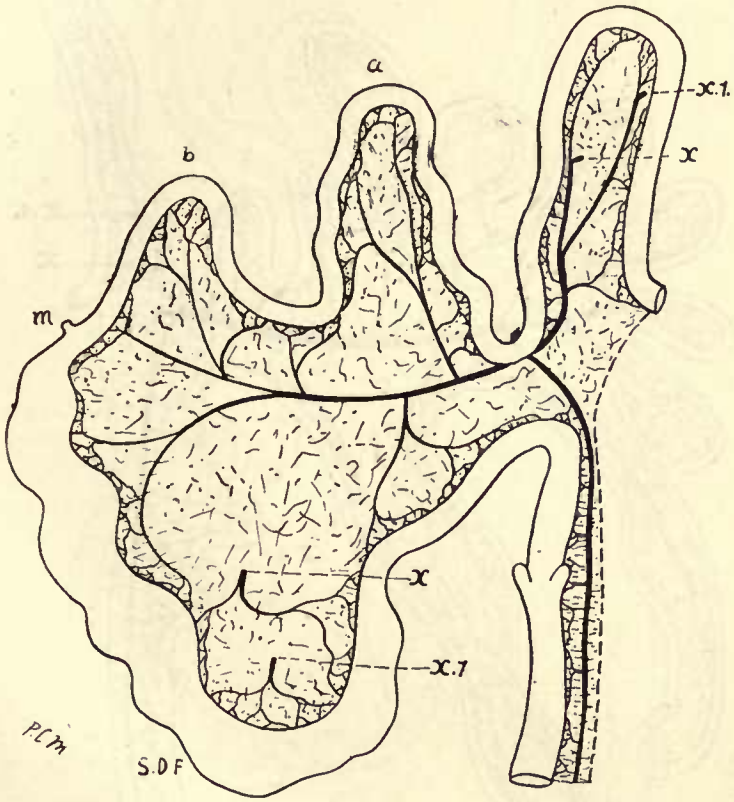


Intestinal Tract of *Thinocorys rumicivorus*. Lettering as in fig. 41.

practically identical with that of *Numenius*; but the fold "*a*" is represented by two loops, and loop "*c*" is partly fused with, or not separated from, the very large supra-duodenal loop to which the long cæca are attached.

GLAREOLIDÆ.—In *Glareola ocularis* (fig. 51), and *G. pratincola* is practically identical in this matter, another very simple modification of the *Numenius* type is displayed. The duodenum is similar; Meckel's tract is relatively shorter, and is thrown into loops "*a*," "*b*" with a small Meckel's diverticulum at its base, and a large and wide supra-duodenal loop, loop "*c*" not being formed. The cæca are attached in the usual way to the supra-duodenal loop, and the rectum is short, wide, and straight.

Fig. 53.



Intestinal Tract of *Parra jacana*. Lettering as in fig. 41.

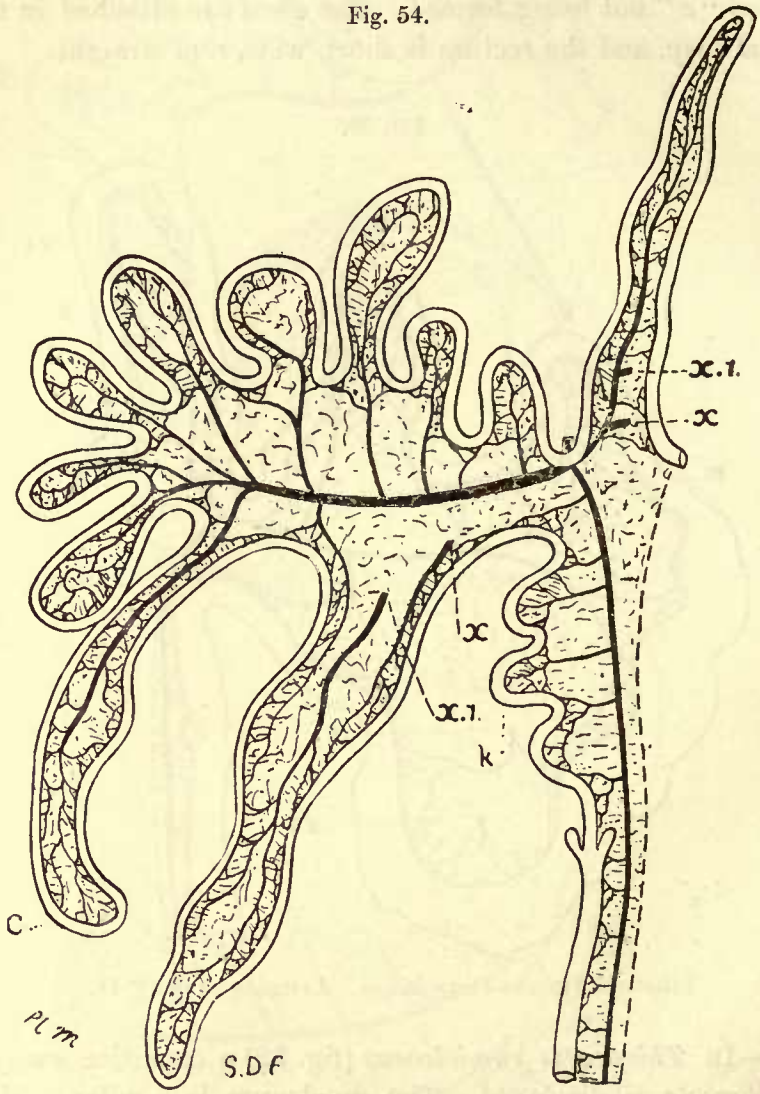
THINOCORIDÆ.—In *Thinocorys rumicivorus* (fig. 52) a condition essentially similar to that found in *Glareola* is displayed. The duodenum is similar; Meckel's tract is suspended at the end of an oval stretch of mesentery, and in it loop "*b*" with the diverticulum at its base is obvious, although in the drawing it is represented as turned up instead of running out in the axial line. Loops "*a*" and "*c*" are not differentiated, and the supra-duodenal loop to which the long cæca are attached is not sharply separated off except at its apex. The rectum is straight, wide, and of moderate length.

ŒDICNEMIDÆ.—In *Œdicnemus scolopax*, the Stone-Curlew, there is displayed a conformation closely similar to that found in *Thinocorys* and *Glareola*. The duodenum

is straight and simple, although rather long. Meckel's tract displays a small loop "*a*," then an axial loop "*b*" with Meckel's diverticulum on its distal limb; loop "*c*" is not differentiated from the supra-duodenal loop, to which the long cæca are attached. The rectum is straight. It is plain that *Œdicnemus* is more archecentric than the ordinary Curlews, and that its nearest allies are the Glareolidæ, Parridæ, and Thinocoridæ.

Parridæ.—In *Parra jacana* (fig. 53, p. 233) the same ground-form is obvious, although

Fig. 54.

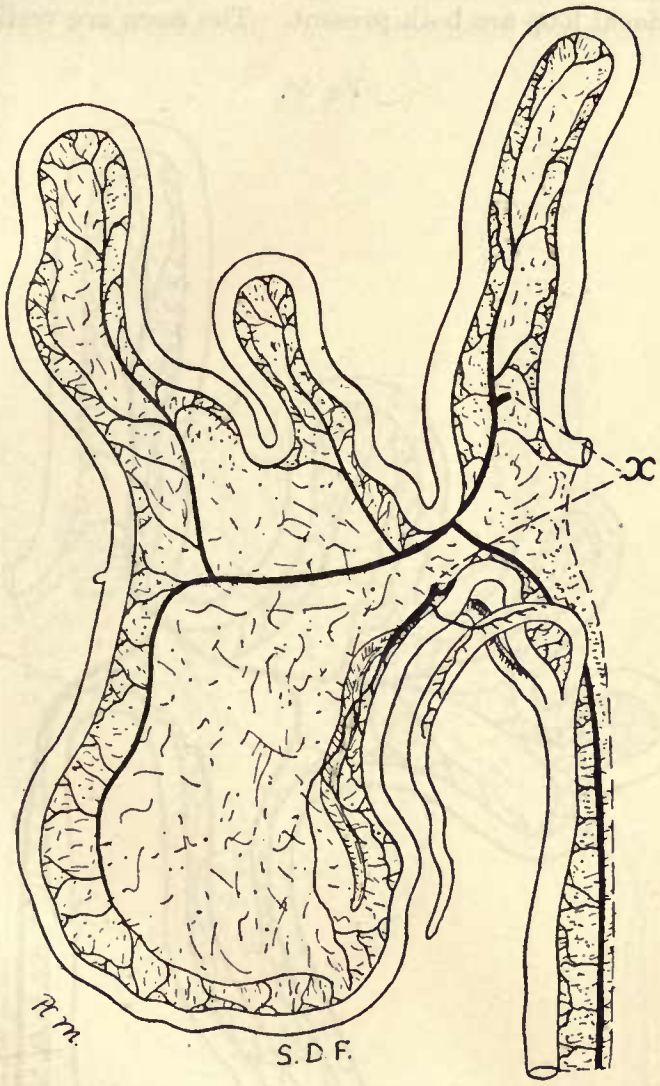


Intestinal Tract of *Pagophila eburnea*. Lettering as before.

there is a good deal of individual specialization. The duodenum is similar. Meckel's tract exhibits loops "*a*" and "*b*," the latter with the diverticulum at its base. There is no trace of loop "*c*," the distal portion of Meckel's tract appearing as a single very large supra-duodenal loop supplied by two "bridging" veins and with the proximal portion of the gut unusually dilated. The cæca are vestigial, and the rectum is short and straight. Except for the vestigial cæca, *Parra* is very like *Œdicnemus*.

It is plain that in the Limicolæ there is displayed a ground-form very close to what I described as the Gruiform metacentre, but rather more archecentric than that. From this condition the Charadriidæ exhibit a striking set of progressively more apocentric modifications, reaching a climax in the conformation of the gut in *Scolopax*. The other

Fig. 55.



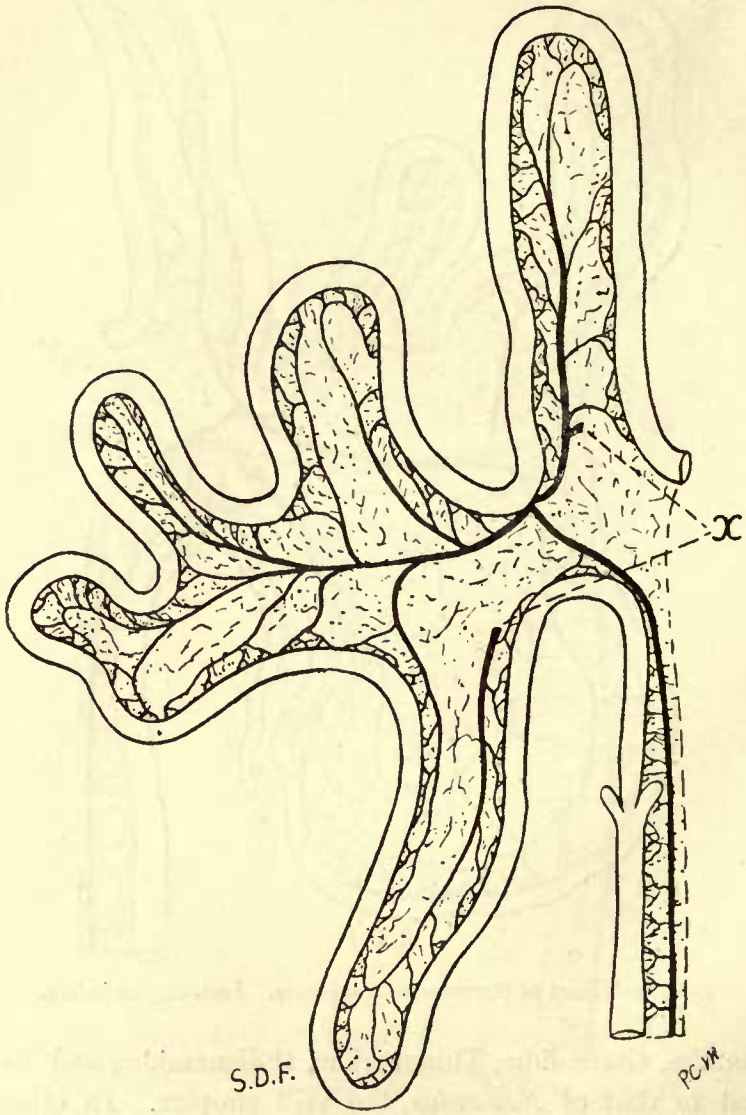
Intestinal Tract of *Stercorarius crepidatus*. Lettering as before.

families, the Chionidæ, Glareolidæ, Thinocoridæ, Œdicnemidæ, and Parridæ, all display types closely allied to that of *Numenius*, but still simpler. In other words, a form of gut like that in *Numenius* is a metacentre common to the Gruiformes and the Limicolæ: from this the Gruiformes have diverged in one direction, the specialized Charadriidæ in another, while the other families cluster about the metacentre.

Lari.

Laridæ.—I have already described and figured the conformation of the gut in *Larus marinus* (26. fig. 17). The duodenum is narrow and straight. Meckel's tract is thrown into a series of irregular loops, the first of which probably represents "*a*," while "*b*" appears as a number of closely-set short loops, proximad of the diverticulum. "*c*" and the large supra-duodenal loop are both present. The cæca are vestigial, and the rectum

Fig. 56.

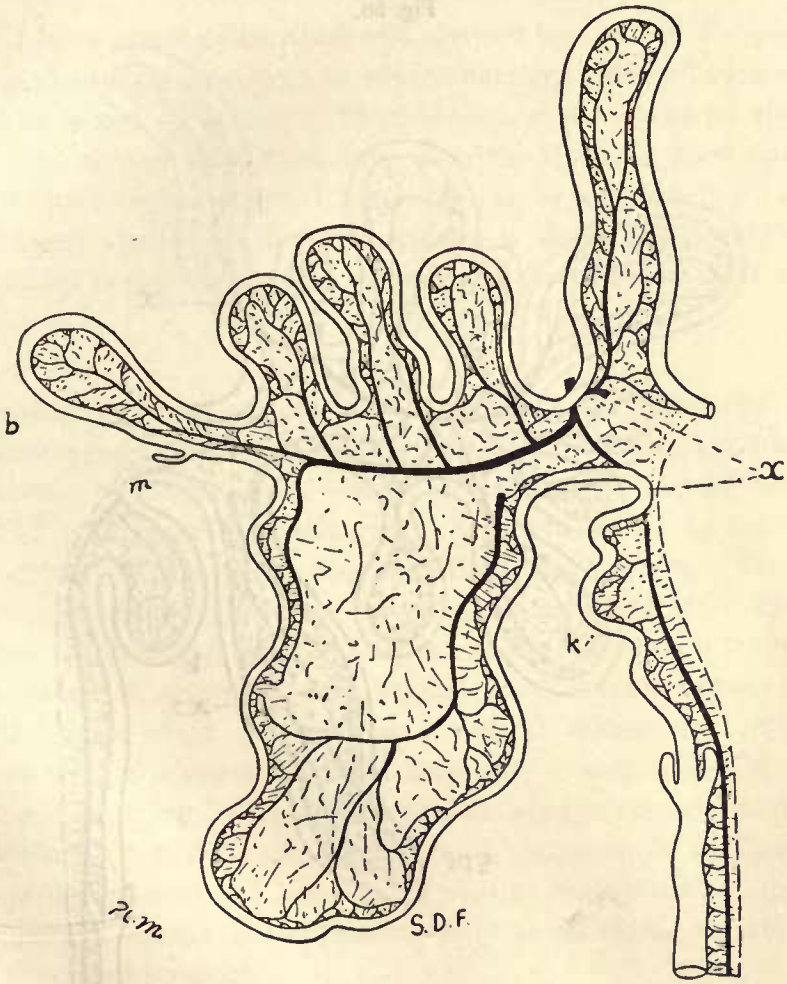


Intestinal Tract of *Sterna hirundo*.

is rather long. Other specimens of *Larus marinus* were identical, except that Meckel's diverticulum was absent, a condition frequent in the Gulls. *Larus argentatus* was closely similar, and *L. ridibundus* differed only in that the loops of Meckel's tract were more definite and were twisted into a common spiral. In *Pagophila eburnea* (fig. 54, p. 234) the general conformation is similar. Loop "*c*" and the supra-duodenal fold are both

larger. However, the most striking circumstance is the appearance above the cæca in the posterior part of Meckel's tract of a set of kinks drained by the rectal vein. In the drawing, the relative importance of these has been slightly exaggerated; but I was anxious to call attention to them, as their presence suggests either an unlikely affinity between the Laridæ (and the Alcidæ) and the Pelargo-Colymbomorphine assemblage, or, more probably, that the existence of this kink is a multiradial apocentricity to which too much importance must not be attached. In *Stercorarius crepidatus* (fig. 55, p. 235) a

Fig. 57.



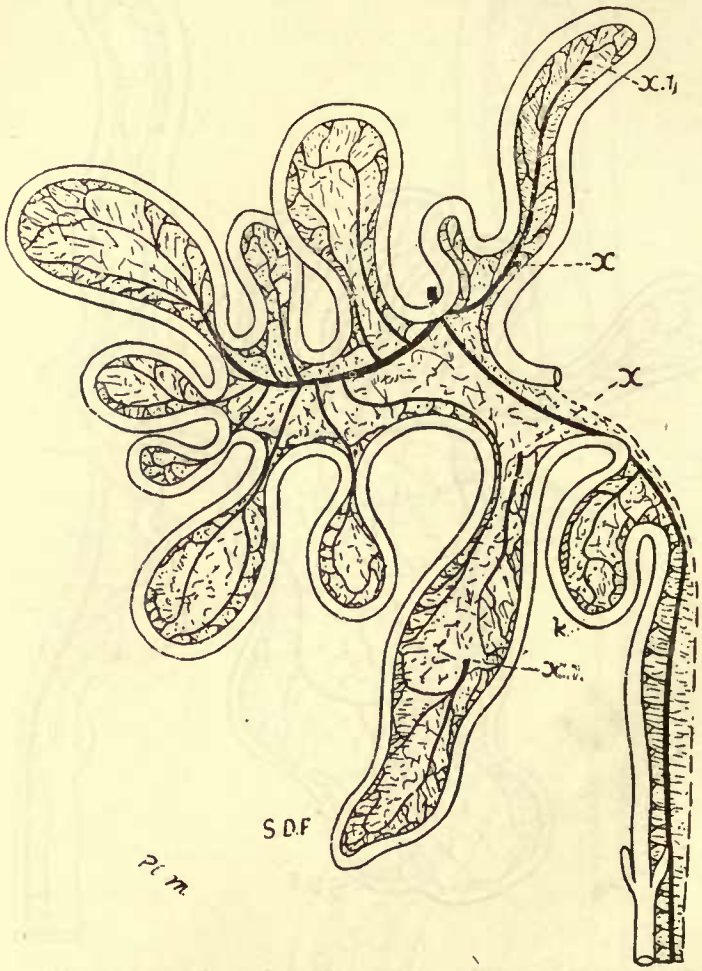
Intestinal Tract of *Fratercula arctica*. Lettering as in fig. 41.

more archecentric type of gut is displayed, the arrangement rather closely resembling that found in *Thinocorys* and *Glareola*. The duodenum is simple. Meckel's tract exhibits two loops proximad of the diverticulum, while distad of it is a very wide area representing a supra-duodenal fold and an undifferentiated loop "*c*." The cæca are long and the rectum is straight. In *Sterna hirundo* (fig. 56) the conformation is more apocentric, and the pattern resembles that in many of the specialized Gruiform and Charadriiform types. Meckel's tract is thrown into three minor loops, which, however, are better left

unidentified, as the diverticulum is not present, and there is a highly specialized supra-duodenal loop left free by the degeneration of the cæca and closely resembling the duodenum in shape. This similar moulding of the duodenum and the supra-duodenal loop is a condition found in many of the higher forms with relatively short guts.

Alcidæ.—In *Fratercula arctica* (fig. 57) a conformation of the same general character as that in many of the Gulls appears. The duodenum is of moderate size and not twisted. The greater part of Meckel's tract consists of a set of short loops, the axial of which bears a large diverticulum in the Ralline position, and of a very large supra-

Fig. 58.



Intestinal Tract of *Lomvia troile*. Lettering as before.

duodenal loop from which there has not been separated loop "*c*." Above the vestigial cæca is the curious supra-cæcal kink to which attention was drawn in certain Gulls. In *Lomvia troile* (fig. 58) a Gull-like pattern is displayed. There is no diverticulum to indicate the exact topography. There is a well-formed supra-duodenal loop and a large supra-cæcal kink. The cæca are vestigial, and the rectum is extremely short.

The Laridæ and Alcidæ are families of birds typically fish-eating, and in which lengthening and narrowing of the gut has to be allowed for. That allowance having

been made, the various conformations exhibited by the different genera of both families (from the point of view of conformation of the gut no distinction can be made between the families) appear obviously to belong to the simpler Ralline and Charadriiform patterns. The only other possible suggestion of affinity is provided by the existence of the supra-cæcal kinks in some Gulls and Hawks; but, as the other portions of the gut are so unlike the conformations found among the Pelargo-Colymbomorphine assemblage, I think the presence of the kinks in these few forms must be taken as a multiradial modification.

Pteroclo-Columbine Assemblage.

PTEROCLES.—I have already described and figured the gut in *Pterocles bicinctus* (26. fig. 19). The duodenum is straight and rather narrow. Meckel's tract is expanded to form three definite loops. The first of these is long, expanded at its apex, and curiously bent on itself. The second is an axial loop bearing Meckel's diverticulum at its apex. The third is a definite supra-duodenal loop, drained by a "bridging" vein and having the long cæca closely applied to it. The rectum is short and straight. In *Pterocles alchata* the condition is exactly similar, except that the cæca are relatively longer.

COLUMBÆ.

I have examined a large number of Columbidæ, including the genera *Calœnas*, *Chalcopelia*, *Chalcophaps*, *Columba* (many species and varieties), *Columbula*, *Geopelia*, *Goura*, *Leucosarcia*, *Ocyphaps*, *Œna*, *Phaps*, *Phlogœnas*, *Ptilopus*, *Starnœnas*, *Treron*, and *Turtur*. The conformation of the gut is best understood by taking it as a simple but more apocentric derivative of the condition in *Pterocles*. The duodenum is a simple loop. Meckel's tract is thrown into the same three folds. The first is simpler than in *Pterocles*. The second or axial loop is usually very much longer, and it may be twisted into an elaborate spiral (26. fig. 19), and as in *Pterocles* bears the diverticulum, or a very small vestige of it marked by a ventral mesentery, or no vestige at all. The third loop is a definite supra-duodenal loop very closely modelled on the duodenum and drained by a "bridging" vein. The cæca are always vestigial and not infrequently are absent. Beddard (2. p. 308) mentions that in an example of *Tympanistria bicolor* only one vestige was present. I have found similar variations not infrequently in the varieties of the genus *Columba*, but apparently only as individual variations. The rectum is always very short and straight.

There is little difference in the conformation of the gut in the different genera and species. The larger forms in most cases have the length of gut relatively greatly increased, and the increase is most noticeable in the spirally twisted axial loop. In some small forms, such as *Œna*, the gut is absolutely and relatively shorter, and there is little trace of the spiral. Precisely a similar state of affairs exists among Passerines, where size is one of the chief factors in determining the length of the whole gut, and the consequent elaboration of the axial spiral. In *Ptilopus* and other fruit-eating Pigeons the whole gut is extremely reduced in length and is very wide. In such cases the relation of the pattern to that in ordinary Pigeons can only be guessed.

From the point of view of conformation of the intestinal tract, it does not appear that the Pteroclo-Columbæ stand in close relation to other Charadriiform birds. The only character in common is the tendency for Meckel's tract to be drawn out into long minor loops, and the particular apocentricity which reaches its climax in the elaborate spiral of the axial loop of Pigeons is different from that in the specialized Charadriidæ such as *Recurvirostra* and *Scolopax*, the difference being made plain by the relative positions of Meckel's diverticulum. The comparison with *Opisthocomus* seems to give a more fertile suggestion.

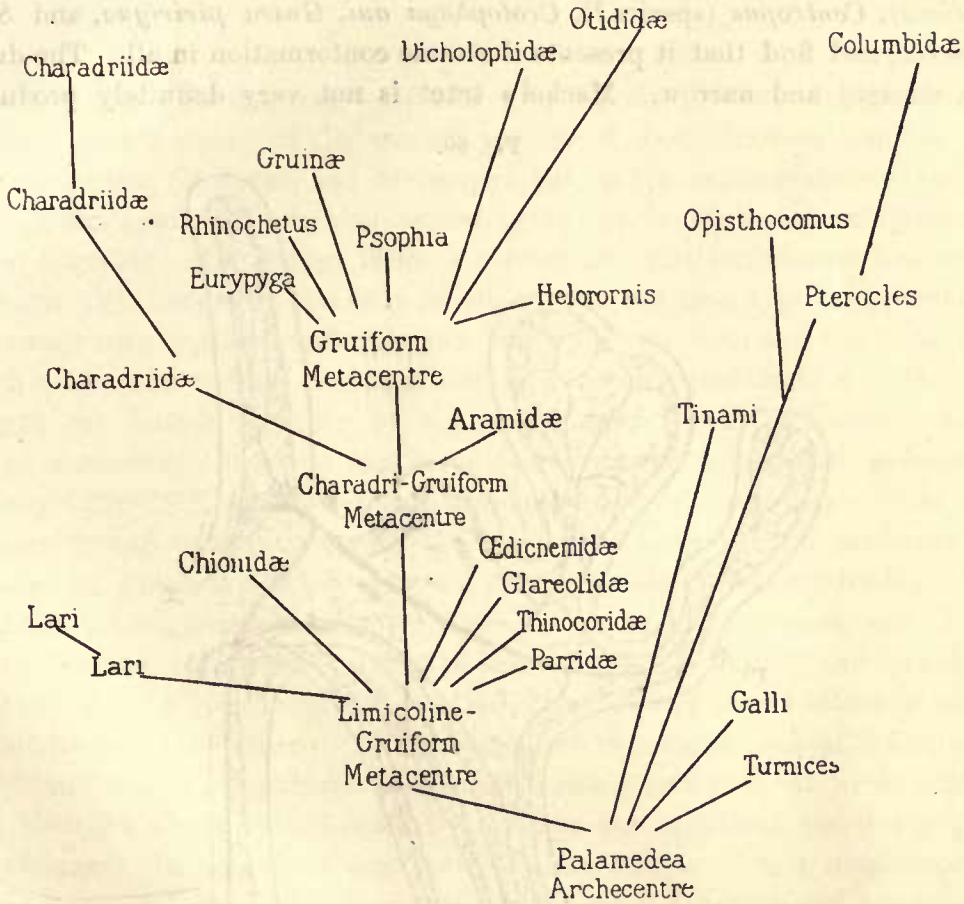
Summary of the Alectoromorphine Legion. (Plate 22.)

Gadow unites the Tinamiformes, Galliformes, Gruiformes, and Charadriiformes into the Alectoromorphæ, the first Legion of his second Brigade, and I propose now to review shortly the characters of the intestinal tract presented in this large assemblage. It must be clear that the conformations of the gut within this group do not follow many of the more generally accepted modes of subdividing the group so readily and naturally as in the case of the Pelargo-Colymbomorphine Brigade. Those, I think, who have paid most attention to the classification of birds will be prepared for this result, for the many and different divisions proposed suggest that the assemblage is still in indifferent order. From the point of view of the subject of this Memoir, it is in the first place clear that the Turnices and Galli stand apart from the other groups, inasmuch as their pattern of intestinal tract has remained markedly archecentric, differing extremely little from that in *Palamedea*. Next, the Tinamidæ retain no suggestion of Struthious affinity; they have moved far apocentrically, while the Ratites, like the Galli, have remained close to the archecentric condition. The Tinamidæ present on the one hand most striking resemblances with the Otididæ, an apocentric type of the Gruiformes. On the other hand, the radius of apocentricity on which they lie suggests that of *Opisthocomus*, *Pterocles*, and the Columbæ. *Opisthocomus*, one of the Galliformes of Gadow, certainly stands far apart from the others, and, so far as the gut is concerned, an affinity with *Pterocles* and the Columbæ is most clearly indicated. The guts of Columbæ and of *Pterocles* are extremely similar, and there is no indication of any affinity with the conformations exhibited in the other Charadriiformes or Gruiformes.

The Galli, Turnices, *Opisthocomus*, and Pteroclo-Columbæ having been disposed of, there is less difficulty in arranging the conformations of the gut in other members of the Alectoromorphine Legion in coherent order. A conformation that is a simple derivative of the archecentric form appears to underlie all of them, and this may be called a Limicoline-Gruiform metacentre. The duodenum is simple; Meckel's tract is slightly elongated, but the elongation is proximad of the diverticulum so that that appears on the distal limb of an axial loop. The distal region of Meckel's tract shows the beginning of separation into a definite supra-duodenal loop to which the long cæca are attached, and into a loop between that and the diverticulum. The rectum is short and straight. The simpler Limicoline families, such as the Chionidæ, Glareolidæ, Thinocoridæ, and Parridæ, are extremely close to this Limicoline-Gruiform metacentre; and the Lari, which from this point of view present no clear distinction into Alcidæ and

Laridæ, are derivatives of the pattern only slightly modified by increased length. A modification of the Limicoline-Gruiform metacentre is found in many of the simpler Charadriidæ such as *Numenius*, and consists in the gradual shaping of Meckel's tract into three loops and a supra-duodenal loop. Of the three, one is axial and carries a large diverticulum on its distal limb. From this Charadri-Gruiform metacentre one line of progressively increasing apocentricity, consisting chiefly in a lengthening of the axial loop, is attended by degeneration of the cæca; it runs through *Tringa* and *Recurvirostra* to *Scolopax*. The Gruiform metacentre is another apocentric derivative of the Charadri-

Fig. 59.



Evolution of the Intestinal Tract in the Alectoromorphine Legion. (For *Helorornis* read *Heliornis*.)

Gruiform metacentre, and is reached by the first three loops of Meckel's tract, including the axial loop, being more clearly marked off and lengthening equally. Most of the Rallidæ remain in this condition. The Gruinæ are apocentric modifications of it in which all the loops, except that immediately following the axial loop, increase in length individually. The Psophiinæ and Heliornithidæ are practically unmodified from it. *Rhinochetus* is modified only in that the first loop of Meckel's tract is represented by two loops, and that the cæca are reduced. *Eurypyga* is more modified, its apparent simplicity being almost certainly secondary. The Dicholophidæ and the Otididæ are very apocentric modifications of it, the apocentricity consisting chiefly in the reduction

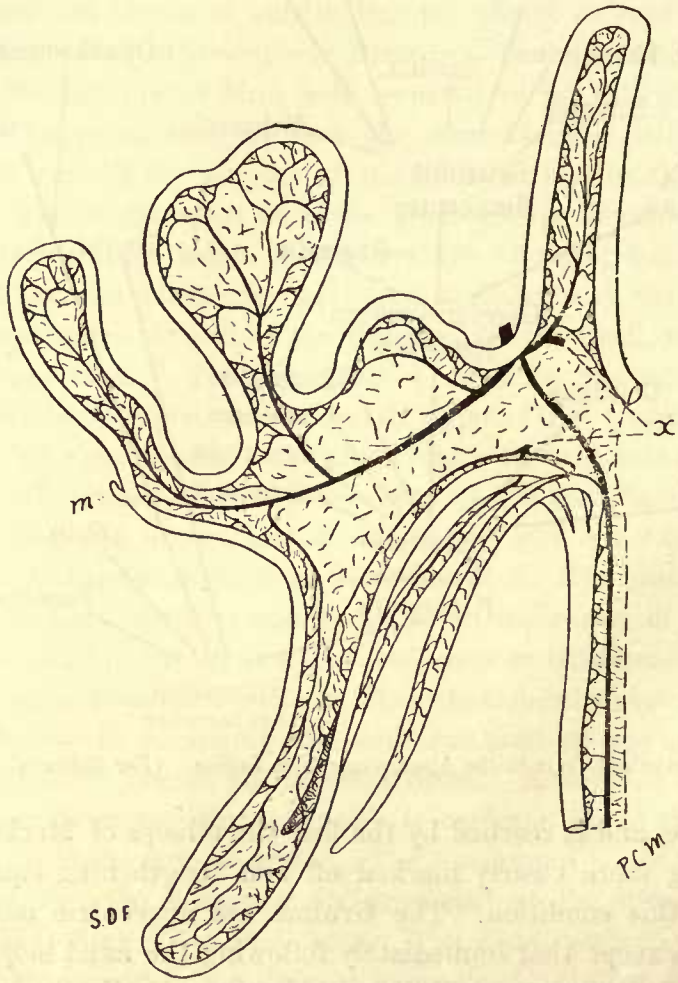
of the first and third loops of Meckel's tract and the great elongation of the axial and supra-duodenal loops. *Aramus* is more difficult to place. It appears to be certainly more archecentric than other Gruiformes, and is to be derived either from the Charadriiform-Gruiform metacentre or, even more archecentrically still, from the metacentre common to the Limicoli and Gruiformes.

CUCULIFORMES.

Cuculi.

Cuculidæ.—I have examined the intestinal tract of *Cacomantis lanceolatus*, *Carpococcyx radiatus*, *Centropus* (species?), *Crotophaga ani*, *Guira piririgua*, and *Scythrops novæ-hollandiæ*, and find that it presents the same conformation in all. The duodenum (fig. 60) is straight and narrow. Meckel's tract is not very definitely produced into

Fig. 60.



Intestinal Tract of *Carpococcyx radiatus*.

loops, but on its periphery there are two loops anterior to the diverticulum, and, posterior to it, one very long supra-duodenal loop to which the long cæca are attached. The rectum is always straight, but differs in length, being extremely short in some Cuckoos.

MUSOPHAGIDÆ.—I have examined several specimens of *Corythaix chlorochlamys* and *C. persa*, and have already figured the intestinal tract (26. fig. 20). The whole gut is short and wide, in obvious association with frugivorous habit. This circumstance and the fact that all the specimens I have seen were affected with tubercular nodules which made the examination of the gut unsatisfactory, make it impossible to say anything very definite regarding these forms. The duodenum is straight and of moderate width. Meckel's tract appears in two portions, the proximal of which is a short, nearly circular expanse on which there was no trace of a diverticulum, and the distal a supra-duodenal loop very closely moulded on the duodenum and supplied by a large bridging vein. The rectum was short and wide, and I found no trace of cæca.

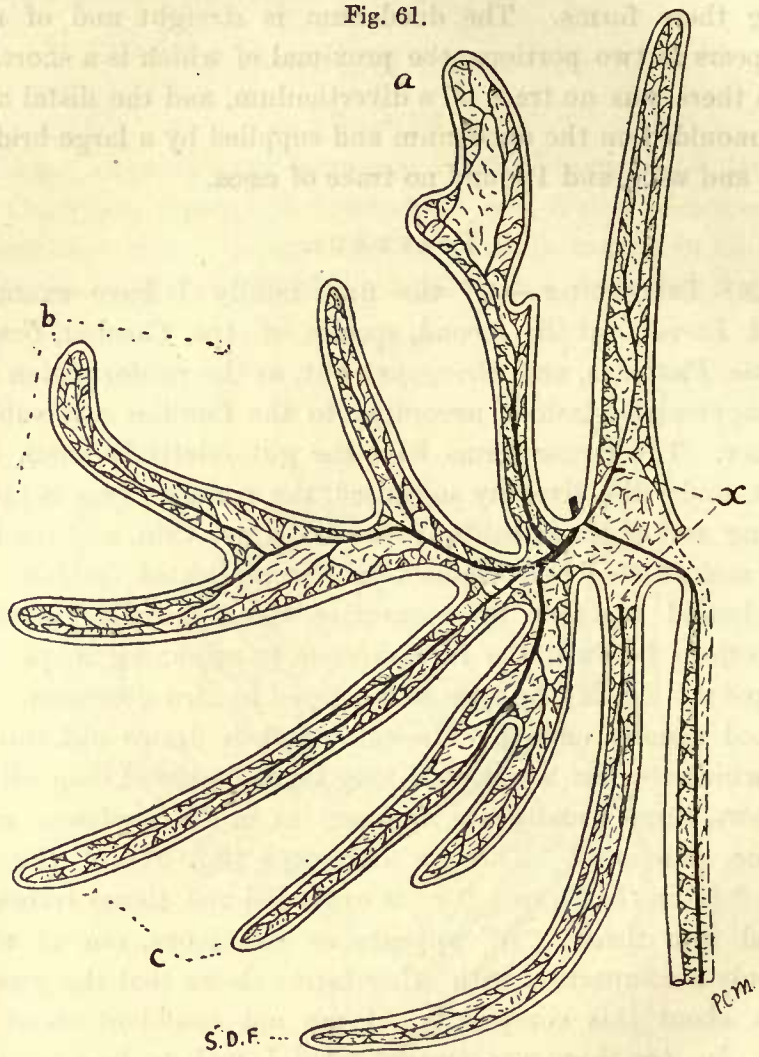
PSITTACI.

TRICHOGLOSSIDÆ: PSITTACIDÆ.—Of the first family I have examined species of *Trichoglossus* and *Lorius*; of the second, species of *Ara*, *Cacatua*, *Conurus*, *Chrysotis*, *Eclectus*, *Palæornis*, *Psittacus*, and *Stringops*; but, as the conformation of the gut does not differ in any appreciable fashion according to the families and subfamilies, I shall treat them together. The larger forms have the gut relatively much longer than the smaller forms, but, under the diversity so caused, the common type is apparent. In all, the gut is very long and of small calibre; the walls are thin, and the loops are folded upon each other, and twisted and doubled in a complicated fashion. The masses of twisted gut are bound together by connective tissue usually loaded with fat, and "bridging" connections between the blood-vessels in adjoining loops are common. I have already figured (26. fig. 21) the type as displayed in *Ara ararauna*. The duodenum is long, narrow, and usually curved. Meckel's tract is drawn out into very long and narrow loops, of which the last is always a long supra-duodenal loop with a "bridging" vein. Of the others, three usually are apparent as in *Trichoglossus*, and any of these three may become compound. Thus in *Stringops* (fig. 61), of the proximal loops (marked "*a*" and "*b*" in the figure), "*a*" is expanded and shows traces of subdivision; "*b*" is subdivided into three; "*c*" appears as two loops, one of which is further subdivided, and only a comparison with other forms shows that the great length of the tract has brought about this complexity. I am not confident about the position of the diverticulum. In *Ara* there was present what I took to be a small representative of it at the apex of loop "*b*," and in one other Parrot I have noted a similarly placed trace. But in the others, including several other specimens of *Ara ararauna*, and in other species of *Ara* there was no trace. The cæca always are absent, and the straight rectum varies in length.

The diet of the Cuculidæ, consisting of insects, fruit, and flesh, is not of a nature to have caused much homoplastic modification, and the conformation of the gut is such as to make it possible to derive it from any fairly archecentric type. Garrod (13) and others have suggested an affinity between the Cuculidæ and the Galli, and, in so far as the conformation of the gut in Galli is archecentric, there is nothing definitely against such an origin of the Cuculine gut. On the other hand, there is nothing definitely in its favour, for such apocentricity as is indicated in the gut of the Galli is different from

that found among the Cuculidæ. In these, as we have seen, the tendency is for the anterior portion of Meckel's tract to be produced into two loops, and this mode of apocentricity is typical of Coraciiform birds. The reduced gut of the Musophagidæ might have come from any simple source. The Psittaci live largely on hard grains and

Fig. 61.



Intestinal Tract of *Stringops habroptilus*.

a, *b*, *c* and S.D.F. are the four loops of Meckel's Tract typical of the Psittaci; *a*, *b*, and *c* being here subdivided, while S.D.F. is a supra-duodenal loop.

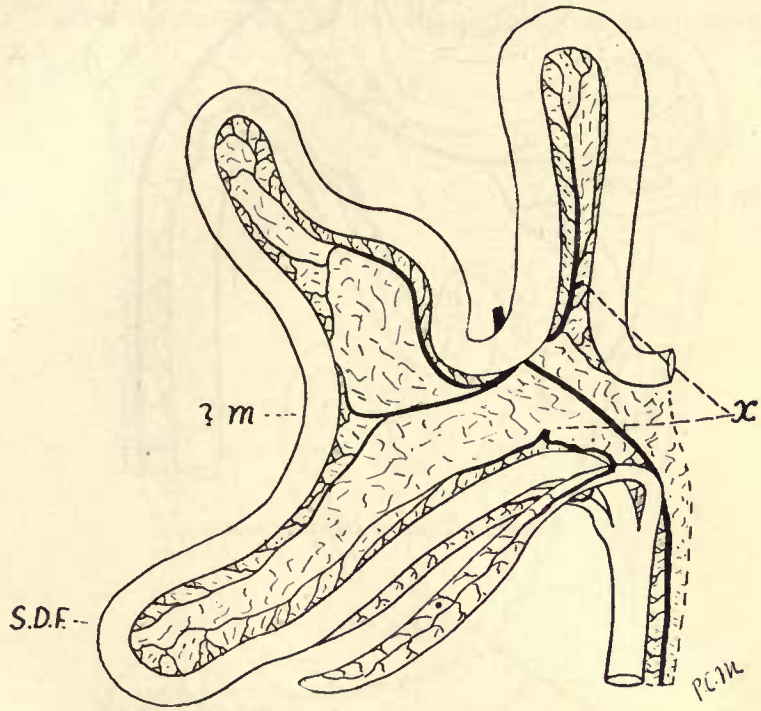
seeds, and this habit, together with the large size of many of the forms, has no doubt greatly added to the length of the gut and helped to disguise its morphological form. That conformation is markedly apocentric, as shown by the complicated folding of the loops, the length of the loops, the individuality of the supra-duodenal loop, and the absence of cæca. No doubt such a type might have been derived independently from any of the more archecentric forms, from, for instance, some of the simpler Galli, as has been suggested, but it is equally easy and perhaps more natural to derive the Psittacine type from that occurring in the simpler Coraciiform birds.

CORACIIFORMES.

Coraciæ.

Coraciidæ.—I have examined the intestinal tract of *Leptosoma* (species ?) and of *Coracias garrula* (fig. 62). In both, which are practically identical, the duodenum is a

Fig. 62.



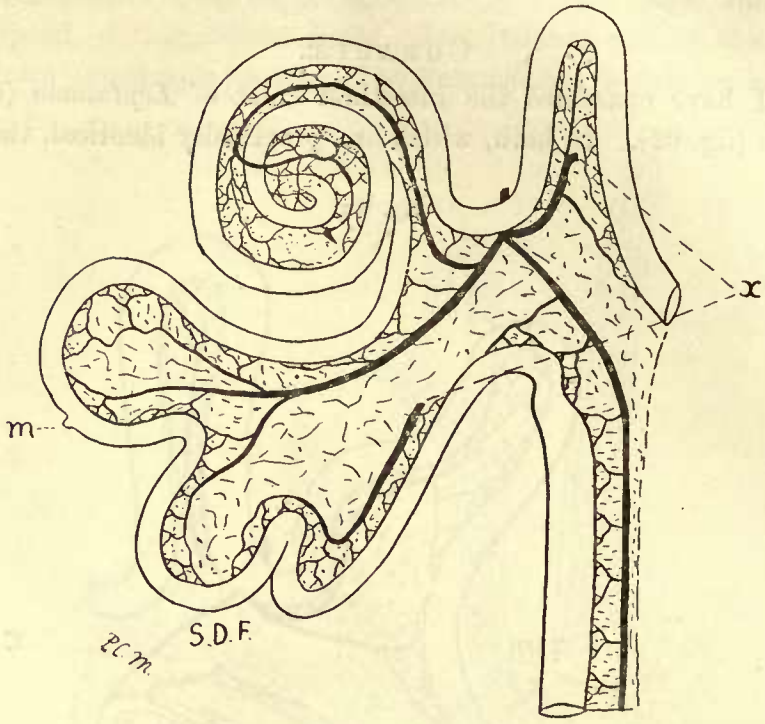
Intestinal Tract of *Coracias garrula*.

short loop relatively rather wide. Meckel's tract is thrown into two rather wide loops which are separated by the diverticulum, the latter being conspicuous in *Leptosoma*, and only faintly indicated by a trace of a ventral mesentery in *Coracias*. The distal loop is a supra-duodenal loop to which the long cæca are attached. The rectum is relatively short, wide, and straight.

Momotidæ.—I have examined *Todus viridis* and some other species of the same genus. The general conformation closely resembles that in the Coraciidæ, but the part of Meckel's tract anterior to the diverticulum is divided into loops and the cæca are shorter.

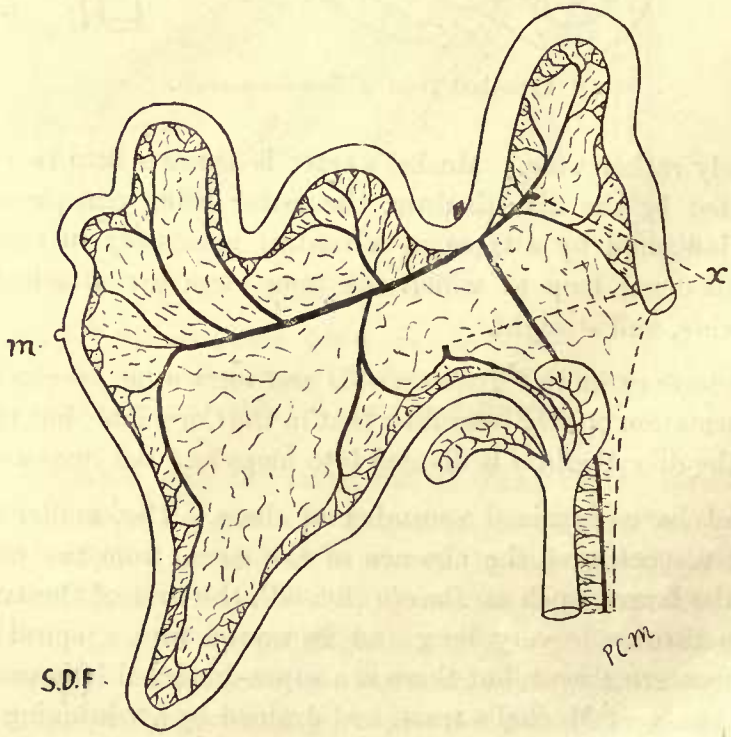
Alcedinidæ.—I have examined a number of these. The smaller forms do not differ in any important respect, save the absence of the cæca, from the conformation in the Momotidæ. In the larger, such as *Dacelo* (fig. 63), the first of the two loops into which Meckel's tract is thrown is very long and is wound into a spiral form. In all the Kingfishers the cæca are absent, but there is a supra-duodenal loop more or less separated from the general sweep of Meckel's tract, and drained by a "bridging" vein. The cæca have disappeared completely, and the rectum is very wide and rather long.

Fig. 63.



Intestinal Tract of *Dacelo gigantea.*

Fig. 64.

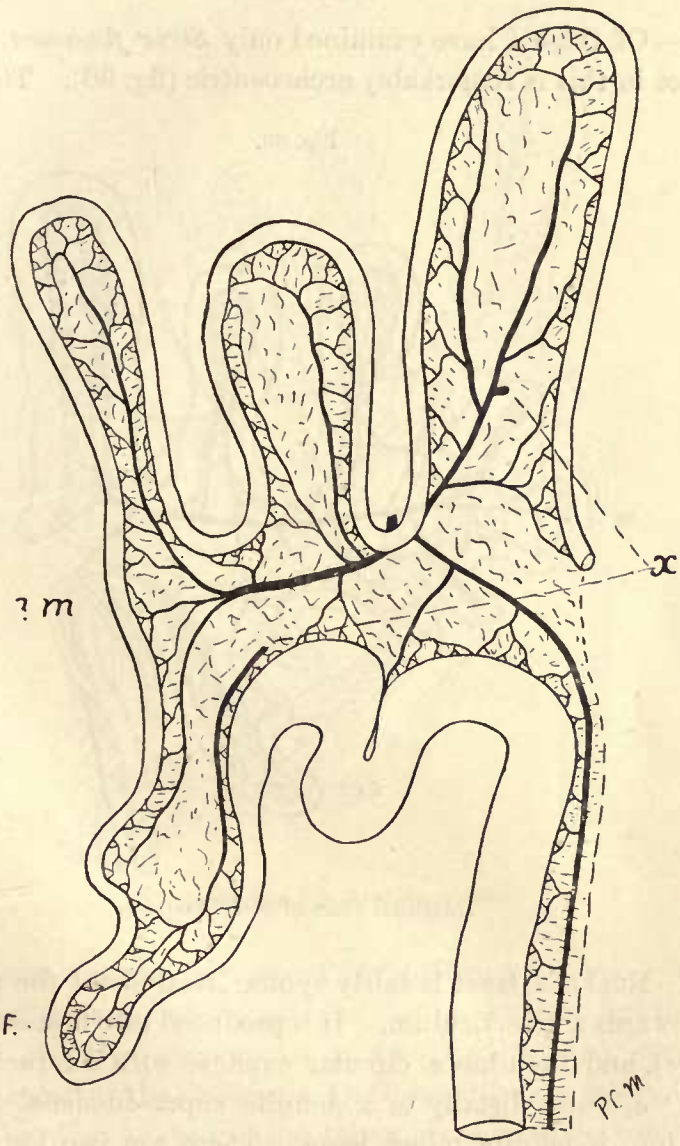


Intestinal Tract of a species of *Merops.*

MEROPIDÆ.—I have examined two specimens of *Merops*, the species not having been identified. In both (fig. 64) the duodenum was short and rather wide. Meckel's tract forms an expanded region, the proximal part of which showed trace of production into two minor loops, while the distal part was a long supra-duodenal loop not well separated from the general sweep of the Tract. The cæca were not long, but were wide and contained fæcal matter. The rectum was short and wide. In the middle of Meckel's tract there occurred a distinct diverticulum.

UPUPIDÆ.—In *Upupa epops* (fig. 65) the duodenum, as in many Coraciiform birds,

Fig. 65.



Intestinal Tract of *Upupa epops*.
?m, probable position of Meckel's diverticulum.

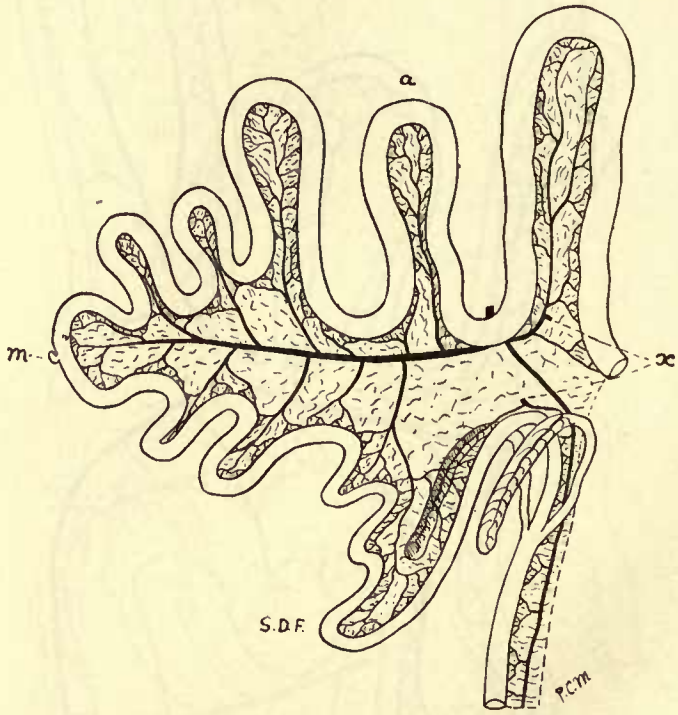
was a wide loop. Meckel's tract displayed two distinct wide loops on its proximal portion, while the distal formed a long supra-duodenal loop drained by a bridging vein. There

were no cæca, and the rectum was long, wide, and partly convoluted. In *Rhytidoceros plicatus* (26. fig. 23), and other Hornbills resemble it, the duodenum is extremely wide. Meckel's tract is thrown into three distinct long loops, of which the last is a well-formed supra-duodenal loop with "bridging" vein. The two anterior loops possibly correspond to the two loops of *Dacelo* and other *Coracii*; but the second, which is much the longer, bears a distinct diverticulum near the apex on its distal limb. There are no cæca, and the rectum is rather wide and straight. It is clear that the character of the gut does not unite the Hoopoes and Hornbills closely.

Striges.

(1) Strigin æ.—Of these I have examined only *Strix flammea*. The conformation of the intestinal tract in this is remarkably archecentric (fig. 66). The duodenum is a large

Fig. 66.



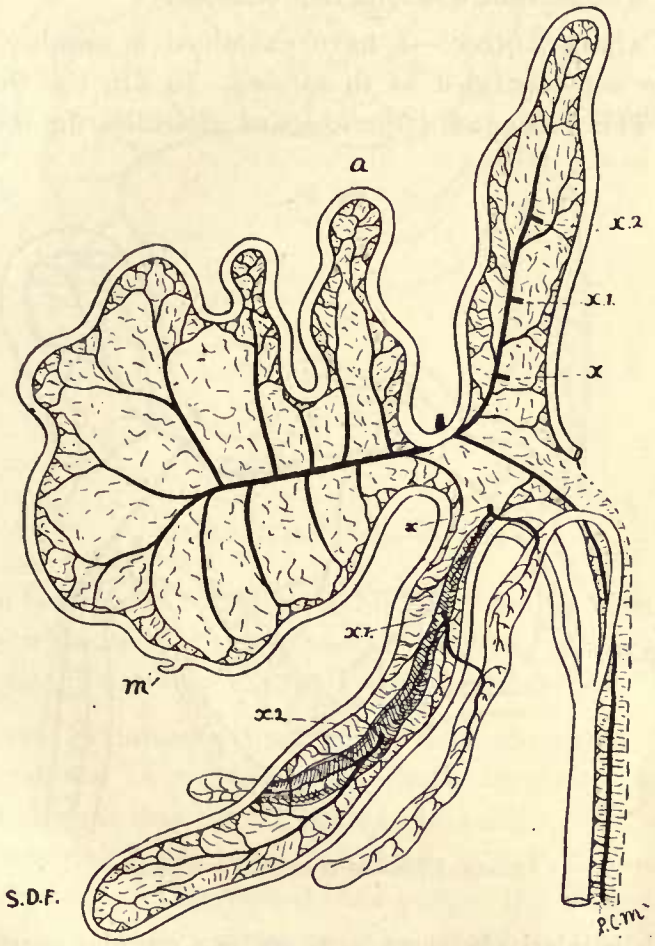
Intestinal Tract of *Strix flammea*.

but simple loop. Meckel's tract is fairly symmetrical about the middle mesenteric vein which runs out towards a diverticulum. It is produced into first one definite loop (marked "*a*" in the figure), and then has a circular expanse with a rather narrow neck, uniting it above to loop "*a*," and distally to a definite supra-duodenal loop. This expanse is partly produced into indefinite minor loops. There are two long cæca attached to the supra-duodenal loop, and the rectum is straight and of moderate length.

(2) Buboninæ.—Of these I have examined species of *Bubo*, *Asio*, *Athene*, *Syrnium*, *Speotyto*, and *Gymnoglaux*. Of these *Bubo maximus*, which I have already figured (26. fig. 22), *Asio*, and *Speotyto* do not differ in any important respect from *Strix*; the

supra-duodenal loop possibly is rather better separated from the general sweep of Meckel's tract. In the others, except *Gymnoglaux*, a slightly more apocentric modification has taken place. In *Syrnium aluco*, for instance (fig. 67), the duodenum is as in the others. Loop "*a*" of Meckel's tract is as in *Strix*, but the region between this and the diverticulum is much enlarged, so that the diverticulum is no longer at the apex of the circular expansion. The supra-duodenal loop has increased very much in size, and is well separated

Fig. 67.



Intestinal Tract of *Syrnium aluco*.

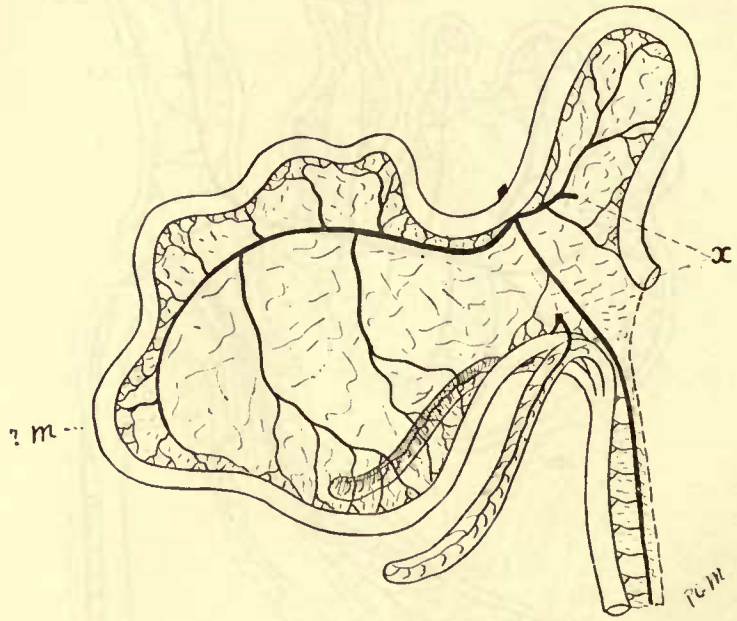
from Meckel's tract, and drained by a series of "bridging" veins. In *Bubo maculosus* and *B. poensis* the conditions are very similar to that in *Syrnium*. but the part of Meckel's tract anterior to the diverticulum appears in two well-marked loops, a conformation which recalls that in many of the Coraciæ. In *Gymnoglaux*, possibly in association with its small size, a simplification of the gut has taken place, with the result that there exists conformation closely resembling that in many of the Rollers and other simple short-gutted Coraciiform birds. Meckel's tract is thrown into two wide loops separated by the diverticulum, the posterior loop being a wide supra-duodenal loop with bridging veins.

Caprimulgi.

Steatornithidæ.—I have examined only a spirit-specimen of *Steatornis*, and that in a fragmentary condition after it had already passed through the hands of other anatomists. It was easy, however, to recognize the general conformation of the gut and its resemblance to the form in other Coraciiform birds. The duodenum was short and rather wide. Meckel's tract showed two loops anterior to the diverticulum and two, not so well separated, distad of it, the second being a distinct supra-duodenal loop with the functional cæca attached to it. The rectum was long and straight.

Podargidæ and Caprimulgidæ.—I have examined a number of these, several of which, however, were not identified as to species. In all, the form of the gut was essentially similar. The duodenum (*Nyctidromus albicollis*, fig. 68) is short and wide.

Fig. 68.



Intestinal Tract of *Nyctidromus albicollis*.

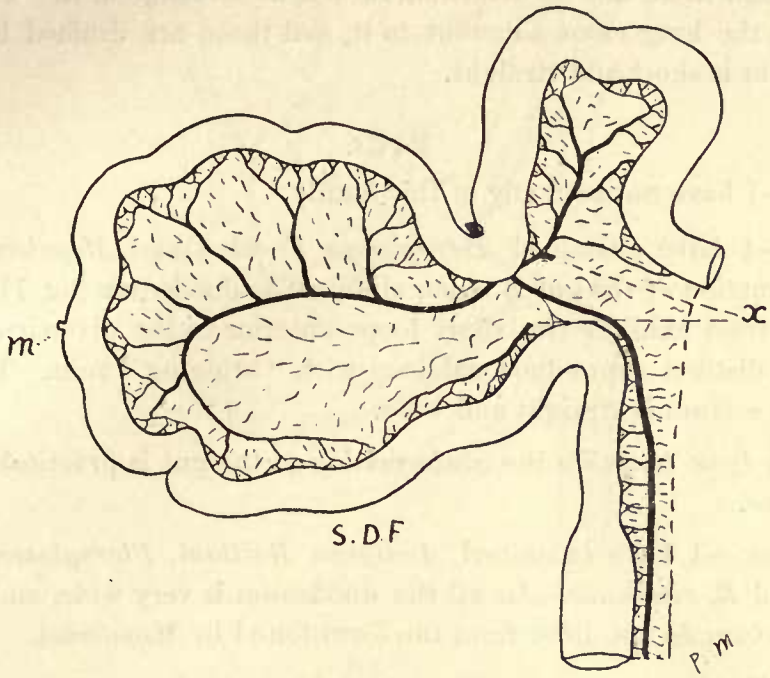
Meckel's tract, which is relatively short, appears as a circular expanse, upon the middle of which the diverticulum was present in most cases, but in some it was absent. The part of the Tract proximad of the diverticulum showed traces of expansion into the two loops so common in Coraciiform birds. The part posterior to it had the long cæca closely applied to it, and these were drained partly by a bridging vein. The rectum was relatively long and straight. This conformation found in the Caprimulgidæ is obviously remarkably archecentric, and is at once comparable with the primitive type.

Cypseli.

Cypselidæ.—I have examined several species of Swifts, and in all found the conformation similar to that in *Cypselus apus* (fig. 69). The duodenum is short and very wide.

Meckel's tract is short, and forms a circular expanse with the diverticulum nearly at the central point. The posterior region of the tract, however, shows traces of former

Fig. 69.



Intestinal Tract of *Cypselus apus*.

complexity, in that it is drained partly by a bridging vein, a circumstance to which I attach importance as evidence that the apparent simplicity of the gut is pseudocentric. The cæca are absent, and the rectum is straight and wide.

Trochilidæ.—I have examined a number of Humming-birds, and found that the conformation of the gut was in every case practically identical with that in *Cypselus*. It is worth while pointing out that the Humming-birds differ clearly in the conformation of the gut from the Passerine Nectariniidæ, although in both the small size has brought about a remarkable simplicity. The Nectariniidæ possess the Passerine nipple-like cæca, and show clear indications of the spiral twist in Meckel's tract which is a striking Passerine character, and there is no trace of either of these peculiarities in the Humming-birds.

Colii.

I have already described and figured the intestinal tract of *Colius capensis* (26. fig. 24). It is relatively shorter and wider than in any other bird that I have examined, and this modification, no doubt due to small size and frugivorous habit, has obliterated practically completely the underlying morphological form. The gut consists of a very wide duodenum, a Meckel's tract bearing a small diverticulum, and consisting of a simple loop similar to the duodenum in size and appearance, and a short, wide rectum. There are no traces of cæca.

Trogones.

In *Trogon puella* (fig. 70) the duodenum is a large loop expanded towards its apex, Meckel's tract shows two loops anterior to the position where I infer the yolk-sac to have been, although there was no diverticulum left as a vestige of it. The distal portion of the Tract has the long cæca adherent to it, and these are drained by a "bridging" vein. The rectum is short and straight.

Pici.

Galbulidæ.—I have not seen any of this family.

Capitonidæ.—I have examined *Tetragonops Frantzii* and *Megalæma asiatica*. In these the conformation of the gut is much alike. The duodenum (fig. 71) is a short, wide loop. Meckel's tract exhibits two short loops anterior to the diverticulum, and, distad of that, forms a distinct supra-duodenal loop with "bridging" vein. There is no trace of cæca, and the rectum is straight and wide.

Iyngidæ.—In *Iynx torquilla* the conformation of the gut is practically identical with that in *Megalæma*.

Rhamphastidæ.—I have examined *Andigena Bailloni*, *Pteroglossus Wiedi*, *Rhamphastos ariel*, and *R. vitellinus*. In all the duodenum is very wide, and Meckel's tract and the short rectum do not differ from the form found in *Megalæma*.

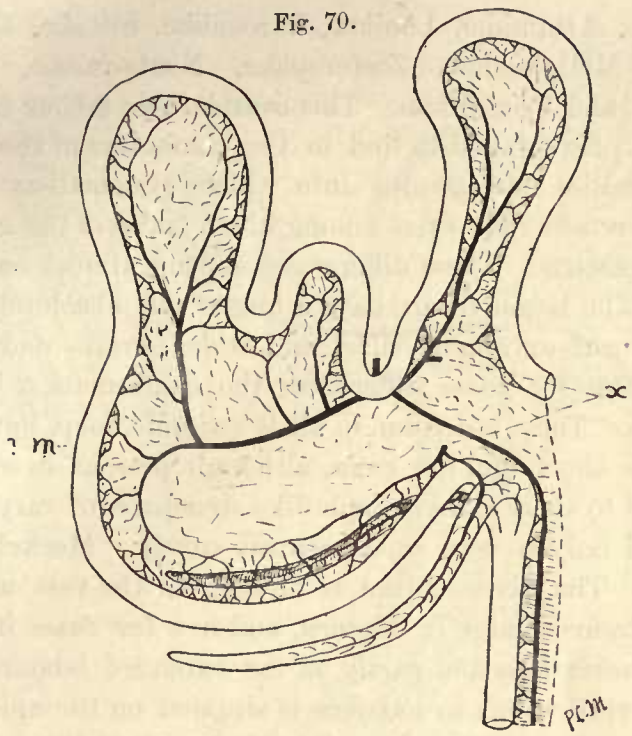
Picidæ.—In *Dendrocopus major*, *Gecinus viridis*, and *Leuconerpes candidus* the conformation of the gut is in every important respect similar to that found in *Megalæma*.

The Coraciiform birds tend generally towards the production of an extremely short, wide, and simple gut. The small size and the frugivorous habit, so common among them, are agencies that have combined in producing this pseudocentric simplicity. Certain forms, such as *Nyctidromus*, are readily comparable with the archecentric type, and present a simple duodenum, a Meckel's tract which is a circular expanse divided by the diverticulum into an anterior portion and a distal portion to which the long cæca are attached, and finally a straight, rather wide rectum. The changes from such a condition depend, first, on a widening of the duodenum; second, on a tendency for the portion of Meckel's tract proximad of the diverticulum to appear in two loops; and, third, for a supra-duodenal loop to become distinct in the distal portion of Meckel's tract. From this condition, various more apocentric modifications of the conformation are produced, chiefly by shortening and simplification of the tract and by reduction of the cæca.

PASSERIFORMES.

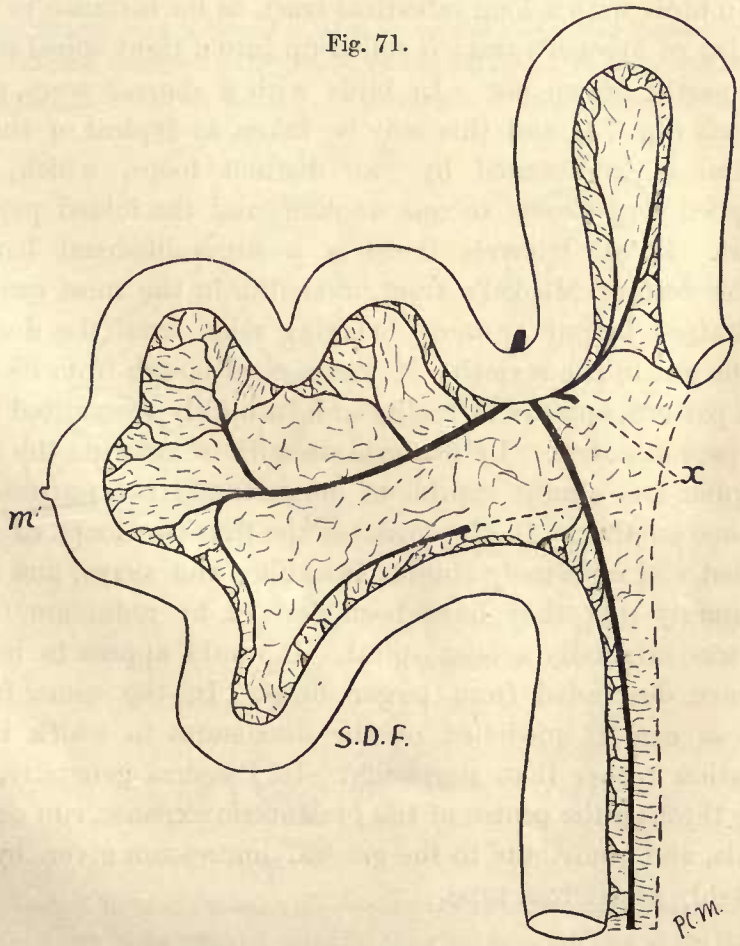
I have examined a very large number of Passeres, belonging to the family Eurylæmidæ of the Subclamatores; to the families Tyrannidæ, Pittidæ, Pteroptochidæ, Dendrocolaptidæ, Cotingidæ, Formicariidæ, and Pipridæ of the Clamatores; of the Suboscines I have examined *Menura*, and of the Oscines members of the families Alaudidæ, Timeliidæ, Pycnonotidæ, Muscicapidæ, Turdidæ, Troglodytidæ, Hirundinidæ, Campephagidæ,

Fig. 70.



Intestinal Tract of *Trogon puella*.

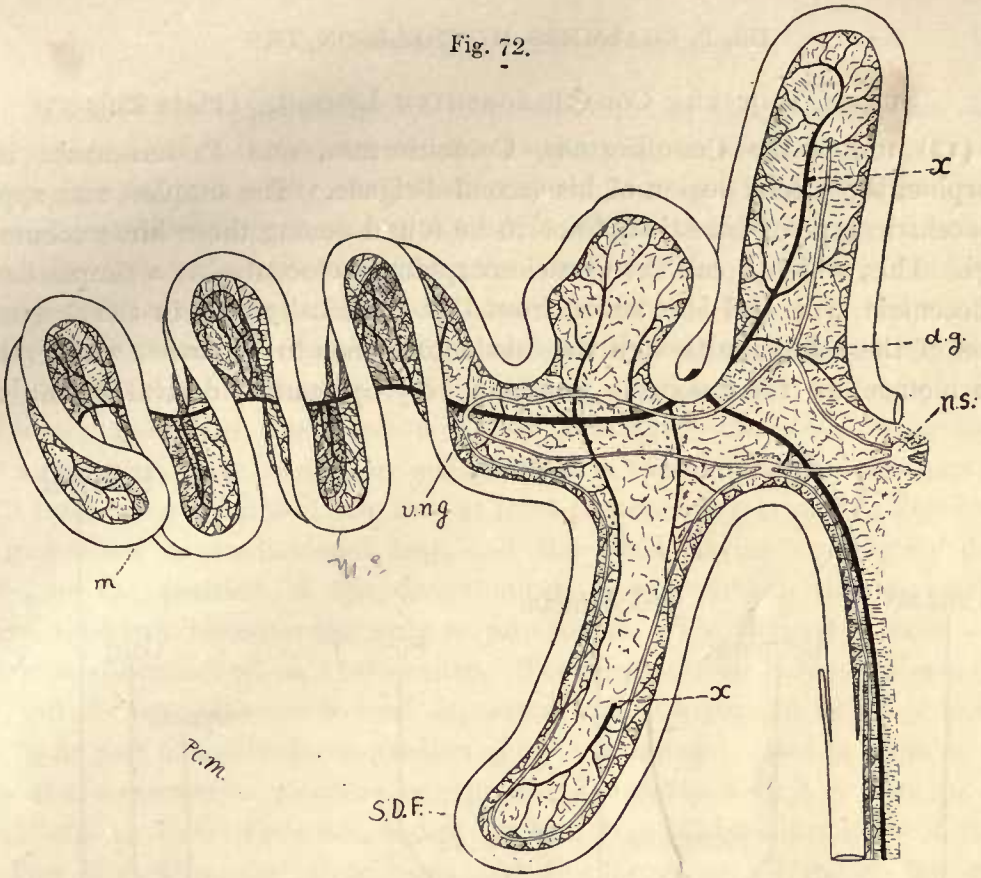
Fig. 71.



Intestinal Tract of *Megalæma asiatica*.

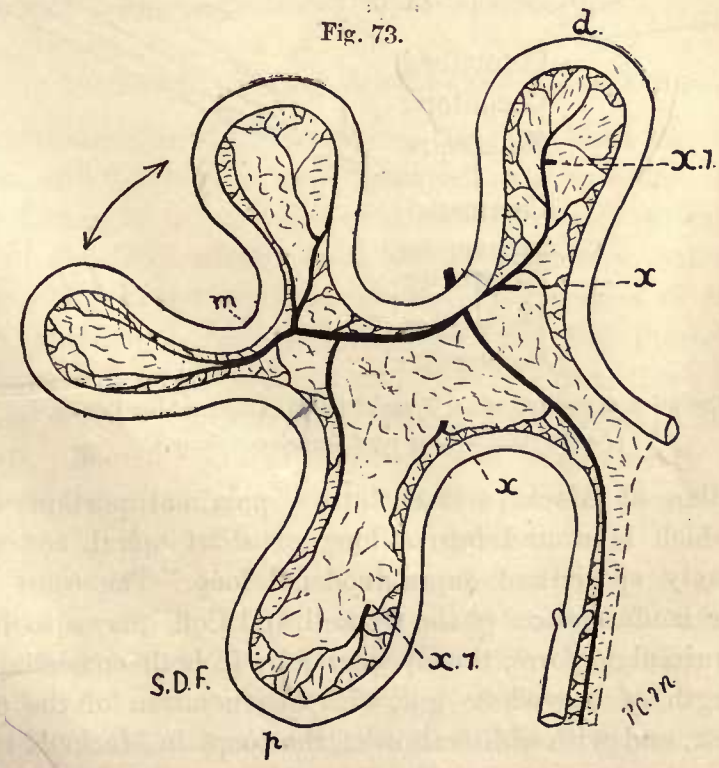
Dicruridæ, Ampelidæ, Artamidæ, Laniidæ, Vireonidæ, Sittidæ, Oriolidæ, Paradiseidæ, Corvidæ, Sturnidæ, Meliphagidæ, Zosteropidæ, Nectariniidæ, Dicæidæ, Cœrebidæ, Mniotiltidæ, Icteridæ, and Fringillidæ. This considerable labour from one point of view had a negative result, for I failed to find in the characters of the alimentary canal any indication of the families and groups into which systematists have subdivided the Passerines. The differences that exist among them traverse the group irrespectively of the divisions of systematists. These differences depend almost entirely on the size and habits of the birds. The larger forms have a longer gut absolutely and relatively; the fruit-eaters have the gut extremely short and wide; grain- and seed-eaters have the gut rather longer. But for these differences the conformation is remarkably similar throughout the group. The duodenum in all is a simple loop, but usually rather wide. The rectum is always short, and the cæca, although present in every case that I have examined, are reduced to short rather nipple-like structures of varying shape, but always with thick walls and only a very small central cavity. Meckel's tract presents the greatest divergences. The diverticulum is missing in the vast majority of cases. As an exception, it is extremely large in *Menura*, and in a few cases it is present. Relying partly on my own observations and partly on the extended labours of Gadow (12), I do not doubt that the diverticulum in Passeres is situated on the apical point of the large portion of Meckel's tract extending from the duodenum to the beginning of the supra-duodenal loop. In birds with a long intestinal tract, as for instance in *Corvus capellanus* (fig. 72), this portion of Meckel's tract is rolled up into a tight spiral which in the figure is represented as partly drawn out. In birds with a shorter tract, as for instance in *Cyclorhis albiventris* (fig. 73), and this may be taken as typical of the vast majority of Passeres, the spiral is represented by two distinct loops, which, in the unfolded condition, are applied very closely to one another, and the folded pair of loops have a slight spiral twist. In all Passeres there is a supra-duodenal loop very distinctly separated from the rest of Meckel's tract, modelled in the most exact fashion on the duodenum, and drained by one or more bridging veins from the duodenal vein. The conformation of the gut in the majority of Passeres, although from its short form it falls into a very simple pattern, appears in reality to be a highly specialized type, the apparent simplicity being pseudocentric. In many birds with short guts the intestinal tract is folded in an irregular and almost capricious manner, and the separate portions bear no exact relation to one another. In the Passeres the first two loops of Meckel's tract are most closely applied and extremely similar in calibre and shape, and their arrangement suggests most strongly that they have been derived by reduction from the proximal portion of what was originally a long spiral. It would appear to be certain that the small Passeres have descended from larger birds. In the same fashion, the supra-duodenal loop is so exactly modelled on the duodenum to which it is applied, as to suggest specialization rather than simplicity. In Passeres generally, the blood-vessels, instead of passing through the centre of the mesenteric expanse, run extremely closely to the intestinal coils, and contribute to the general impression given by the conformation of the gut as a highly specialized type.

Fig. 72.



Intestinal Tract of *Corvus capellanus*; type of long-gutted Passerine.
x, bridging factor of duodenal vein from S.D.F. the supra-duodenal loop; *m*, position of Meckel's diverticulum at the apex of the spiral; *n.s.*, *d.g.*, *v.n.g.*, ganglia of the antonomic nerve-chain.

Fig. 73.

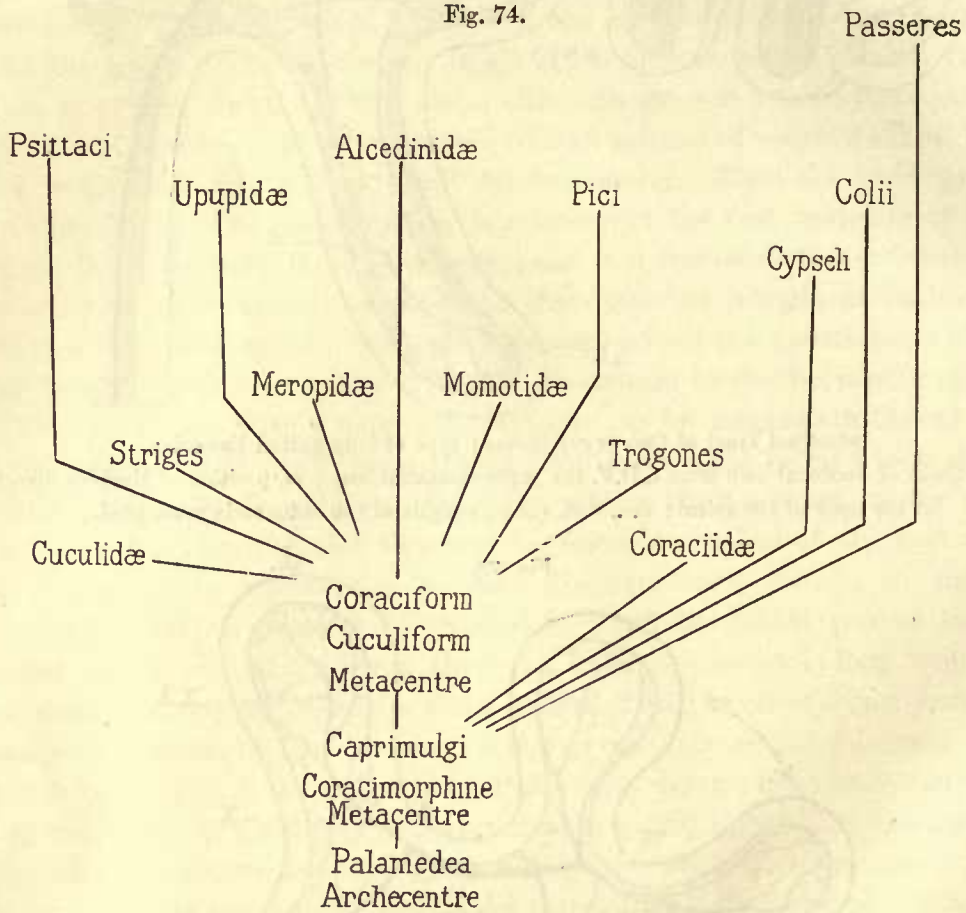


Intestinal Tract of *Cyclorhis albiventris*; type of short-gutted Passerine.
d, apex of duodenum, which in the unfolded condition is applied to *p*, the apex of the supra-duodenal loop; *m*, position of Meckel's diverticulum, corresponding to apex of spiral in fig. 72.

Summary of the Coraciomorphine Legion. (Plate 23.)

Gadow (12) unites the Cuculiformes, Coraciiformes, and Passeriformes into the Coraciomorphæ, the second legion of his second Brigade. The simplest and apparently most archecentric type of intestinal tract to be found among these birds occurs in the Caprimulgi. This, which I call the Coraciomorphine metacentre, is a simple derivative of the archecentric type, and is changed from that practically only in the shortness and straightness of the rectum, although the duodenum tends to be rather wider relatively. From this metacentre the Passerine gut is a very apocentric derivative, the changes

Fig. 74.



Evolution of the Intestinal Tract of the Coraciomorphine Legion.
(*For* Coracimorphine *read* Coraciomorphine.)

being the specialization of Meckel's tract into a proximal portion which bears the diverticulum, and which is wound into a long or short spiral, and a distal portion which is an extremely specialized supra-duodenal loop. The cæca have also been reduced in size. The conformation of the Cypseli and Colii may also be an apocentric derivative of the Caprimulgid form, the apocentricity in both consisting of an immense reduction in the length of the whole gut, with degeneration of the cæca so that no vestige of them is left, and with obliteration of the loops in Meckel's tract; there may or may not be a supra-duodenal loop. The Coraciidæ present a less apocentric modifi-

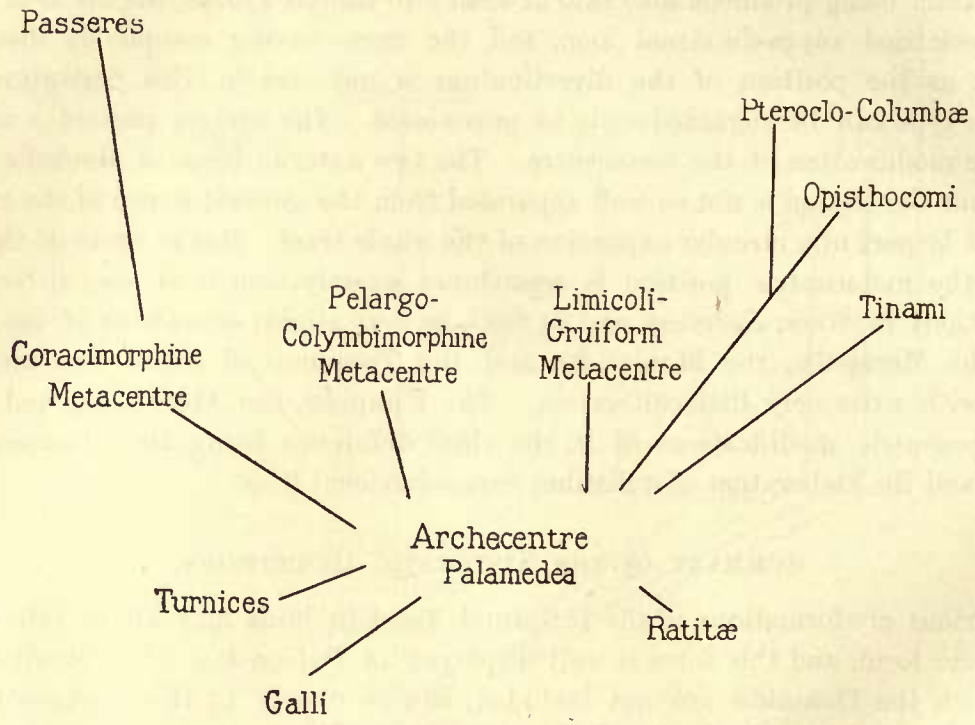
cation. Meckel's tract appears in two loops separated by the diverticulum, the posterior loop having attached to it the long cæca and so forming an incipient supra-duodenal loop. Underlying the conformations in the other types there is a central pattern which I call the Coraciform-Cuculiform metacentre, and in which the duodenum is frequently but not invariably wide; Meckel's tract is produced into two loops anterior to the diverticulum, and a single, rather wide supra-duodenal loop to which the long cæca are attached. The Cuculidæ retain this metacentral form, only slightly altered by increase of length, due no doubt to the relatively large size of these birds. It is possible to derive the Psittacine type as a very apocentric modification of this metacentre, the two anterior loops having become enormously long, and often complicated in themselves, the posterior portion of Meckel's tract being produced also into at least two complex loops, the distal of which is a well-specialized supra-duodenal loop, and the cæca having completely disappeared. However, as the position of the diverticulum is not certain, this derivation of the Psittacine type can be regarded only as provisional. The Striges present a much less apocentric modification of the metacentre. The two anterior loops of Meckel's tract are present, but the second is not so well separated from the general sweep of the tract, and appears to be part of a circular expansion of the whole tract. But in some of the species of *Bubo* the metacentric position is reproduced exactly, and it is easy to regard the conformations in *Strix*, *Syrnium*, and so forth as very slight alterations of the common form. The Meropidæ, the Momotidæ, and the Trogones all retain the metacentric position with extremely little alteration. The Upupidæ, the Alcedinidæ, and the Pici are all apocentric modifications of it, the chief difference being the disappearance of the cæca and the elaboration of a distinct supra-duodenal loop.

Summary of the Systematic Description.

The various conformations of the Intestinal Tract in birds may all be referred to an archecentric form, and this form is well displayed in *Palamedea*. The Struthious birds (with which the Tinamidæ are not included) adhere closely to this archecentric type. The Turnices and the Galli adhere to it almost as closely, but among the Galli an apocentricity, consisting in the expansion of the distal portion of Meckel's tract, begins to appear. The Tinamidæ, the Opisthocomidæ, and the Pteroclo-Columbæ present apocentric conformations which are not easy to derive from those in any other groups, although there are certain suggestions of affinity with the type displayed by Gruiform birds such as *Otis*. For the present, however, it is preferable to regard the forms in these birds as separate, although allied derivatives of the central type. The Passeres again do not show any clear affinity with the types in other birds. The conformation displayed must be regarded as having come separately from an archecentric type, perhaps from that common to the other Coraciomorphine birds, but which has progressed very far apocentrically along a radius of its own. The conformations in all other birds may be referred without difficulty to three main metacentres, which are all simple, but different modifications of the archecentric type. The metacentre of all the birds in the Pelargo-Colymbomorphine Brigade is a conformation in which the

symmetry of Meckel's tract about the median mesenteric vein and the Meckel's diverticulum is retained, but in which Meckel's tract tends to be produced into a number of long and narrow loops, the most distal of which is a supra-duodenal loop to which the long cæca are attached. The metacentre of the Limicoline-Gruiform assemblages (which contains the Alectoromorphine Legion without the Tinamiformes, Galliformes, and Pteroclo-Columbæ) is a derivative of the archecentre in which Meckel's tract is no longer symmetrical about the middle mesenteric vein and the diverticulum, but in which the region anterior to the diverticulum is produced beyond it so as to form an axial loop, on the distal limb of which the diverticulum lies and which may be greatly

Fig. 75.



Evolution of the Intestinal Tract in Aves.

(*For* Coracimorphine and Colymbimorphine *read* Coraciomorphine and Colymbomorphine.)

prolonged as in *Scolopax*. The members of the Coraciomorphine Legion, except the Passeres and a few pseudocentric types, may be derived from a metacentre in which the duodenum tends to widen, and in which the part of Meckel's tract anterior to the diverticulum is produced into two loops. In Plates 21, 22, and 23, and in figures 35, 59, 74, and 75, the evolution and affinities of the conformations of the intestinal tract are represented, and by no means necessarily the pedigrees and affinities of the birds containing these conformations.

Intestinal Portion of the Autonomic Nervous System.

It was only at a late stage of this investigation that my attention was directed to the peculiar features in the Sympathetic, or, to use the modern term, the Autonomic Nervous System of Birds. In certain birds (for instance the Megapodidæ and Cracidæ) the

so-called intestinal nerve is unusually large and visible, and it was in members of these families that I first noticed it. In the majority of cases, however, it is not readily seen; moreover, much of my material consisted of rather badly preserved spirit-specimens, or of birds that had died of disease in which tubercular and fatty degenerations of the mesentery were a conspicuous feature, and I am able only to give a few almost casual notes, which, however, may serve the purpose of redirecting the attention of anatomists to a very peculiar and interesting set of structures. A good deal is known about the paired ganglionated mesenteric chain (*Grenzstrang* of the German writers), thanks to the observations of many writers, of whom the chief are Wiedersheim, Gadow, Gaskell, and Marage. In the cervical region [Wiedersheim (36. p. 350), Gadow (12. p. 394), and Marage (23, *passim*)] it divides into a deep and a more superficial portion, and irregular traces of this division persist in different birds in the posterior parts of the body. In all cases it appears to have more autonomy; that is to say, to be in less intimate connection with the metameric spinal nerves than in most other vertebrate forms. In the lumbar region there arises from this a very complex plexus with large ganglia on the edge of the stomach, on the ovary, on the supra-renal capsule, and further back near the rectum. It is from these ganglia that the so-called intestinal nerve of birds arises. Concerning this peculiar nerve the literature is very scanty. Remak (32, 33) appears to have called attention to it first, but most later writers pass it over almost completely Thus Gadow, Wiedersheim, Fürbringer, and Beddard, in their ornithological and anatomical treatises, pass it by. Oppel, in his great work on the anatomical tract (30), is content with discussion of the plexuses actually in the wall of the gut. Gegenbaur (14), in the most recent edition of his 'Text-book,' mentions the existence of such a nerve in reptiles, and states that it is best developed in birds ("Am meisten sind diese Nerven bei Vögeln entwickelt. Ein den Mitteldarm begleitender Nervenstamm geht am Enddarme in mehrere ansehnliche Ganglien"), and adds that it is undeveloped in mammals. Marage (23) has given the best account of it, and states that it differs in its arrangement in different birds; but his figures are rather difficult to follow, and he is incorrect in stating that it does not occur in rapacious birds, and he seems to have overlooked it in the Ratites. As I have already stated, I do not pretend to have made anything that approaches to a complete study of it, and the figures that I have been able to give must be taken only as rough anatomical notes. Special study by special methods on material in good condition is required*. I can say, however, that in every case since I was aware of its existence, where the material was in sufficiently good condition, I found it present, and I do not doubt that this presence is invariable. It arises usually from two or three main nerves, which leave the ganglia corresponding to the solar plexus and the ganglia over the ovary and supra-renal capsule, and enter the mesenteric expanse which is the support of Meckel's tract. These, or some of these, are represented in figures 1 and 45, and I have worked them out in several unfigured cases. In fig. 72 there is a

* Since writing this memoir, my attention has been directed to a beautiful memoir by Thébault (34), which contains, *inter alia*, an elaborate study of the modes of origin of the intestinal nerve in various types of birds.—P. C. M.

large ganglion at entrance of these to Meckel's tract, and I could make out only two nerves forming the origin of this ganglion. One of the three nerves frequently runs independently to the duodenum, as in *Otis* (fig. 45) and in *Andigena Bailloni*; but no doubt there may have been a cross connection between this and the main intestinal nerve, as certainly is the case in the Pigeon. In the duodenal-fold loop usually at least one distinct and large ganglion is present (fig. 45, *v.nx.*; fig. 72, *d.g.*). The main intestinal nerve which supplies Meckel's tract starts in common with the duodenal nerve as in *Palamedea* (fig. 1) and the Passeres (fig. 72). It courses round the mesenteric expanse of the tract, giving off a series of minute branches to the gut, and where the tract passes into the rectum it frequently receives one of the entering nerves, or is in connection with the ganglion at the entrance to the mesentery of Meckel's tract, and then turns down parallel to the rectum, and comes again into connection with the posterior portion of the Grenzstrang. On its course this main intestinal nerve may follow Meckel's tract more or less closely. Thus in *Palamedea* (fig. 1), *Pandion* (fig. 34), *Talegallus* (fig. 38), it forms a loop corresponding to, but not absolutely identical with, the course of the tract. In *Falco melanogenys* (fig. 32) it follows the general course of the tract much more closely, having a loop following the supra-duodenal loop. In *Crax Daubentoni* (fig. 39) it has a curious elongated and narrow distal portion, which corresponds exactly with the typical apocentricity of these birds, in which the tract itself is enlarged on its distal portion. This intestinal nerve in many cases—Struthious birds, *Palamedea* (fig. 1), *Talegallus* (fig. 38), *Crax* (fig. 39), other Galli, *Falco* (fig. 32), *Pandion* (fig. 34)—presents a very large number of small ganglia evenly distributed along its course. In other birds, e. g., *Otis* (fig. 45), *Columba*, *Andigena*, and *Corvus* (fig. 72), there are a smaller number of much larger ganglia. As to the systematic value of these differences, it is impossible to say anything definite on so small a range of information; but the subject is very promising. It appears as if the chain with many ganglia were more primitive than the nerve with a limited number of large ganglia; and it is certainly the case that such birds as *Otis*, *Columba*, the Toucan, and the Passeres, where the number of ganglia is very small, are more specialized forms than those with multi-ganglionated chains. It has to be remembered, however, that although the nervous systems of many invertebrates with a small number of large ganglia appear to have been produced by the concentration of multi-ganglionated chains, we have no right to extend such a principle to other forms. The origin of this intestinal nerve in birds requires to be worked out, and in this connection the observations of Andersson (1), who found that in the Urodele Amphibia the main sympathetic chain was subdivided into a *Grenzstrang* and a *Collateralstrang*, are worthy of attention.

It is to be noticed that this intestinal nervous system lies, as the blood-vessels lie, between the two layers of the mesentery, and therefore outside the cœlom. In larger forms, such as the Emu, it is often comparatively easy to strip off one layer with its load of fat from the mesenterial expanse supporting Meckel's tract, upon which the ganglionated nerve-chain come plainly into view. However, just as it occasionally happens that some of the blood-vessels pierce the mesentery and form "bridging" vessels traversing the portion of cœlom between two loops which happen to lie in contact, so in

certain cases nerves may "bridge," or rather bore through, the mesentery and pass across a narrow portion of cœlomic space. The most obvious case of this occurrence is where, as in *Otis*, nerves leave a ganglion in the duodenal loop and pass to the cæca or the supra-duodenal loop. I am practically certain that this happens in many of the small Passerines, where the supra-duodenal loop is a structure of considerable importance, but I am not yet prepared to demonstrate this.

Morphology of the Intestinal Tract.

The chief writers on this subject within comparatively recent times have been Toldt (35), who deals chiefly with the tract in Man; Klaatsch (18), who in two extremely important memoirs dealt with the relation of the tract and its ancillary viscera to the mesentery; and Mathes (24), who followed closely the work of Klaatsch, but dealt chiefly with the development of the mesenteries in the Amphibia. None of these writers has paid special attention to the conditions that exist among Birds, but their work has been of great assistance to me in interpreting and coordinating my own investigations. It is plain that in all the higher vertebrates the intestinal tract is thrown into three main portions which are homologous throughout the series. Of these, the first is the Duodenum, which in birds is always a closed loop lying ventral to the rest of the tract. It arises extremely early in ontogeny, and while in the majority of cases it remains simple, it may develop many minor complexities, sometimes simply becoming wider, sometimes being thrown into numerous minor folds, and sometimes being twisted into more or less regular spirals, the spiral duodenum being in some cases (Storks) wound with the spirally twisted proximal loop of Meckel's tract. Concerning the relations of the duodenum to the supra-duodenal loop I shall presently have more to say. The distal extremity of the duodenum, however the course of that may have been complex, always returns to the dorsal edge of the mesentery very close to the starting point of the anterior limb, and there passes into the second portion of the gut. This portion, which I name Meckel's Tract, extends from the duodenum to the insertion of the cæca. The first important point about this large region of the gut is that it represents an outgrowth of only a very small section of the primitive gut. Its proximal extremity approaches its distal extremity so closely in the line of the dorsal attachment of the mesentery, that in the majority of cases it would be possible to remove the whole of Meckel's tract and suture the cut edge of the duodenum to the cut proximal edge of the rectum, and almost without dislocation reconstruct a primitive straight intestinal canal. In actual development Meckel's tract, in all the vertebrates in which it is developed, arises as a simple narrow loop in the line of the principal mesenteric artery. Toldt's figures, and others given by Kollman (19), show this beautifully in the case of human embryos, and general comparative anatomy from the Frog to Man makes the morphological nature of Meckel's tract extremely plain. There can be no doubt that this is the most recent phylogenetic development of the Vertebrate gut, and that it corresponds to not more than two, or possibly three, of the primitive somites of the body. When the development and comparative anatomy of the intestinal nervous chain in Birds has been worked out,

it is to be expected that the origin of that system from not more than three entering nerve-branches will be given an importance which as yet can only be suspected. The nature of Meckel's tract as a recent outgrowth of a portion of the gut corresponding only to a very limited number of segments has an important bearing on medical work, as it is being found that there is an organic sympathy through the nervous system between certain superficial areas of the skin and certain visceral organs or portions of the organs; the sympathy depending on a common relation to the primitive segmentation of the body, and being of practical value in the diagnosis of affections of internal organs. In those creatures in which there is a yolk-sac or umbilical cord, the outgrowth of Meckel's tract from the primitive straight gut is opposite the vessels running to these structures; and it seems tempting to regard the origination of Meckel's tract as being dependent on this mode of embryonic nutrition. However, as Meckel's tract is equally definite and equally metamerically limited in the Frog, we cannot lay much stress on this possible mode of origin.

The large intestine, from the cæca to the cloaca or anus, is the third distinct portion of the intestinal tract. It always lies in the primitive position of the straight gut, dorsad of all the other portions, and phylogenetically it is the oldest portion and corresponds to the greatest number of somites. It appears to be homologous throughout the vertebrate series; but this homology depends on the identification of the paired cæca of Birds with the unpaired cæcum of Mammals and Lizards—a homology not apparent when a bird with a short gut is taken, but much more convincing when the comparison is made between a form such as *Palamedea* (fig. 1) or a Struthious bird and a Mammalian or Lacertilian intestinal tract. In the more primitive types the large intestine is very long, and may show traces of division into colon and rectum; in the higher forms, partly in correlation with the greater development of the thoracic portion of the viscera, the duodenum and whole intestinal tract has shifted far distally, with the result that the large intestine is extremely small, and is here referred to simply as rectum (see footnotes, pp. 176 and 271).

Meckel's Diverticulum.

Examination of the embryo of any bird makes it plain that this structure is the vestige of the yolk-sac, and its retention in adult birds has been described by a number of anatomists. It has been termed by most writers who understood its nature the *Diverticulum cæcum vitelli*; but as it is obviously homologous with the cæcum described by Meckel as an abnormality in Man, and as in human anatomy it bears the well-known name of Meckel's diverticulum, I have preferred to give it that name in birds. I have not found it present in any adult reptile, and I can find no record of its occurrence there. Nor have I found it in any mammal other than Man. In human anatomy its frequency of occurrence has received recent attention, and Birmingham (4) states that it is present in about 2·2 per cent., varying from half an inch to five inches in length. In birds it is present much more frequently; indeed, its presence throughout life is a character of very many groups. Gadow (12), summing up his own very numerous observations and those of earlier writers, states that it is retained throughout life by

Swimming-birds and most Waders, but that it disappears very early in Birds of Prey, Parrots, Woodpeckers, and Singing-birds. He regards it as a functionless rudiment. Lönnberg and Jägerskiöld (21) examined a large number of birds, chiefly Sea-birds and Waders, for it, not contenting themselves with single individuals, and found it absent in most Gulls and Terns, present in Waders, Ducks, Herons, and some others. As at an early stage in my investigations I found it an important point of morphological orientation, I searched for it in each of the very large number of birds upon which this communication is based, and found its presence much more frequent than has been stated. An interesting feature in connection with it is, that in a large number of cases it is supported by a vestige of the primitive ventral mesentery. Usually this appears only as a small fold of tissue tying down the diverticulum to the ventral edge of the gut, but sometimes a strong band runs from this towards the liver, the latter of course being developed in the primitive ventral mesentery. Occasionally when the diverticulum itself was absent, its place was indicated by the presence of a mesenterial vestige, as in many Pigeons.

I have found the Diverticulum present and large in all the Ratitæ; of the Colymbiformes absent only in *Podiceps*; present in the Sphenisciformes; present in the Procellariiformes; of the Ciconiiformes, present and large in all the Steganopodes but small in *Plotus*, and present and large in the Ardeidæ, Scopidæ, Ciconiæ, and Phœnicopteri, in many of the Ciconiiformes being very large; present and large in all the Anseriformes; present in all the Falconiformes (except a *Buteo*), and very large in the Falconidæ, but usually small in the others; present and large in the Tinamiformes; present but usually very small in the Galliformes (except *Turnix*); present and very large in all the Gruiformes, often extremely large, but, as a solitary exception, absent in *Heliornis*; present and very large in all the Limicolæ; among Lari small and often absent in the Laridæ, small, but usually present, in the Alcidæ; present in the Pterocletidæ, but usually absent and always extremely small in the Columbidæ, a feature in which they stand in marked contrast with the Charadriiformes generally; of the Cuculiformes, always present although small in the Cuculidæ; absent in the Musophagidæ, and probably always absent in the Psittaci; of the Coraciiformes, always small, but present rather more often than not in the Coraciæ, present and small in most of the Striges, very small but present in most Caprimulgi; always very small and absent more often than present in the Cypseli, Colii, Trogones, Pici; of the Passeriformes, absent in the vast majority of cases, when present extremely small except as a solitary case in *Menura*, where it was very large. In making this review I have excluded those specimens which were marked in my notes as obviously chicks or quite young birds, and the list may be taken as representing with fair exactness the incidence of the diverticulum among the Avian groups.

In all the cases where I have mentioned, in the paragraph above, that Meckel's diverticulum was *small*, I think that it was a vestige in the true sense, that is to say a functionless rudiment of an embryonic structure. Sometimes the lumen remained, and contained a few fragments of material resembling yolk, and doubtless remains of the yolk. Rather more frequently the "small" diverticula had no lumen, and were mere nodular excrescences on the wall of the Tract. Among the cases which I have noted as large there are certainly some (Ratites, *Palamedea*, etc.) in the same category. The curious feature

therefore exists that a functionless vestige is retained universally in some groups and not in other groups—a circumstance to which the attention of those naturalists may be directed who would see a purpose or "selection-value" in every systematic character.

Meckel's diverticulum presents another condition of great interest. Lönnberg and Jägerskiöld (21) drew attention to the fact that in certain cases where the diverticulum is large, it has a patent lumen and a thick wall, and is slightly constricted from the gut (21, cited in Oppel 30, p. 559). These authors, while they suggest that the vestigial organ has been transformed into a gland, do not go further in their microscopical investigation than to point out that the mucous membrane of the diverticulum in these cases is thickened by a series of folds. I have examined the microscopical structure in several Anatiformes, Gruiformes, and Charadriiformes, and find that glands occur frequently in the foldings of the mucous membrane, and that the diverticulum in such cases corresponds, with its folded wall containing glands and lymphoid nodules, very closely to the structure of the cæca in Passerines and Columbæ. I am inclined to think, therefore, that in many cases, particularly in the groups that I have mentioned (and possibly in the Falconinæ), Meckel's diverticulum has acquired a new function. It is at the least suggestive that where the diverticulum has become glandular, the paired cæca are either rudimentary and functionless, or they are very large, thin-walled, and full of fæcal matter. Where, on the other hand, the paired cæca are chiefly glandular, the diverticulum is either a functionless vestige or has disappeared. This, however, is not a complete account of the relations of the two organs; for, in the first place, it is based only on a relatively small number of observations of microscopical structure, and in the second place there are instances, such as the Psittaci, where both diverticulum and paired cæca are absent in the adult.

The Subsidiary Loops of Meckel's Tract.

In the section dealing with systematic description, I have already said all or nearly all that I have to say regarding the minor loops into which the Tract so frequently is produced. I have tried to show that these display patterns which persist through systematic groups, the persistency referring to their position with regard to the diverticulum and to their number. The arrangements of these minor loops, in fact, are instances of what I term uniradial apocentricities. When Meckel's tract is elongating, in a large bird or in a bird the habits of which demand a great length of gut, the elongation does not take place at random, but in special regions and in special modes. The combination of position and complexity is of a kind not likely to be repeated independently, but to have common origin, and so to prove of systematic value. The explanation of how these different and complex combinations came into existence I have not attempted. Before that could be done, there is necessary the great labour of following out in every stage of individual development the relations of the growing folds of the gut to the blood-vessels, regions of the cœlom, liver, air-sacs, sternum, stomach, and so forth. The beautiful work of Klaatsch and of Mathes, elaborate and prolonged as it was, does little more than to open up the lines of such enquiries. Until something is known in each individual case of the nature of the "growth-forces" in contiguous

organs, of their compromises and co-ordinations, in fact of their places with regard to one another and to the whole corporeal republic in every stage of the growing embryo, nothing more can be said but that such complex uniradial apocentricities, if not in themselves possessed of "selection-value," may stand in correlation with structures that have such value.

The Supra-duodenal Loop.

In its natural condition the duodenum lies folded ventrally under the other portions of the gut, and comes in very close relation with the distal portion of Meckel's tract. Cuvier drew attention to the fact that in birds as in mammals the duodenum comes into intimate relation with a posterior portion of the gut, a relation so intimate that the mesenterial folds suspending the two portions may fuse after the fashion explained by Klaatsch. This portion of the gut which comes into relation with the cæca I have called the supra-duodenal loop, preferring not to call it "colon" as was done by Cuvier, since that term is applied in Mammalian anatomy to a portion of the gut posterior to the cæca, and therefore belonging to what I have been terming the rectum. Within the group of birds various stages in the evolution of this curious inter-relation between the proximal and distal portions of the gut are displayed. Thus in *Palamedea* (fig. 1) there is no supra-duodenal loop, and the gut may be unfolded without any difficulty or cutting of blood-vessels. The same conditions obtain in a number of the archecentric types, and in the systematic portion I have referred to these. Even in *Palamedea*, however, the earliest stage in the formation of the connection is apparent. A short recurrent factor of the duodenal vein runs in the mesentery at the dorsal portion of Meckel's tract across from the terminal portion of that tract and assists in draining the cæca. As the cæca increase in size this vessel becomes larger and of more importance, and, in many cases which I have referred to in the systematic portion, the recurrent vein along with a second and sometimes a third accessory recurrent vein run to nearer the apex of the duodenum, having traversed the mesentery as "bridging" veins, and arisen from the long cæca and the posterior portion of Meckel's tract. In such a mode, an intimate relation is established between the duodenum and the distal portion of Meckel's tract, and, as in *Otis*, this relation may involve not only the veins but the nerves. The portion of the Tract to which the cæca are adherent is not distinctly marked off from the more proximal portion of the Tract in very many of the less apocentric types. But, as I have shown in the systematic portion, *pari passu* with the establishment of the "bridging" veins, the distal portion of the Tract becomes a distinct loop clearly marked off from the general sweep of the Tract. Finally, in those birds where the cæca have degenerated either completely or have shortened to glandular nipples, the supra-duodenal loop is retained with its separateness from the rest of the Tract and with its "bridging" veins. In such a form the supra-duodenal loop generally becomes very accurately moulded to the contour of the duodenum, and its presence and completeness are important reasons for seeing in the apparent simplicity of the gut in many of the higher forms, such as the Passeres, a pseudocentricity—a condition apparently simple, but still retaining evidence of past complexity. I do not think it can be doubted

that wherever in short-gutted birds without large cæca the supra-duodenal loop is present in its elaborate form, these birds at one time had a longer gut, and almost certainly possessed longer cæca. Where a gut is long, and where its irregularly folded loops lie closely together in a narrow space, the establishment of an intimate connection between any of the crowded loops would call for little remark. Where, as in the Passeres and many other short-gutted forms, there appears to be abundant space, and yet the duodenum and the supra-duodenal loop are accurately moulded, the one on the other, and in intimate vascular, nervous, and mesenterial connection, we must seek for the origin of the complexity in the past history.

There can be no doubt, I think, that the presence of a specialized supra-duodenal loop marks a high degree of apocentricity in the intestinal tract possessing it, but it is equally plain that this apocentricity is multiradial and no guide to affinity. The presence of cæca of at least moderate length is a fundamental or archecentric character of birds; and, if the supra-duodenal loop has arisen in the mode I have indicated, it is clear that it may have arisen repeatedly, and in my systematic description I showed that actually it does appear, repeatedly and apparently independently, in the different groups. The probably multiradial nature of the structure is also supported by the occurrence of similar formations among Mammals, these formations not even being on exactly homologous parts of the gut. The mammalian structures with which the Supra-duodenal Loop may be compared are the loop which in Man has the transverse colon as its apical portion, and the sigmoid flexure, which in embryonic Man reaches much further towards the duodenum. Naturally, I do not propose to enter at present into the various modifications presented by these structures; it is enough to say that the connections in Mammals between the duodenum and posterior regions of the gut are frequently present, but less frequently than in the case of Birds.

Dealing with its occurrence in Man, Toldt sees in these connections between the proximal and distal portions of the gut the mere result of apposition. Klaatsch criticises this view, and rightly points out that, although many of the other loops are in equally close spatial relations, fusion does not necessarily occur among them. In Birds, however, as I have shown, secondary fusions and "bridging" veins are not absolutely confined to the duodenum and supra-duodenal loop. Thus in Psittaci they are frequent among the numerous long and narrow loops into which Meckel's tract is thrown. In Anatidæ secondary fusions and "bridging" veins are of frequent occurrence in the case of different portions of the same loop, notably in the axial loop, and in *Spatula* in the long loop distal to Meckel's diverticulum (fig. 24). Finally, in the Ciconiæ bridging veins and secondary fusion of the mesentery occur between the duodenum and the proximal minor loop of Meckel's tract. These occurrences, however, are less important and much less frequent than the supra-duodenal connections. Klaatsch accounts for these in the case of Reptiles and Birds by the mode in which the cœlomic divisions are broken up by the intruding blood-vessels and viscera. I think, however, that, in birds, the formation may serve a useful purpose; the supra-duodenal loop is maintained and made even more elaborate after the degeneration of the cæca, although it arose in relation to the cæca; moreover, it is specially perfect in cases where there is no reason to

suppose that want of space played a part in its ontogenetic appearance. Plainly, when the pyloric valve relaxes and the contents of the stomach are poured into the duodenum, the shock will be transferred to the supra-duodenal loop which lies closely applied to the duodenum and sometimes in special nerve-connection with it. And thus discharge of the contents of the posterior region of the gut into the rectum may be set about without the necessity of peristaltic waves traversing the whole length of Meckel's tract.

The Colic Cæca.

Gadow (12), Fürbringer (9), Beddard (2), and Oppel (30), in their respective treatises have devoted so much attention to the voluminous literature concerning the colic cæca of birds that I need not refer to older writers. The archecentric condition of these organs in birds, a condition which is probably an heritage from Reptilian ancestors, is the existence of a pair of cæca growing from the point where the distal end of Meckel's tract passes into the rectum. Such primitive cæca proximally are applied more or less closely to the posterior portion of Meckel's tract. They are of moderate length; their walls are not specially thickened, their lumens are widely open to the gut, and their contents consist of food-material in a state more akin to that in the rectum than to the state in Meckel's tract. When, as happens frequently, there is a difference in colour apparent through the intestinal wall and marking the different stages of metabolism, the colour of the cæca approximates to that of the rectum. These primitive cæca probably had a digestive function of some sort, for the presence in their walls of glands, of absorbing veins, and occasionally of villi show that they were not mere reservoirs of fæcal matter. From the primitive condition various apocentric modifications have arisen. The cæca may increase very greatly in size, and may develop spirally arranged septa protruding more or less into the cavity and deeply marking the exterior, as in *Chauna* and some of the Ratites and Gruiformes, or the whole external surface may be prolonged into a number of papilliform hollow outgrowths, as in *Calodromas* described by Beddard (2). These enlarged cæca appear to retain their digestive functions. Secondly, the cæca may become very much reduced, but in such apocentric reduction I am convinced that there are two quite different conditions to be noted. In the one case, the reduction may be nothing more than the degeneration of an organ that has become functionless; and almost any stage from the archecentric size to complete absence may exist. In the Columbidæ, for instance, the cæca if present are always small and frequently are thin-walled, irregular (I have noted many cases of individual absence of one cæcum), and sometimes pigmented. In the fruit-eating Pigeons, and indeed in many other Pigeons apart from the nature of their food, the vestiges have disappeared completely. Precisely a similar series of events occurs among most Falconiform birds. The cæca are small in all, and when present appear to be functionless, thin-walled vestiges, frequently unsymmetrical (here, again, absence on one side has been noted in different birds by different observers). Sometimes they appear to be absent, but inflation of the wall of the gut reveals the presence of slight, thin-walled rudiments in their place. In the Vultures they are sometimes totally absent, and a similar absence is a

character of the Cathartidæ. However, there is yet another condition possible among these reduced cæca. Numerous observers have shown that in the cæca of many birds, whether these be long or short, there occur in different regions masses of lymphoidal tissue. Such masses may occur at the apex of long cæca as in the Owls, or in scattered patches as in Ducks and Fowls, or in concentrated swellings as in *Otis*. Berry (3) has recently shown that the occurrence of these lymphoid masses, in concentrated regions forming vermiform appendices, or in scattered masses, is frequent in Vertebrates, and he suggests that the vermiform appendix of Man is a specialized and not a degenerate structure. The reduced cæca of many birds (*e. g.* Passerines) are quite different from the obviously vestigial cæca that I have mentioned. They are regularly formed, nipple-like structures, the lumen of which is greatly reduced by closely-set villi and folds. In these, small glands and lymphoid tissue are abundant; and in the Sparrow I have noted the presence of abundant dark granules which are apparently matter in process of excretion. I distinguish therefore in the conditions of the cæca among birds the following:—

1. *Archecentric Character.*—Cæca large, thin-walled, containing food-material on which some process of digestion is taking place, but which may have in addition the beginning of secretory or excretory function.
2. *Apocentric Characters.*
   A. Cæca enlarged, partly digestive, and partly secretory or excretory.
   B. Cæca functionless, vestigial or absent.
   C. Cæca reduced but transformed solely to glandular organs, secretory or excretory or both.

PALAMEDEA. Cæca archecentric. *Chauna* apocentric A.

RATITÆ. Cæcæ archecentric or apocentric A.

COLYMBIFORMES. Archecentric.

SPHENISCIFORMES. Apocentric B. but according to Gadow archecentric in some.

PROCELLARIIFORMES. Apocentric B, occasionally one only present.

CICONIIFORMES. Archecentric in the Pelecanidæ, apocentric B in the Phaethontidæ, Sulidæ, Fregatidæ, and Phalacrocoracidæ (in *Plotus* one may be absent); apocentric B in the Scopidæ, Ciconiidæ, and Ardeidæ, in the latter one only as the normal but not invariable condition. In the Phœnicopteri archecentric.

ANSERIFORMES (excluding the Palamedeidæ). Apocentric A, usually with large rows of glands, but in *Mergus* apocentric B and one occasionally absent.

FALCONIFORMES. Apocentric B, vestigial with frequent irregularities and absent in Cathartidæ.

TINAMIFORMES. Apocentric A, extreme specialization in some.

GALLIFORMES. Apocentric A in Galli and Opisthocomi; archecentric in Turnices.

GRUIFORMES. In the Rallidæ apocentric A; of the Gruidæ archecentric in the Araminæ, apocentric A in the others. In the Dicholophidæ and Otididæ apocentric A (extremely so in *Otis*); in the Rhinochetidæ archecentric; in the Eurypygidæ apocentric, probably C; in the Heliornithidæ archecentric.

CHARADRIIFORMES.

Limicolæ. In the Glareolidæ archecentric; in the Chionidæ, Thinocoridæ, and Charadriidæ apocentric A, but in some of the latter family apocentric C. In the Parridæ, Alcidæ, and most of the Laridæ apocentric B and sometimes practically quite absent, but in *Stercorarius* archecentric.

Pterocletidæ. Apocentric A.

Columbidæ. In the vast majority apocentric B, occasionally one and very often both absent, but in *Columba livia* and *Columba œnas* traces of glandular structure and so apparently apocentric C.

CUCULIFORMES.

Cuculi. Archecentric to apocentric A in the Cuculidæ; in the Musophagidæ apocentric B, and usually, if not always, quite absent. In the Psittaci apocentric B.

CORACIIFORMES. In the Coraciidæ, Momotidæ, and Meropidæ archecentric; in the Alcedinidæ and Upupidæ apocentric B.

Striges. Apocentric A.

Caprimulgi. Archecentric.

Trogones. Archecentric.

Cypseli, *Colii*, and *Pici* are apocentric B.

PASSERIFORMES. All that I have examined are apocentric C.

Gadow (12. pp. 688-693) has made a very careful study of the relations between the character of the cæca and the nature of the diet, and I have gained further information from Finn (8) and from Evans (7), and from the keepers at the Zoological Gardens as to the diet of birds. There is very far from an exact correlation between the apocentricities and particular diets, but there is enough to make it plain that many of the modifications are homoplastic; that is to say, that they are multiradial apocentricities on which no argument as to affinity can be based.

Archecentric Type.—The diet in these forms is by no means uniform, but there is a preponderance of feeding on insects and caterpillars, grubs, and so forth; in fact, of what may be taken as more typical reptilian diet.

Apocentric Type A. A very large number of birds displaying much enlarged cæca live on vegetable diet in which cellulose bulks largely, and it is to be remembered that the digestion of cellulose occurs in the large cæca of some mammalia.

Apocentric Type B. Carnivorous diet, piscivorous diet, and especially frugivorous diet are specially associated with the degeneration of the cæca to functionless vestiges, or even with the complete disappearance of the cæca.

Apocentric Type C. When it is remembered that the vast majority of the Passeres display this type, and that yet almost every possible form of diet is found among them, it is at once clear that diet is no complete explanation of the character of the cæca. I am more inclined to think that type C is to be associated with a high development of the Avian structure, and that it is a peculiar secretory or excretory organ.

Some parallels may make the complexity of the problem of the cæca apparent. The Passeres display all diets and one type.

The Owls and the Falconiformes have almost identical diet, the larger forms of both being carnivorous, the smaller forms chiefly insectivorous; the Owls all exhibit apocentricity A, the Falconiformes apocentricity B.

Fowls and Pigeons (except the fruit-eating Pigeons) have a similar diet; Fowls all exhibit apocentricity A; Pigeons apocentricity B or rarely C.

The Gulls have a similar diet consisting of fish and garbage; most exhibit apocentricity B, but *Stercorarius* is archecentric.

On the other hand, *Phœnicopterus* is distinguished from other Ciconiiformes by a nearly purely vegetable diet, and it has the longest cæca in the group. The Mergansers are distinguished from the other Anatidæ by their typically piscivorous diet, and they alone among the Anatidæ have apocentricity B as in most other fish-eaters.

Characters and Classification.

In the systematic descriptive part, my task was to treat the characters of the patterns displayed by different birds as nearly as possible as if the gut were the whole animal, and the various phylogenetic figures and the three Plates display what I take to be the relations of the intestinal tracts, and not necessarily the relations of the possessors of these tracts. I have been taking, in fact, the anatomical structure as the unit, and not the individual or the species. In a sense, this is a return to the old Hunterian method; but its purpose reflects on the new problem of the nature and evolution of varieties and species of genera and families. Granting that the Plates attached to this paper represent with approximate accuracy the phylogeny of the intestinal tract in birds, we have yet to learn the relation of the phylogenetic tree of this structure to the phylogenetic trees of other structures, and the relation of all these to the phylogenetic trees of these impermanent combinations of characters that we call species. Although the coincidence of such trees is frequently assumed, there is no *à priori* reason to support such a proposition; and there is much recent work on the nature of characters and of their inheritance to throw doubt on the proposition. The nature of the anatomical structure in any organism depends in the first place on the nature of certain material transmitted from the parents in the fertilized ovum (naturally it does not matter to the argument whether the transmitted substance be what we call "matter" or "state of matter" such as mode of rhythm). Among other writers de Vries (6) has recently brought strong experimental evidence to show that at least in plants the hereditary material is composed of independent units which may be sorted out and recombined in each sexual generation. Of such independent variables underlying the fully developed anatomical structures of animals, we know practically nothing as to their number, nature, or modes of sorting out and recombination as they pass from generation to generation. Next, the anatomical structures of animals depend on the environment in which the combination of transmitted units come to maturity as actual adult organs; that is to say, they depend on the

various correlations with other organs and with external conditions established during embryonic, youthful, and adult life. In the case of the alimentary canal we know just enough, from the transforming experiments of Hunter and others, to feel certain that a large part of the final structure is determined by the conditions in which the hereditary material is grown. The phylogenetic tree of an organ such as the alimentary tract may be little more than the exhibition of a long series of experiments in growing similar or identical "germs" in different culture media. And, finally, we know nothing as to how far these hereditary masses, as they were marshalled into the actual branches of the actual phylogenetic tree of the organisms that contained them, carried within themselves historical limitations or determinations towards further development in specialized directions.

Such questions, however they may seem remote from an actual study in comparative organogeny, in reality lie at the root of every attempt to use characters in classification: if by classification there is implied more than the convenient disposal of particular animals in particular pigeon-holes according to their possession of obvious anatomical characters. The study of characters by themselves and for themselves must precede the attempt to use these characters in genealogical classification.

In the study of characters, the first proposition is whether they are primitive or modified, archecentric or apocentric. So far as the subject-matter of this paper is concerned, I have tried to show that for Aves the presence of a specialized duodenal loop, of a Meckel's tract consisting of a nearly circular expanse of mesentery with a simply convoluted gut suspended at its periphery and symmetrical about a median vein running towards a vestige of Meckel's diverticulum, of a pair of colic cæca with free lumen of moderate length and with walls partly glandular and partly absorbing, and of a rectum relatively long, are archecentric characters. When birds possess many or even all of these characters, we are tempted to say, but we cannot say definitely, that they are closely akin. The retention by some descendants of a common stock of an ancestral heritage in the ancestral form does not imply that such members are more closely akin than other members that have dissipated or improved the common heritage. I have shown that in all the great accepted groups of birds there are some members with the archecentric condition.

The second proposition that may have to be made regarding characters is that they are modified from the archecentric condition, or apocentric, and in this modification degrees of apocentricity may be exhibited. I have shown that the lengthening and twisting of the duodenum, the appearance of asymmetry in Meckel's tract and its production into variously-formed and variously-placed loops, the special formation of the loops described as supra-cæcal kinks and supra-duodenal loops, the great lengthening of the colic cæca or their reduction to vestiges or to short compact glands, and the shortening and straightening of the rectum *, are apocentric characters. That two birds possess

* Since writing this memoir, I have been interested by noticing that Professor Metschnikoff attributes many of the digestive troubles of man to inheritance of a long rectum. The higher birds of every group apparently have passed through a similar condition, but have succeeded in very greatly reducing the length of the rectum.—P. C. M.

apocentricity in an organ is no evidence of their affinity. In the first place, the apocentricity may be the mere result of growing the same inherited "germs" in similar culture media. I call such apocentricities multiradial, implying that they are the result of similar conditions on the same plastic material. The lengthening of the whole gut and the spiral twisting of portions of it, and in particular the lengthening of the cæca, are plastic or multiradial effects and can have no direct bearing on affinity. The extreme shortening and widening of the whole gut and the disappearance of the cæca, or even their transformation to nipple-like excretory organs, are multiradial. The production of a supra-duodenal loop and its retention after shortening of the long cæca in connection with which it arose are multiradial apocentricities. These again give us no clue to affinity. There is no reason to suppose that even in the actual phylogenetic tree of birds, a branch the members of which now possess an organ with archecentric character, may not have come from a branch the members of which now possess an apocentric character in the same organ. For, in the first place, the apocentricity may have arisen after the branching; and, in the second place, if the apocentricity be truly plastic, the transmitted germs in another environment may grow only into the ancestral form. It is probable, however, that apocentricities, even if multiradial, leave some legacy of complexity in their simplified descendants, and such conditions of character I have called pseudocentric. The conclusion to which consideration of multiradial apocentricity leads is that even if the phylogenetic trees based on the study of the intestinal tract be absolutely correct, and if they be compared with equally correct trees based on the examination and valuation of other characters, these trees may not coincide.

Apocentricities, however, may be so definite, so precise, or anatomically so complicated, that they appear to imply a phylogenetic contraction of the range of variability in respect to the structure in question. Such a demarcation of modification along a single and definite radius I have called uniradial apocentricity. When further divergent modifications occur on a single radius, there is formed what I have termed a metacentre, and what seems to imply that the range of variability has been limited or defined, with the result that future modifications all retain an indication of their more limited or defined starting-point. I take it that the archecentre of the alimentary canal of birds is a metacentre of the alimentary canal of the Sauropsida, and that, again, is a metacentre of the alimentary canal of the whole vertebrate stock. I have tried to show that the uniradial apocentricities of the intestinal tract of birds relate to the number and position of the minor loops into which Meckel's tract is produced.

The obvious use of the study of characters as regards classification is, then, the valuation of characters as archecentric and apocentric, and the discovery among the apocentricities of the uniradial modifications with their metacentres. When these have been determined and valued, the characters have yielded all the material that they afford for genealogical enquiry. When one set has been exhausted, recourse must be made to another set. In other words, the work of the anatomist whose goal is the achievement of natural classification, is the study of the definition and limitation of variation within groups. There is, however, another and most important side to this valuation of

zoological characters. When the archecentricities and apocentricities of a number of organs or structures have been mapped out, the questions are opened as to how far archecentric conditions of different organs are combined in the same animal; how far apocentric conditions are so combined; how far archecentric conditions of one set of structures are associated with apocentric conditions of other sets. In general terms, the problem is how far different organs become modified or remain unmodified independently or in association in the same individuals. If we compare the Dog-fish and the Frog, we find that, in relation to the general characters of the Ichthyopsida, the Dog-fish is archecentric as regards its skeletal system, apocentric as regards its urino-genital system, while the Frog is apocentric in its skeleton and archecentric in its urino-genital system. Naturally, in a paper dealing with part of one system, this problem of association has not been raised, but I desire to add my conviction, based on a general study of birds and a particular study of small groups of birds, that the larger the number of forms in a group and the narrower the anatomical range within which the group is confined, the more close is the association of apocentric modification of different organs.

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EXPLANATION OF THE PLATES.

Plate 21.

Evolution of the Intestinal Tract in the Pelargo-Colymbomorphine Brigade.
(*For* Colymbimorphine *read* Colymbomorphine.)

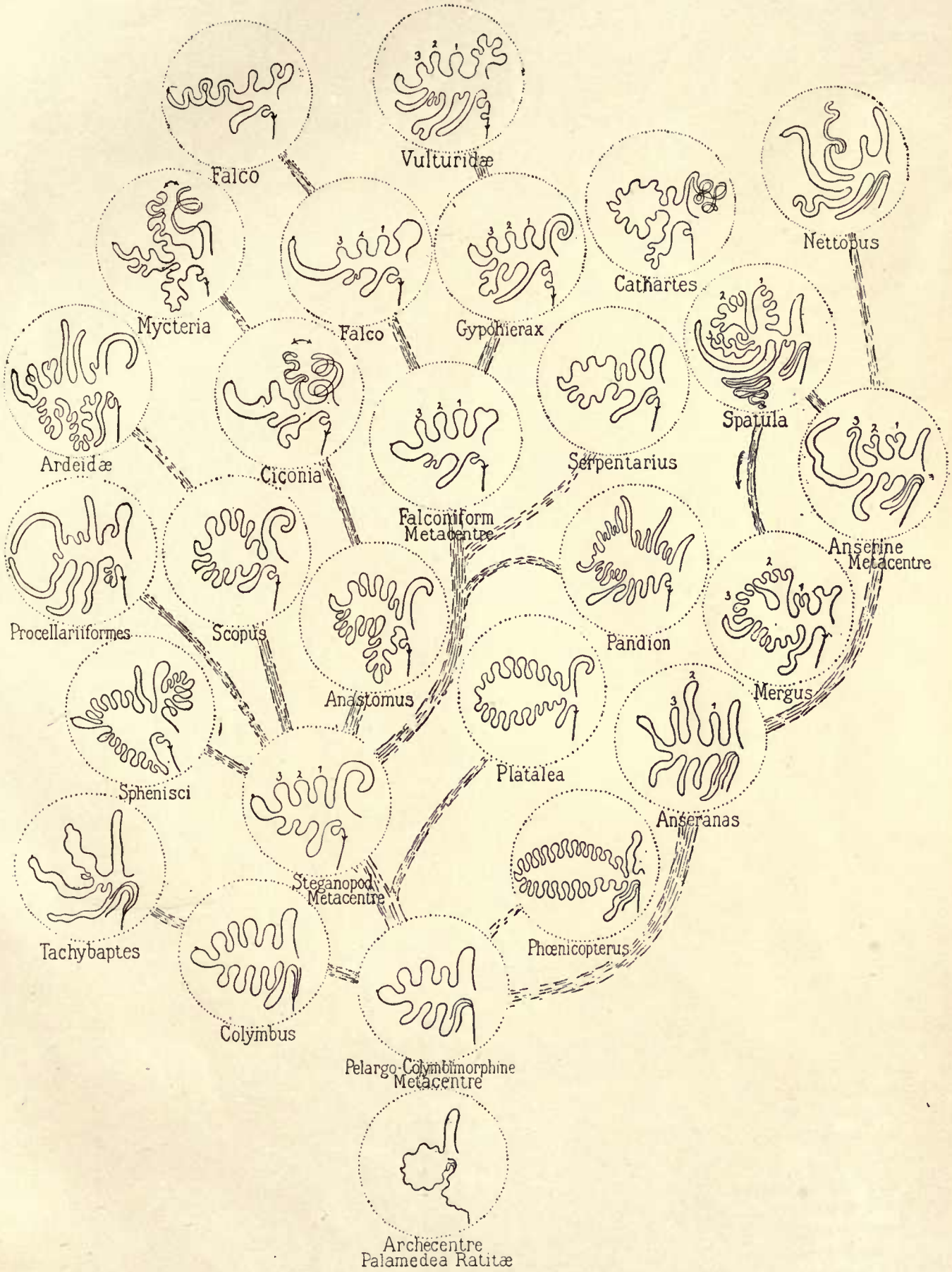
Plate 22.

Evolution of the Intestinal Tract in the Alectoromorphine Legion.

Plate 23.

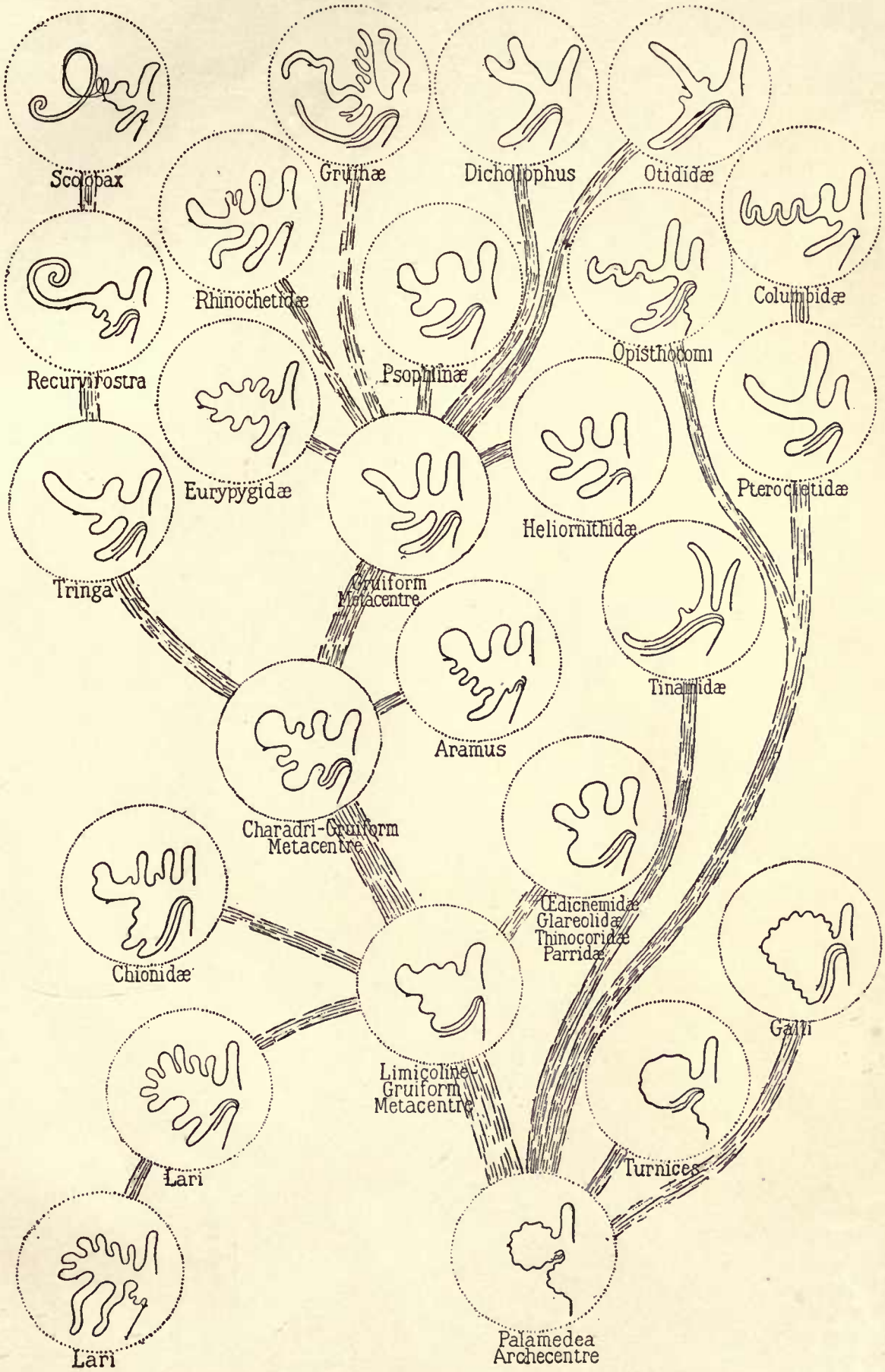
Evolution of the Intestinal Tract in the Coraciomorphine Legion.
(*For* Coracimorphine *read* Coraciomorphine.)

In these Plates the affinities of the conformations of the Intestinal Tracts and not of the birds are indicated. The outline of the coils of the tract in the unfolded condition is given; the line of attachment of the mesentery to the body lies to the reader's right. The diverticulum is represented as a dark spot on the left. The duodenum lies towards the upper end of the Plates, the rectum towards the lower end, with the cæca, when present, as a pair of dark lines.



P C M del

INTESTINAL TRACT OF BIRDS
PELARGO-COLYMBIMORPHINE BRIGADE.



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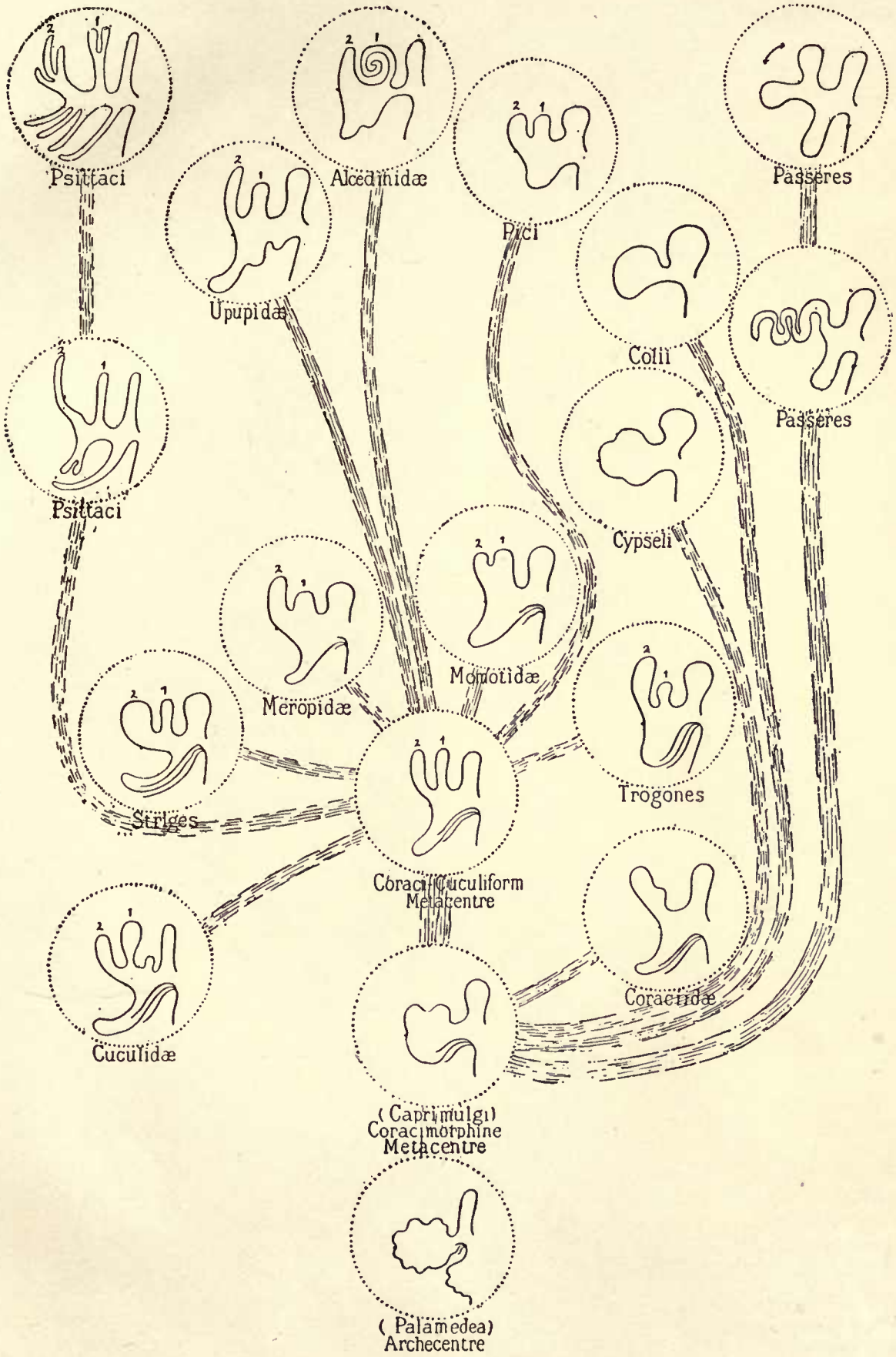
INTESTINAL TRACT OF BIRDS
ALECTOROMORPHINE LEGION.



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INTESTINAL TRACT OF BIRDS
CORACIMORPHINE LEGION.