2. On the Respiratory Organs of *Apteryx*. By Thomas H. Huxley, F.R.S., F.Z.S.

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I am not aware that the structure of the respiratory organs of *Apteryx* has been investigated since the publication of Professor Owen's Memoirs on the Anatomy of the Southern Apteryx, in the second and third volumes of the 'Transactions' of this Society. Professor Owen gives a detailed description of a structure which he terms the diaphragm, and compares it with that organ in mammals; the account of the anatomy of the lungs and of the air-sacs, on the other hand, is less full. The important fact that no air-sac extends into the abdomen is noted; but only four air-sacs on each side are mentioned, and no attempt is made to identify these with the air-sacs of other birds.

The question whether *Apteryx* presents any real approximation to mammals in the structure of its breathing-apparatus is of considerable interest, from its bearing upon the general problem of the affinities of birds to other groups of vertebrated animals. Having recently examined a specimen of *Apteryx* (which, although it had been many years in spirit, was still in a very fair state of preservation) with reference to this point, I have come to the conclusion that its respiratory organs differ in no essential respect from those of other birds—though they exhibit those peculiarities which are peculiar to and characteristic of the class Aves in a less developed condition than that which obtains in all those Carinatæ and Ratitæ which have been carefully studied.

The admirable monograph by Sappey [1], chiefly based on the study of the respiratory organs of the Duck, contains the most complete and accurate account extant of the general disposition of these organs in their highest condition of development. Rainey [2] supplemented this by the important discovery of the existence of intercapillary air-passages; and, more recently, Campana [3] has contributed a very elaborate study of the respiratory organs of the Common Fowl. It is not difficult to verify the chief statements of these anatomists. Nevertheless it is any thing but easy to find a succinct and precise account of the facts; and the terminology at present employed appears to me to be for the most part cumbrous and inappropriate. I make no apology, therefore, for endeavouring to amend this state of matters.

The lungs of birds lie, one on each side of the vertebral column, between the first thoracic rib in front and the anterior end of the kidney behind. On the dorsal aspect they rise, on the sides of the vertebræ, as high as the tubercular transverse processes of the ribs. On the ventral aspect they descend to a variable distance towards the

[1] Recherches sur l'appareil respiratoire des Oiseaux: 1847.

[2] "On the minute Structure of the Lung of the Bird," Medico-Chirurgical Transactions, xxxii. 1849.

[3] Les lois de l'Evolution animale.—La respiration des Oiseaux: 1875.

ends of the vertebral ribs. The lowest point of the ventral margin lies on one of these ribs, not far from its articulation with the sternal rib; and the hinder part of this margin, or the *posterior ventral margin*, slopes upwards and backwards, while the *anterior ventral margin* is inclined upwards and forwards from this point, which may be called the *ventral angle* of the lung. The whole ventral margin of the lung is very thin; its dorsal margin, on the other hand, is thick and rounded off into the outer or lateral face of the lung, which is convex from above downwards. The dorsal margin and the lateral face are closely applied to the parietes; and the former presents deep notches, into which the necks and dorsal portions of the bodies of the ribs are received.

The mesial face of the lung is divisible into three facets:—a *superior*, which is closely applied to the lateral faces of the vertebræ and to a fibrous lamella, the *median vertical septum*, which proceeds from the ventral faces of the vertebræ in the middle line; and an *anterior inferior* and a *posterior inferior* facet, which occupy that slightly concave face of the lung which is turned towards the thoracic cavity. These last facets are divided by a ridge or elevation of the surface of the lung, which ascends from the ventral angle to the insertion of the bronchus. This is always situated at some considerable distance from the anterior end of the lung.

The anterior inferior and posterior inferior facets of the lung are closely invested by a thin fibrous membrane, which may be termed the *pulmonary aponeurosis* ("diaphragme pulmonaire," Sappey; "diaphragmite antérieur," Milne-Edwards). The mesial edge of this is continuous with the median vertical septum; the lateral edge is inserted into the parietes of the thorax immediately beyond the ventral edge of the lung. Around the pneumatic apertures, or *ostia*, the pulmonary aponeurosis is closely adherent to their margins; it is, in fact, perforated by them.

Broad flat bands of striated muscle (the *costo-pulmonary muscles*) take their origin from the vertebral ribs[1], at some distance below the attachment of the pulmonary aponeurosis, and, proceeding obliquely dorsad and forwards, spread out and are inserted into that part of the aponeurosis which covers the posterior inferior facet. They are supplied with branches of the intercostal nerves. This pulmonary aponeurosis with its muscles is one of the two structures which have been compared to the mammalian diaphragm.

The second so-called "diaphragm" ("diaphragme thoraco-abdominal," Sappey; "diaphragmite thoraco-abdominal," Milne-Edwards) is a more or less aponeurotic fibrous membrane, continuous with the ventral edge of the median dorsal septum and suspended by it, like the roof of a tent, across the thoraco-abdominal cavity. In the middle line, this *oblique septum* slopes downwards and forwards to the dorsal and anterior face of the pericardium, with which its fibres become firmly connected on their way to their attachment to

[1] In many birds there are additional "*sterno-pulmonary*" *muscles*, which proceed from the antero-lateral part of the sternum to the aponeurosis covering the anterior inferior facet.

the sternum. From the median line, the two halves of the oblique septum slope laterally and ventrally until they attach themselves to the parietes of the abdomen behind, to those of the thorax more anteriorly, and to the margins of the sternum in front, at a considerable distance from the attachment of the pulmonary aponeurosis. It follows that a wide interspace is left, on each side, between the pulmonary aponeurosis, dorsally and laterally, the dorsal median septum in the middle line, the oblique septum ventrally and below, and the parietes of the body laterally; and, as the mesial attachments of the pulmonary aponeurosis and of the oblique septum are very much closer together than their outer attachments, the whole cavity has somewhat the form of a wedge with the narrow edge towards the middle line. This *subpulmonary chamber* is divided into four *loculi* by three *dissepiments*, which pass transversely from the lateral face of the oblique septum to the mesial face of the pulmonary aponeurosis. Each loculus lodges one of four *postbronchial* saccular diverticula of the wall of the lung, constituting the proper air-sacs, which thus fill up the subpulmonary chamber, between the insertion of the bronchus and its posterior extremity. Another air-sac lies in front of the insertion of the bronchus, on the mesial side of the anterior extremity of the lung.

Thus, on each side, there are five air-sacs, the lateral and superior face of each of which abuts against a particular region of the lung. The most anterior is that just mentioned, which may be called *præbronchial* ("réservoir cervical," Sappey), as the bronchus lies between it and the next, or *subbronchial* ("interclavicular," Sappey). The dissepiment which separates the loculus of this sac from the next is attached mesially along the oblique elevation which runs from the insertion of the bronchus to the ventral margin of the lung. The following dissepiment is attached dorsally, near the origin of the cœliac artery from the aorta, which lies in the median dorsal septum, and thence to the pulmonary aponeurosis, along a line which is inclined more or less obliquely backwards, to the posterior ventral margin. It separates two loculi, which lodge the *anterior* and the *posterior intermediate* air-sacs ("réservoir diaphragmatique antérieur et postérieur," Sappey). The third dissepiment, still more inclined, divides the loculus of the posterior intermediate air-sac from that of the *posterior* air-sac ("réservoir abdominal," Sappey).

Thus, that part of the thoraco-abdominal cavity which lies dorsad and anterior to the oblique septum lodges no other viscera than the lungs and the air-sacs, and may therefore be distinguished, as the *respiratory cavity*, from the *cardio-abdominal cavity*, which contains the heart and the rest of the viscera, and lies below and behind the oblique septum. The respiratory cavity is further divided into two lateral chambers by the median dorsal septum; and each of these chambers is subdivided by the pulmonary aponeurosis into two stories, of which the upper is occupied by the lung, and the lower by the loculi with their contained air-sacs.

The dorsal aorta traverses the median dorsal septum from before backwards, giving off, from its ventral aspect, the cœliac and the

mesenteric arteries, which thus appear in the middle line of the oblique septum when this is viewed from below and behind. The vena cava inferior enters the pericardium just behind the attachment of the oblique septum to it.

Immediately after the bronchus has entered the lung, it enlarges somewhat to form a dilatation, which has been termed the *vestibule*. A trunk which continues the direction of the bronchus through the centre of the parenchyma of the lung backwards, leaves the posterior end of the vestibule, and ends at the superior end of the posterior ventral margin in the *posterior ostium*, by which it opens into the posterior air-sac. This trunk may be termed the *mesobronchium*, by way of distinction from certain others which have a superficial position on either the lateral or the mesial face of the lung; and which may be distinguished, respectively, as *ecto-* and *ento-bronchia*.

Toward the middle of its course the mesobronchium gives off a wide branch, which passes backwards and downwards to the posterior ventral edge of the lung, and opens there by a very wide *posterior intermediate ostium* into the corresponding air-sac.

The *entobronchia* ("bronches diaphragmatiques," Sappey) are four in number. They take their origin in wide openings of the dorsal wall of the vestibule. The *fourth* is hindermost, runs almost directly backwards to the posterior end of the lung, and ends there cæcally. Branches are given off only from its ventral wall.

The *third* entobronchium runs parallel with this, giving off a number of close-set branches from its dorsal side, which are distributed over the superior facet. Close to the entrance of the bronchus, this presents the large *anterior intermediate ostium* for the corresponding air-sac.

The *second* entobronchium passes directly dorsad, and ramifies over the middle of the superior facet. A wide branch descends to the *subbronchial ostium*.

The *first* entobronchium curves sharply round the entrance of the bronchus, and from its anterior or convex wall gives off a number of branches to the anterior part of the superior facet and to the anterior inferior facet. One of these branches passes directly forwards, and opens by the *præbronchial ostium* into the præbronchial air-sac; while the inferior end of the trunk opens below the bronchus, into the subbronchial ostium, and, in that way, communicates with the subbronchial air-sac.

Thus the mesobronchium and the first entobronchium are each connected with two air-sacs—the former with the posterior two, and the latter with the anterior two; while the middle air-sac (anterior intermediate) communicates with the third entobronchium so close to the vestibule that it might almost be said to open into the latter.

Behind the vestibule, the mesobronchium gives off successively several (usually six or seven) branches, which are directed laterally and dorsally towards the lateral or costal face of the lung. These are the *ectobronchia* ("bronches costales," Sappey).

Those parts of the walls of the various bronchia and their ramifica-

tions, which are in relation with the pulmonary parenchyma, are perforated by minute rounded apertures. These lead into canals which are directed, at first, more or less at right angles to the surfaces of the bronchia upon which they open, and pass, side by side, sometimes anastomosing with one another, to some other bronchium than that from which they start. They may be termed *parabronchia* ("canaux tertiaires," Cuvier; "bronchial tubes," Rainey; "Lungenpfeifen" of the Germans). The lumina of these canals are interrupted at pretty regular intervals by transverse circular folds which contain unstriped muscular fibres. The interspaces between these folds are more or less subdivided by oblique or longitudinal folds of a similar nature into *fossæ*; and the walls of these fossæ present smaller depressions or *fossulæ*, which directly, or indirectly, open into the *intercapillary air-passages*. These last occupy the meshes of the capillary network into which the pulmonary vessels resolve themselves.

This description (with possibly some variation in the number of the ostia and air-sacs) applies to the respiratory apparatus of every known bird, and to that of no other animal; but it also applies, almost word for word, to *Apteryx*. Hence there can be no doubt that the respiratory organs of this bird are thoroughly and typically ornithic, and that they present not the slightest approximation to those of the Mammalia.

If the organs of respiration of *Apteryx* are compared with those of a carinate bird of similar size and form of trunk, such as a Duck, the resemblances and differences between the two can be easily traced.

1. The Duck's lungs are considerably larger both absolutely and relatively.

2. The anterior ventral margin in the Duck is longer than the posterior. The reverse obtains in *Apteryx*.

3. The pulmonary aponeurosis of the Duck is very delicate; in *Apteryx* it is strong and thick.

4. The median vertical septum in the Duck is much deeper, and anteriorly it is supported by the long hypapophyses of the anterior thoracic vertebræ. At the same time it is far less strongly fibrous than the corresponding structure in *Apteryx*. The mesial attachment of the pulmonary aponeurosis is to the ventral edge of the septum, close to that of the oblique septum, in the Duck; while in *Apteryx* the two are separated by a considerable interval, throughout which the thin and membranous part of the dorsal median septum divides the mesial ends of the intermediate and posterior loculi from one another.

In the Duck, the median dorsal septum lies throughout between the superior facets of the internal faces of the two lungs. In other words, this superior facet is much deeper in the Duck than in *Apteryx*.

5. The oblique septum is extremely thin and weak in the Duck; while in *Apteryx* it is a very strong aponeurotic membrane, with interlacing fibres diverging from two tendons attached to the under face of the posterior thoracic vertebræ. In the Duck it contains, on

Fig. 1.

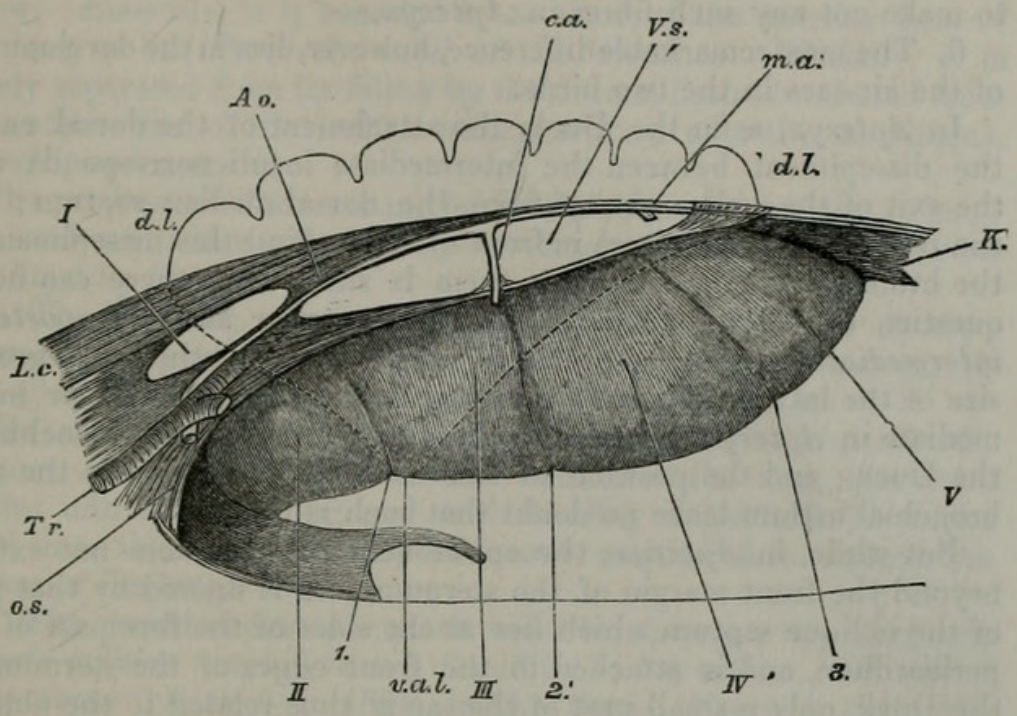

Fig. 2.

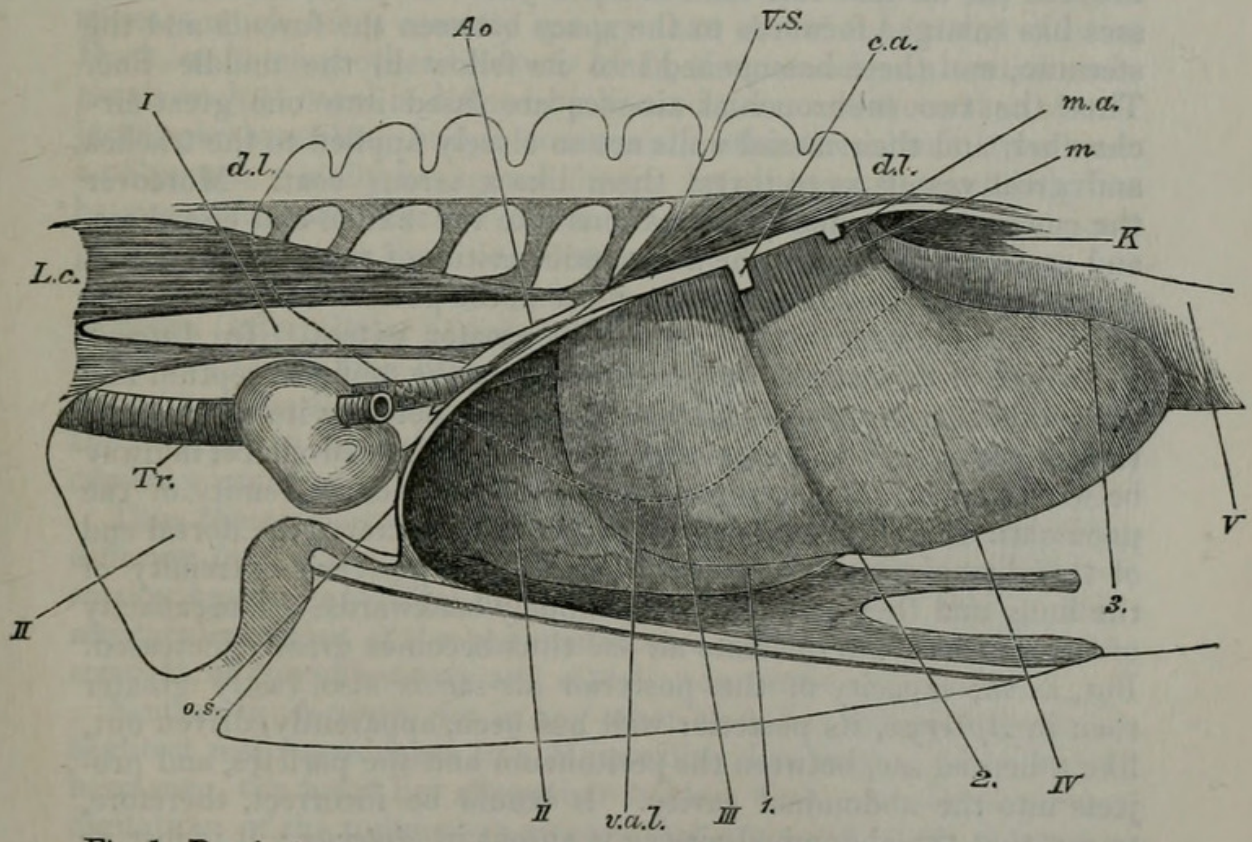

Fig. 1. Respiratory organs of *Apteryx*; and Fig. 2, of a Duck having the trunk of nearly the same dimensions. In each the vertebral column and the left wall of the thoracic and abdominal cavities are supposed to be removed; while the median vertical septum, the right half of the oblique septum, and the air-sacs of the right side are left. The contour of the right lung is indicated.

d. l, dorsal margin of the lung; *v. a. l*, ventral angle of the lung; I, præbronchial, II, infrabronchial, III, anterior intermediate, IV, posterior intermediate, V, posterior air-sac; 1, 2, 3, dissepiments.

L. c, *longus colli*; *V. s*, vertical median septum; *o. s*, oblique septum *Tr*, trachea; *Ao*, aorta; *c. a*, cœliac artery; *m. a*, mesenteric artery; *K*, kidney. *m*, smooth muscular fibres in the oblique septum of the Duck.

each side, a layer of unstriped muscular fibres. I have not been able to make out any such fibres in *Apteryx*.

6. The most remarkable difference, however, lies in the development of the air-sacs in the two birds.

In *Apteryx*, as in the Duck, the attachment of the dorsal end of the dissepiment between the intermediate loculi corresponds with the exit of the cœliac artery from the dorsal median septum; and the relation of the air-sacs in front of and behind this dissepiment to the bronchia which open into them is such, that there can be no question of their homology with the *anterior* and the *posterior intermediate* air-sacs in the Duck, notwithstanding the vastly greater size of the latter. Hence the air-sac in front of the anterior intermediate in *Apteryx* must be the homologue of the subbronchial in the Duck; and the position of this sac and its relation to the subbronchial ostium leave no doubt that such is the case.

But while, in *Apteryx*, the subbronchial air-sac does not extend beyond the front margin of the sternum, and is floored by that part of the oblique septum which lies at the sides of the fore part of the pericardium and is attached to the front edges of the sternum, in the Duck only a small part of the sac is thus related to the oblique septum, and even this extends much further backwards and more towards the median line than in *Apteryx*. In front, each of these sacs has enlarged forwards to the space between the furcula and the sternum, and there has opened into its fellow in the middle line. Thus the two subbronchial air-sacs are fused into one great air-chamber, and their mesial walls are so closely applied to the trachea and great vessels as to invest them like a serous coat. Moreover the common sac sends prolongations into the axillæ and elsewhere, and communicates with the pneumatic cavities of the adjacent bones. A similar modification has taken place in the posterior air-sacs of the Duck, but has been carried to a still greater extent. In *Apteryx* the whole of this sac is enclosed between the oblique septum and the pulmonary aponeurosis, the dissepiment between its loculus and that of the posterior intermediate sac being situated almost midway between the second dissepiment and the posterior extremity of the pneumatic chamber. In the Duck, on the contrary, the dorsal end of this dissepiment is attached close to the posterior extremity of the lung, and thence slopes very obliquely backwards. The capacity of the posterior intermediate air-sac thus becomes greatly increased. But, as the capacity of the posterior air-sac is also vastly greater than in *Apteryx*, its posterior wall has been, apparently, driven out, like a hernial sac, between the peritoneum and the parietes, and projects into the abdominal cavity. It would be incorrect, therefore, to say that the abdominal air-sac is absent in *Apteryx*: it is just as much present as in any other bird; but its small size and the small relative development of the posterior intermediate sac permit it to occupy a different position.

7. The first or præbronchial air-sac has hitherto been overlooked in *Apteryx*. It is of a long ovate or spindle-shape, 21 millim. long by 8 millim. wide in the middle, and lies between the *longus colli*

with the vertebral column above, and the œsophagus and bronchus below. Laterally, it is bounded by so much of the anterior facet of the lung as lies above the level of the bronchus. Mesially, it is widely separated from its fellow by the fibrous tissue continued from the anterior end of the median vertical septum onto the œsophagus, bronchi, and aorta.

The præbronchial air-sac in the Duck is fully three times as long, and sends off prolongations to the vertebral column, which have been described by Sappey.

8. The vestibule, mesobronchium, and entobronchia of *Apteryx* present no important differences from those of the Duck, except that the branches of the entobronchia are less numerous.

The ectobronchia, on the other hand, are much smaller, and only the most anterior reaches the lateral surface of the lung, and there divides into an ascending and a descending superficial branch of small size; the others break up into parabronchia before reaching the surface of the lung.

9. The parabronchia are much wider in *Apteryx*, the diameters of their cavities varying from 1·5 millim. to 0·8 millim., while they range from 0·8 to 0·4 millim. in the Duck Moreover the intervening vascular parenchyma is relatively much narrower in *Apteryx* than in the Duck. Hence a section of the lung of the former appears much more coarsely spongy than one of the latter. In the Duck, as in many other Carinate birds, the parenchyma around each parabronchial canal is defined by linear interspaces from that of adjacent parabronchia; and in transverse section these boundaries have a polygonal, usually hexagonal form. In *Apteryx*, the parenchyma between the parabronchial tubes is continuous, and the intercapillary air-passages show no interruption.

In the Duck, as in most Carinatæ, the fossulæ lead into branching passages (intercellular passages of Rainey), which radiate towards the periphery of the area of parenchyma which belongs to each parabronchium, finally ending in the intercapillary passages. In *Apteryx*, the fossulæ are mere shallow pits which open at once into the intercapillary passages.

Thus the respiratory organs of *Apteryx* are thoroughly ornithic, differing from those of other birds chiefly in the greater width and smaller aggregate surface of the respiratory passages, in the rudimentary condition of the pneumatic sacs, and in the much greater strength of the pulmonary and septal aponeurotic expansions.

Neither in *Apteryx*, nor in any other bird, has either of these the slightest real resemblance to a Mammalian diaphragm. For, as has been seen, the heart lies altogether behind both, and the muscular digitations of the pulmonary aponeurosis are supplied by the intercostal nerves, the phrenic being absent. The vertical and oblique septa really answer to the fibrous tissue of the posterior and middle mediastinum in Mammals.

In this, as in all other cases, the meaning of ornithic peculiarities of structure is to be sought, not in Mammals, but in Reptiles. It is only among Reptiles that we meet with pneumatic bones similar

to those of birds (Crocodilia, Pterosauria, Dinosauria), pulmonary air-sacs (Chamæleonidæ), and membranous expansions which are comparable to the septa in birds.

In Crocodiles, which approach birds in so many other ways, the resemblance is closest. As in birds, the liver lies between the stomach and the pericardium, and has a peculiar peritoneal investment shut off from the great sac of the abdomen; and, as in the Ostrich, the whole circumference of the stomach is united by fibrous tissue with the parietes. A fibrous expansion extends from the vertebral column over the anterior face of the stomach, the liver, and the dorsal and front aspect of the pericardium, to the sternum and the parietes of the thorax, separating the thoraco-abdominal space into a respiratory and a cardio-abdominal cavity, and representing the oblique septum of the bird. The respiratory cavity is similarly divided into a right and left chamber by a very deep median septum, traversed from before backwards by the œsophagus, trachea, and pneumogastric nerves, and containing the aortic arches. Each of these chambers is occupied by one of the lungs, the mesial face of which is closely adherent to the septum, while the lateral face, though quite free, naturally fits closely to the parietes. As there are no air-sacs, each chamber has only one story.

When the lung is distended, its dorsal margin extends far up on the sides of the bodies and arches of the vertebræ, the height of which seems to be related to this dorsal expansion of the lung [1]. A broad, thin muscle arises, on each side, from the anterior margin of the pubis; and its fibres pass forwards, diverging as they go, to be inserted into the ventral face of the posterior part of the pericardium and into the ventral and lateral parts of the fibrous capsule of the stomach, passing between that organ and the adherent posterior face of the liver, and being inserted into the fibrous aponeurosis which covers the anterior face of the stomach, and represents the oblique septum.

Each bronchus is continued directly backwards into a wide canal, which dilates into an oval sac-like cavity at the posterior end of the lung, representing the mesobronchium with the posterior air-sac in birds.

In the dorsal and mesial wall of the mesobronchium there are five or six apertures, which lead into as many canals, representing the entobronchia in birds. These pass, the anterior two almost directly forwards, and the others more or less obliquely, to the dorsal margin; and they lie quite superficially on the mesial face of the lung. The first is very much larger than the others, and ends in a dilatation at the anterior end of the lung. It is united with the second by transverse branches. Along the ventral margin of the lung there are four sac-like chambers, which communicate, in the case of the two anterior, with the entobronchia, and, in the case of the two posterior, with the mesobronchium. Finally, there are two very large canals, external to these, which communicate with the mesobronchium by large aper-

[1] It seems not improbable that the great height of the bodies and arches of the anterior thoracic vertebræ in some Dinosaurians may be connected with a similar modification of the lungs.

tures in its dorsal wall, and give off branches to the outer face of the lung, representing the ectobronchial system of birds. The orifices with which the surfaces of all these canals, except the anterior half of the mesobronchium, are thickly set, lead into depressions, which are often so deep as to become cylindrical passages, simulating the parabronchia of birds.

Thus, notwithstanding all the points of difference, there is a fundamental resemblance between the respiratory organs of Birds and those of Crocodiles, pointing to some common form (doubtless exemplified by some of the extinct Dinosauria), of which both are modifications.

3. Contributions to the Anatomy of Passerine Birds.—Part VI.[1] On *Xenicus* and *Acanthisitta* as types of a new Family (*Xenicidæ*) of Mesomyodian Passeres from New Zealand.

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A few months ago I received, through the kindness of my friend Prof. Jeffrey Parker, of the University of Otago, New Zealand, a small collection of birds in spirit from that country, which included most of the peculiar forms of Passeres found there. Amongst them were single specimens of *Xenicus longipes* and *Acanthisitta chloris*, the examination of which has proved to be of especial interest.

The genus *Xenicus* was founded by the late Mr. G. R. Gray [2] for the reception of the *Motacilla longipes* of Gmelin [3], Lafresnaye having some twenty years previously established *Acanthisitta* for Sparrman's *Sitta chloris* [4].

Subsequent ornithological writers have pretty unanimously assigned both these forms to the "Certhiidæ" or their immediate neighbourhood, in company with *Sitta*, *Sittella*, and their allies. The peculiar structure of the tarsus in *Xenicus* first induced me to examine these birds more closely, with the unexpected result that I find that the two genera in question are true Mesomyodian forms, and therefore in no intimate degree related to such Oscines as those just mentioned.

The subjoined drawings of the syrinx of *Xenicus*—with which in all points *Acanthisitta* appears to agree in every essential respect—will show that it has none of the complex nature of that organ in the Oscines, the thin lateral tracheal muscle terminating on the upper edge of a somewhat osseous box formed by the consolidation of the last few tracheal rings, and there being no other intrinsic

[1] For Part V. *vide antea*, p. 544.
[2] Ibis, 1862, p. 218.
[3] Rev. Mag. Zool. 1842, Ois. pl. xxv
[4] Mus. Carls. fasc. 2, no. 33.