AVIAN RESPIRATION

by

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Introduction

It is important for members of the veterinary profession to have a reasonable understanding of avian respiration for the following reasons:

(1) In the context of world agriculture, the economic importance of domestic avian species has shown a dramatic increase in recent years. In Britain alone poultry products were worth about £350,000,000 last year.

(2) A number of serious respiratory diseases such as Newcastle disease, infectious bronchitis, infectious laryngo-tracheitis, psittacosis, avian influenza and aspergillosis affect poultry health and thus productivity and profitability. The importance of these diseases is obviously increased by modern methods of poultry husbandry by which 10,000 birds may be kept in the same house.

(3) Poultry pathologists know a good deal about the virology and immunology of these diseases but for a balanced understanding of the situation a knowledge of the avian respiratory system is obviously an essential prerequisite.

(4) For a really adequate understanding of any disease process, and here we are thinking of an avian respiratory disease, it should be possible to present a picture, well documented by experimental and clinical observation, of the cellular interaction between the pathogenic organisms and the infected tissues. With the electron microscope we should be able to illustrate these events from the initial invasion of the cells through destruction, to their final repair.

This ultrastructural picture should be paralleled by an equally detailed account of immunological responses, antibody formation and activity, systemic effects on feeding, sleeping, growth and the distribution both inside and outside the body of infective material that might cause the spread of the disease. It is probably true to say that no disease of any species, human, domestic mammal or bird, has so far been described with this degree of detail.

(5) Avian respiration is worth studying for its own sake, because it is an intellectually rewarding thing to do. The avian respiratory system, as a piece of biological engineering, is quite different from the mammal and probably a good deal more efficient.

In this general account an attempt has been made to provide a simple introduction to the subject for those who may never have thought about it before; but at the same time to provide sufficient of the latest information for those who know much of it already.

References to specific research have been kept to a minimum but a few general publications, in addition to those quoted in the text, have been added at the end. Fortunately these are quite recent and so include reference to all but the very latest research.

Main differences between avian and mammalian respiratory systems

The avian respiratory system differs fundamentally from that of the mammal. In the mammal the body cavity is divided by a powerful muscular diaphragm, into thorax and abdomen which follow completely opposite pressure regimes throughout the respiratory cycle. In the bird there is nothing even remotely comparable to the mammalian diaphragm and, in spite of the existence of various septa, the pressure throughout the whole of the body cavity is the same at any given instant. Of course this pressure changes with the respiratory cycle but does so uniformly throughout the body cavity as a whole.

On inspiration air enters the mammalian lung to fill millions of expanded blind ending alveoli, and during expiration, largely by the elastic recoil of the lung, stale air leaves the system. A considerable amount of dead space is an inevitable result of this mechanism. Inspiration in the bird results in fresh air being drawn into the relatively indistensible lung and also right through it into large bellows-like containers, the air sacs. During expiration this reserve of fresh air is pumped back through the lung following the same route taken by the fresh air during inspiration. There is thus an almost continuous stream of fresh air flowing through the lung of the bird, in the same direction during both phases of respiration and as a result dead space is virtually eliminated. Clearly this is very different from the mammal.

Component parts of the avian respiratory system

In order to understand how the system works we must know a good deal about its structure. We can find this out by employing a wide range of techniques which include straight dissection, making a cast of the system (preferably in rubber latex), histology, transmission and scanning electron microscopy, histochemistry and radiography. All these have been used to provide the description which follows.

A long trachea runs down the neck from the larynx at the top to the syrinx at the bottom. The syrinx houses the vocal fold in birds. Beyond the syrinx the trachea bifurcates into two primary bronchi and after a short distance each enters the craniomedial part of the lung.

The lungs are situated under the first four ribs and are so tightly applied to them that lung tissue actually surrounds part of these ribs. Avian lungs are smaller than those of a mammal of comparable size and are relatively indistensible. They consist of a series of tubes or bronchi connected together in a fairly complicated way (see later).

Beyond the lungs, and connected to them by some of the bronchi, are several air sacs (Fig. 1). These are air-filled spaces amongst the viscera which act like bellows to suck fresh air through the lung on inspiration and to puch fresh air through the lung on expiration.

Some of the air sacs are extended into air-filled spaces inside certain bones which are thus called pneumatic bones, although they will have very little, if any, bearing on respiration as such.

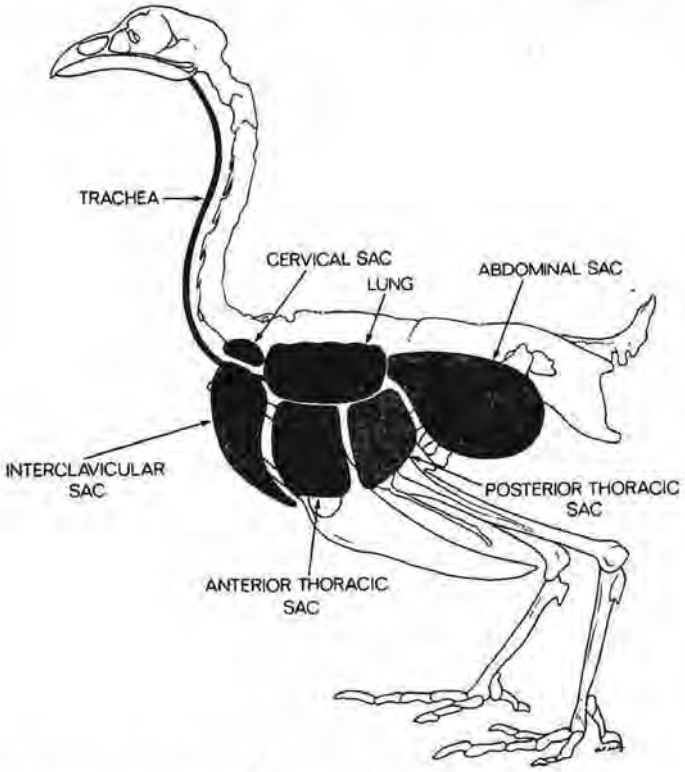


Fig. 1

General arrangement of lung and air sacs. Here the cervical sac has been placed above the interclavicular sac, although in fact the latter tends to enclose the former which extends back between the lungs.

Arrangement of bronchi within the lung

Each primary bronchus enters a lung on its craniomedial side, follows a flattened S-shape rout through the lung and leaves at the caudolateral corner (Figs. 2, 3). Immediately after entering the lung, the primary bronchus connects with a group

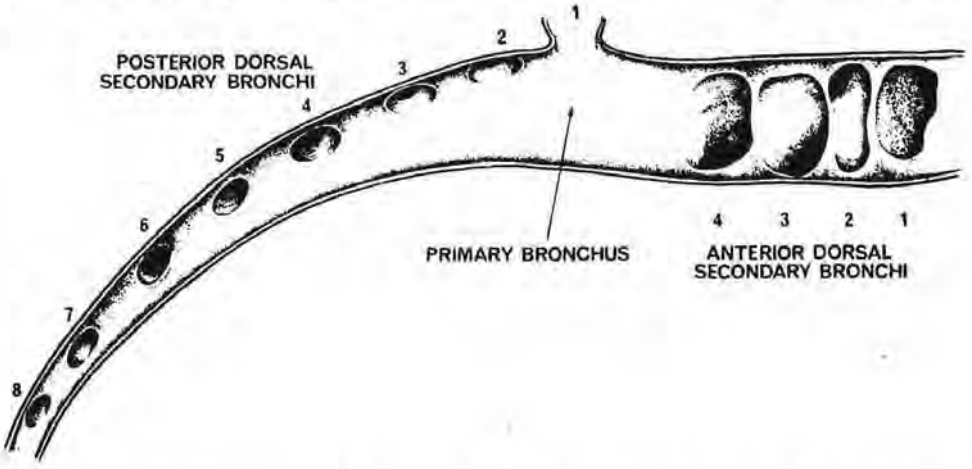


Fig. 2

Medial half of left primary bronchus. The head is to the right. The four large openings to the anterior dorsal secondary bronchi can be seen separated by thin septa. They occupy virtually the whole of the medial wall, from mid dorsal line at the top, to mid ventral line at the bottom. Of the posterior group, only the posterior dorsal secondary bronchi are shown. Their openings are much smaller than those of the anterior group and whilst the first is directly in the mid dorsal line, the others move progressively round to the medial wall.

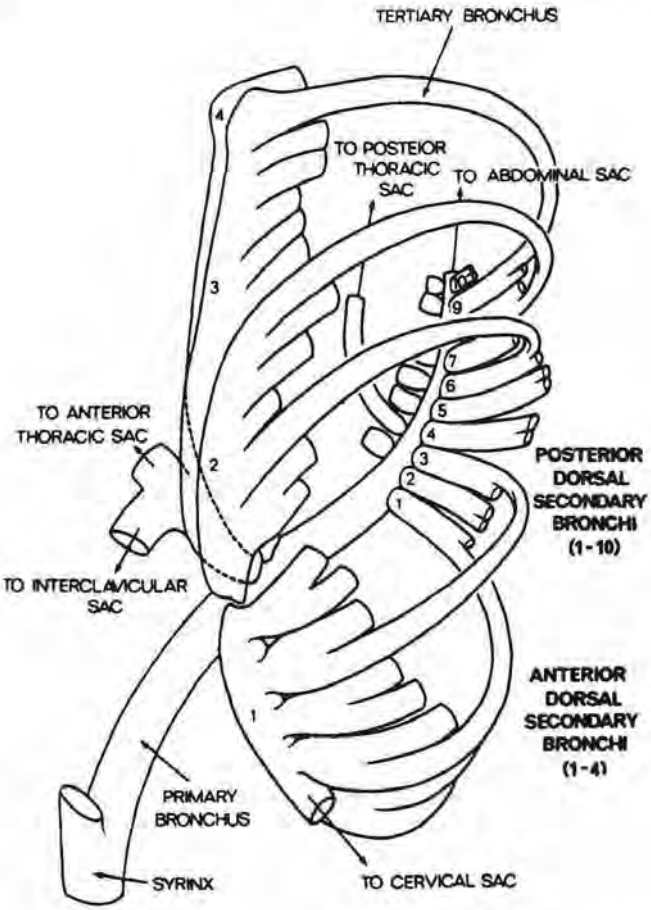


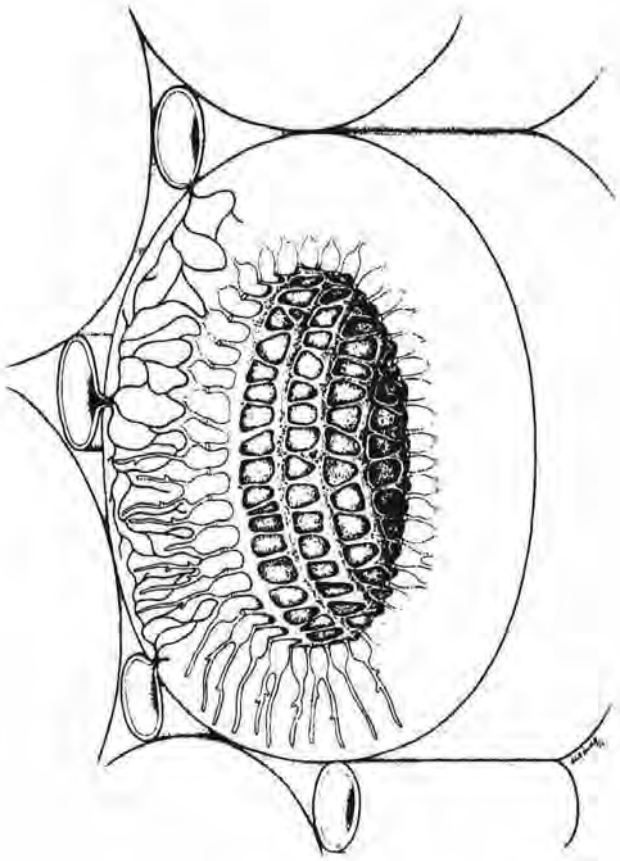
Fig. 3

Left lung, craniomedial view. The anterior and posterior groups of secondary bronchi are shown joined by tertiary bronchi. In this illustration the gap between the two groups of secondary bronchi is rather greater than it should be. Fig. 2 is more accurate in this respect.

of four anterior dorsal secondary bronchi (Figs. 2, 3). These are large ducts, and their points of connection with the primary bronchus occupy almost the whole of its medial wall. After a short distance, a posterior group of secondary bronchi connects with the primary bronchus along its dorsal and ventral surfaces. These have been called posterior dorsal and posterior ventral secondary bronchi respectively (Figs. 2, 3). These two groups of secondary bronchi are connected together by a large number of tertiary bronchi. Because the primary bronchus enters the lung on the medial side and leaves on the lateral side the distribution of the anterior and posterior groups of secondary bronchi is such that they tend to face one another across the width of the lung. Many of the tertiary bronchi are thus oriented across the lung from its lateral to its medial side. There is a certain amount of interconnection between them and it is important to appreciate the fact that tertiary bronchi constitute the bulk of the lung. For this reason we must look at one in some detail.

A tertiary bronchus (Figs. 3, 4) is a uniform air-filled tube, about $\frac{3}{4}$ mm in overall diameter with a thick spongy wall. The innermost part of the wall consists of a layer of pouches (about 100 μ diameter) whose entrances connect directly with the central airway, and are surrounded by thick bands of smooth muscle (Fig. 4). From the bottom of each pouch two or three small ducts (about 20 μ diameter) lead towards the outermost part of the tertiary bronchus. From these ducts there originate hundreds of extremely delicate tubes, the air capillaries, (6-10 μ diameter), which ramify throughout the rest of the thickness of the tertiary bronchial wall.

Fig. 4



Transverse section of tertiary bronchus. Thick muscular bands are shown surrounding the entrances to the pouches. Between 6 and 7 o'clock ducts, which will give rise to air capillaries, are shown leaving the pouches. Between about 9 and 11 o'clock blood capillaries are shown in the wall of the tertiary bronchus. Between 7 and 9 o'clock blood and air capillaries are shown together.

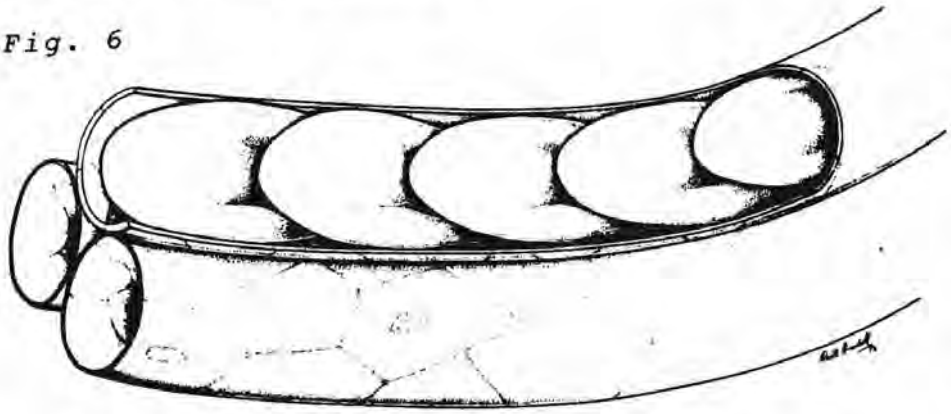
Fig. 5



A tertiary bronchial unit. This refers to a single pouch, all the air capillaries originating from it, the associated blood capillaries and the nerves which innervate the smooth muscle bands surrounding the entrance to the pouch. Only about 1/3 of the capillary zone is shown (cf. Fig. 4).

Branches of the pulmonary artery are distributed between the tertiary bronchi. These give rise to blood capillaries which enter the wall of a tertiary bronchus and ramify amongst the air capillaries (Figs. 6, 7). About a ¼ to 1/3 of the thickness of the tertiary bronchial wall is taken up by the pouches. The remaining 3/4 to 2/3 consists of a capillary zone in which air and blood capillaries ramify in the most intimate proximity.

Fig. 6

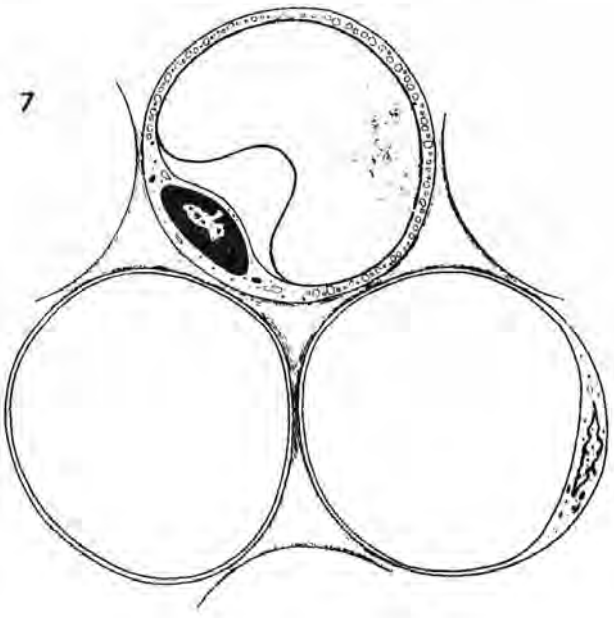


A blood capillary above two air capillaries. Both are about 5 or 6 μ in diameter. Avian red blood cells are about 7 x 14 μ and so have to be rolled up to pass through the blood capillary. They also ovelap one another by about 1/3 of their length. This is quite different to the mammalian arrangement.

The concept of a tertiary bronchial unit has been proposed (Fig. 5) to describe what may be the smallest functionally integrated part of the lung. It refers to a single tertiary bronchial pouch with all the air capillaries connected to it, together with their associated blood capillaries and the nerves that innervate the smooth muscle which surrounds the entrance to the pouch. Each tertiary bronchus would thus consist of an air-filled central cavity surrounded by thousands of tertiary bronchial units occupying the thickness of its spongy wall.

It should be pointed out that there is a certain amount of variation in the terms used by different people to describe the primary, secondary and tertiary bronchi of the avian lung. Alternative names are given in brackets after the terms that have been used in these notes:

Fig. 7



Blood and air capillaries, transverse section. The capillary zone of the tertiary bronchi is made up almost entirely of these two types of capillary, with virtually no support tissue between them. The vascular endothelium is about 80 nm wide. The air capillary epithelium is about 40 nm wide, with a separation of between 60 and 80 nm containing the minimum of basement membrane. The total distance for gaseoeus diffusion is probably something less than 200 nm.

Primary bronchus (mesobronchus); *anterior dorsal secondary bronchi* (craniomedial secondary bronchi, ventrobronchi, entobronchi); *posterior dorsal secondary bronchi* (caudodorsal secondary bronchi, dorsobronchi, ectobronchi); *posterior ventral secondary bronchi* (caudoventral secondary bronchi, laterobronchi); *tertiary bronchi* (parabronchi).

Details of air sac connections to the lung

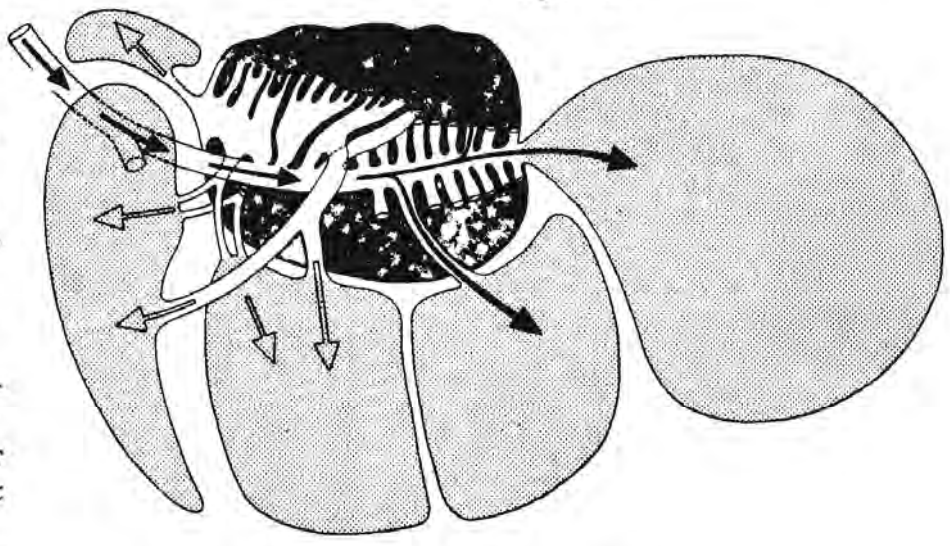
In the adult fowl each lung is connected to five air sacs. These can be divided into two groups: an anterior group consisting of cervical, interclavicular and anterior thoracic; and a posterior group consisting of posterior thoracic and abdominal air sacs (Fig. 1). The cervical and interclavicular sacs are shared by the two lungs whereas each of the other sacs is paired, one for each lung.

The primary bronchus terminates in the abdominal air sac and because it is tapered it has approximately the same diameter at this point as the two or three tertiary bronchi which also join this sac at approximately the same place. There is thus a small cluster of apertures, each a little less than 1 mm diameter, by which air can enter and leave the abdominal air sac. The posterior thoracic air sac is connected directly to the second posterior ventral secondary bronchus and, in a similar way to that by which the primary bronchus enters the abdominal sac, it is closely associated with a small group of tertiary bronchi. These tertiary bronchial connections to the two posterior sacs are not shown in any of the illustrations.

The interclavicular and anterior thoracic air sacs are connected to a large diameter branch from the third anterior dorsal secondary bronchus. There is also a group of about eight tertiary bronchi connecting to each of these sacs, but they are somewhat apart from the secondary bronchial connection (Fig. 8).

The single cervical air sac is connected to the first anterior dorsal secondary bronchus in each lung. This is the only air sac without any tertiary bronchial connections.

Fig. 8



Right lung and air sacs to show air movement during inspiration. Here the connection from the third anterior dorsal secondary bronchus to the interclavicular and anterior thoracic air sacs has been grossly extended to simplify the illustration. In fact it is very short inded. Fresh air enters the lung mainly by way of all the posterior secondary bronchi. It also enters the posterior air sacs. Stale air is sucked out of the lung by the anterior air sacs. Black arrows represent flow of fresh air. White arrows represent flow of stale air.

Surfactant

This phospholipid material which is essential for the normal functioning of the mammalian lung is also produced by the avian lung. It is a surface tension reducing agent and in the mammal prevents the alveoli from collapsing completely at the end of expiration.

It is normally first produced in human embryos just before birth so that the surfactant will be immediately available when the newborn infant takes its first breath. If surfactant is not produced, and if special steps are not taken, then the infant may die of the respiratory distress syndrome.

Nobody knows whether or not baby chicks ever die of their version of this syndrome. However, surfactant is produced in the normal chick and adult fowl by epithelial cells which cover the smooth muscle bands of the tertiary bronchi and which line the tertiary bronchial pouches. It is possible that this material spreads from the pouch down into the air capillaries, although it is not synthesised by the epithelial cells of the capillaries.

Whilst it is not yet known how this phospholipid is synthesised in the cells, it is easy to recognise by the electron microscope in the form of osmiophilic inclusion bodies. These are roughly spherical bodies which take up osmium tetroxide, a common electron dense stain, and thus show up as dark laminated structures under the electron microscope. This material is discharged by the cells to form a thin layer over the surface of the pouch and possibly of the air capillaries as well.

The mechanics of avian respiration

During inspiration, as a result of muscular activity, the sternum hinges down and the ribs hinge outwards, the abdominal muscles relax and the body cavity as a whole enlarges. The pressure in the body cavity falls, this is immediately referred to the air sacs so that a pressure gradient is established and gas enters all the expanding air sacs.

Fresh air enters the trachea, flows along the primary bronchus and fills the two posterior air sacs. Fresh air also enters the tertiary bronchi of the lung by way of the posterior group of secondary bronchi (Fig. 8).

Stale air which is already in the lung is sucked into the anterior sacs by the pressure gradient caused by their expansion. In this way, all the sacs fill with gas. Fresh air fills the posterior sacs, stale air fills the anterior sacs and a stream of fresh air flows along the tertiary bronchi from the caudolateral, towards the craniomedial part of the lung (Fig. 8).

During expiration, as a result of active contraction by the abdominal muscles, gas is squeezed out of all the air sacs. The fresh air in the posterior air sacs is directed into the posterior dorsal secondary bronchi and so enters the tertiary bronchi to flow along them in the same direction as occurred during inspiration.

The stale air in the anterior sacs is forced out of the system by way of the anterior dorsal secondary bronchi and the trachea. It is also joined by stale air from inside the lung. There is thus a more or less continuous unidirectional, caudocranial flow of air along the tertiary bronchi of each lung throughout both inspiration and expiration, with a resultant elimination of dead space. This unique and highly efficient system requires a considerable amount of explanation some of which is not yet available.

Explanation of unidirectional air flow through the tertiary bronchi

Although this is not easy to explain, the fact that it happens is now well established by direct measurement of air flow. This was achieved very recently, more or less simultaneously and quite independently in three widely separated laboratories (Bretz and Schmidt-Nielsen, 1971; Scheid and Piiper, 1971; Brackenbury, 1971). In all these experiments air flow was measured directly in the largest of the posterior dorsal secondary bronchi using anaesthetised ducks and geese. It was shown that air always moved in the same direction along these secondary bronchi, away from the primary bronchus and into the tertiary bronchi, during both phases of respiration.

It is interesting that this recent experimental work should confirm the inspired and imaginative reasoning of earlier workers who proposed essentially the same system of unidirectional ventilation nearly fifty years ago (Brandes, 1924; Bethe, 1925; Dotterweich, 1936; and Hazelhoff, 1943, 1945). It has been suggested by Brackenbury (1972) that flow of air through the tertiary bronchi during inspiration is driven mainly by suction of stale air from the lung into the anterior sacs, whilst tertiary bronchial flow during expiration is powered mainly by the forced expulsion of fresh air from the posterior sacs.

During inspiration fresh air flows rapidly along the primary bronchus and, possibly because of its momentum, only a small amount enters the large openings of the anterior dorsal secondary bronchi (Fig. 2). Aerodynamically it may be that these entrances are not favourably placed for air to enter during inspiration. The fact is that very little does and instead the bulk of this incoming stream of fresh air sweeps past the anterior dorsal secondary bronchi to enter the posterior group of secondary bronchi, and particularly the posterior dorsal secondary bronchi. At about the same time as this is happening, although possibly very slightly beforehand, the anterior sacs are sucking air out of the anterior part of the lung. This may establish a slight caudocranially directed pressure gradient within the lung which may help the fresh air, which is entering by the posterior dorsal secondary bronchi to flow along the tertiary bronchi (Fig. 8).

For a proper explanation of this subject a detailed analysis of aerodynamics and fluid flow in converging and diverging tubes; the nature and behaviour of turbulence and boundary layers at tube junctions; and the realisation that none of these factors is static in a biological system, would all have to be taken into consideration. In fact no complete explanation has yet been presented and none will be attempted here. However one or two fairly obvious facts will be pointed out which will certainly have a bearing on the problem.

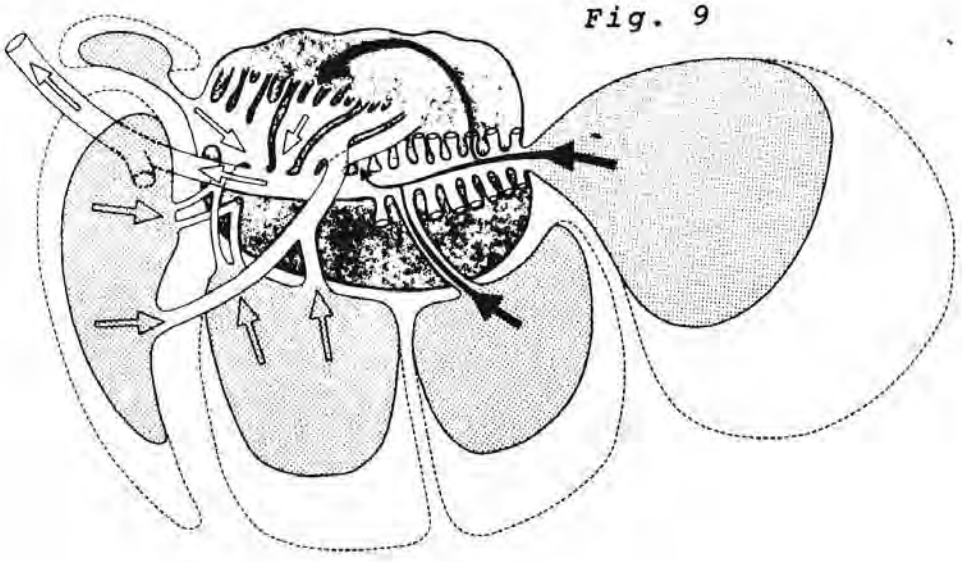
It is well known to physicists that a fluid (and air is a fluid) flowing along a tube has pressure energy and kinetic energy. If the tube is narrowed over a certain region, then the fluid flows faster and pressure energy is converted to kinetic energy. On the other hand, if the tube abruptly dilates beyond a constricted segment the opposite happens. The fluid flows more slowly in the dilated part and its pressure energy increases.

With these simple facts in mind we may note that all the secondary bronchi connect with the primary bronchus by a narrow neck. If we consider the posterior dorsal secondary bronchi as air flows into them during both phases of respiration; this air is accelerated through the narrow neck, beyond which it will slow down. Kinetic energy will be converted to pressure energy and this increased pressure will contribute to the pressure gradient across the lung and so to the flow of air through the tertiary bronchi.

During expiration the fresh air in the posterior sacs is forced out. A glance at Figures 3 and 9 shows that the posterior thoracic sac discharges its air, by way of the second posterior ventral secondary bronchus, straight across the primary bronchus into the openings of the first few posterior dorsal secondary bronchi, and so into the tertiary bronchi. Fresh air leaving the abdominal sac enters the posterior dorsal secondary bronchi many of which are favourably angled to receive it.

In this way a more or less continuous unidirectional, caudocranially directed air stream flows along the tertiary bronchi of the lung. The thick smooth muscle bands which surround the central airway of the tertiary bronchi may disturb the smooth flow of air, causing turbulence which could favour the flow of air into the pouches (Figs. 4 and 5). From here air would diffuse into the air capillaries where gaseous exchange takes place (Figs. 6 and 7).

Fig. 9



Right lung and air sacs to show air movement during expiration. By active contraction of intercostal and abdominal muscles all the air sacs empty. Most of the fresh air in the posterior sacs enters the tertiary bronchi of the lung by way of the posterior dorsal secondary bronchi. A continuous unidirectional flow of fresh air, through the main tertiary bronchial circuits, is thus provided during both phases of respiration. The stale air in the anterior sacs together with that inside the lung is forced out by way of the anterior dorsal secondary bronchi, anterior part of the primary bronchus and the trachea.
Black arrows represent flow of fresh air.
White arrows represent flow of stale air.

Fig. 10



Pulmonary blood supply to the tertiary bronchi

The illustration opposite shows the pulmonary arterial supply, in white, being distributed at the periphery of two tertiary bronchi.

Terminal branches of the pulmonary artery run between tertiary bronchi and at right angles to their long axis. They finally spread out over the outer surface of the tertiary bronchi where they give rise to a mass of interconnecting capillaries.

These blood capillaries are distributed throughout the entire thickness of the capillary zone of each tertiary bronchus, on the lumen side of which they lead into the first rudiments of the pulmonary vein.

Pulmonary venous rudiments (in black) then pass through the capillary zone, joining others, finally to form the main branches of the pulmonary vein.

Remember that gaseous exchange takes place between blood and air capillaries in the capillary zone of the tertiary bronchi. Compare this illus-

Control of avian respiration

This is a subject of active research at the present time in many parts of the world, and a clear solution to the problem has not yet emerged. We have seen that the avian lung does not expand significantly during inspiration, so that a Hering-Breuer reflex based on stretch receptors is unlikely to occur. However there is reason to think that something similar may exist, based on CO_2 sensitive chemoreceptors.

Experiments have been carried out by which a continuous stream of air is made to flow down the trachea and out of one of the posterior air sacs. With this arrangement the gas content of the air stream can easily be modified. If recordings are now made from individual sensory axons in the cervical vagus nerve, their responses to changes in the perfusing air stream can be recorded.

Under these experimental conditions and with 5% CO_2 in the perfusing air, it has been shown that there is a slow but regular discharge in some sensory axons. When this CO_2 was abruptly removed from the air stream the discharge frequency immediately, and dramatically increased.

Clearly there are CO_2 - sensitive chemoreceptors which respond to a reduction in the concentration of CO_2. It seems likely that a reflex control system exists based largely on these receptors, but the possibility that there are stretch receptors as well should not be completely disregarded. They might be in the walls of air sacs.

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