ON THE

MINUTE ANATOMY

OF

THE LUNG OF THE BIRD,

CONSIDERED CHIEFLY IN RELATION TO THE STRUCTURES WITH WHICH THE AIR IS IN CONTACT WHILST TRAVERSING THE ULTIMATE SUBDIVISIONS OF THE AIR-PASSAGES.

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A DIFFERENCE in structure between the membrane lining the bronchial tubes, and that lining the air-cells of the lungs, has long since been inferred and insisted upon by Dr. Addison and others purely from pathological considerations; but, prior to the communication of a paper of mine, upon the Minute Structure of the Lungs, to the Royal Medical and Surgical Society in 1845, I believe no direct proof that there is a decided difference in the structure of these parts had been advanced; that is, it had not been shown that the membrane and epithelium which line the bronchial tubes are not present also in the air-cells.

Notwithstanding the facts adduced in my paper, and the facility which the examination of lungs, recently and properly injected, affords, in determining the precise structure of the walls of the air-cells, and in proving, so far as a negative question is susceptible of proof, that they are destitute of a lining of epithelium, it is still maintained by some authors that the air-cells are lined with ciliated epithelium. The demonstration of this supposed fact has been attempted by filling the air-passages with tallow or size, and then submitting the lung thus treated, and the casts taken from the air-cells, to examination with the microscope. I may observe that all the ramifications of the bronchial tubes have a very complete lining of ciliated epithelium, which, by

such a mode of preparation, might easily have been detached and broken up, and fragments of it forced into the air-cells, hence such a mode of procedure seems ill calculated to determine a point of so much delicacy. I am ready to admit that corpuscles of various kinds may occasionally be found in the air-cells, but these have not the most remote resemblance either in their quantity or manner of arrangement to a lining of epithelium, especially of that kind which is called ciliated epithelium. Mr. Addison was the first who described an epithelium lining the air-cells, which he states to be in the form of round nucleated scales, with from one to fifteen or more nuclei observable in a single scale. (Philosophical Transactions, 1842, Part ii, p. 162.) It is very evident from this description that Mr. Addison must have mistaken the nuclei in the coat of the capillaries for an epithelium, an error which it is very easy to commit in examining the uninjected lungs, and which error can only be corrected by comparing the lungs uninjected with those in which the capillaries have been filled with injection. I have frequently seen the curve formed by a capillary projecting beyond the free border of the pulmonary membrane, where it forms a communication with an adjoining cell, presenting so much the appearance of a delicate epithelium that, had I not more than once seen a vessel in a similar situation in the injected lung, I might have mistaken it for a portion of epithelium lining an air-cell, and considered that the air-cells have a lining, if not of ciliated, yet of pavement, epithelium, as some anatomists of the present day imagine.

Notwithstanding, however, all that has yet been advanced on both sides concerning the presence or absence of an epithelial lining to the air-cells, this subject will probably be considered by many as undecided, and as requiring further confirmation. I am convinced this circumstance, even in the present state of the discussion, is not due to a deficiency of evidence on the negative side of the question, but to the difficulty which there always is in supporting a negative position against a positive one; the arguments in defence of the former being necessarily indirect and rational, and

frequently deducible only from laborious observations and difficult experiments, whilst mere assertions, resting sometimes only upon the credit of the person who makes them, are all that is necessary to support the latter. But fortunately this is one of those questions which, if it cannot be determined in one class of animals, admits of being decided by an examination of the structure of the lungs in another class; furnishing an example of the advantage of comparative anatomy in leading to a clear comprehension of the structure of organs, which, in their pathological and physiological interest, must be classed among the most important in the body: and it is with this view that I have extended my inquiry to the minute anatomy of the lung of the bird and inferior mammals, to be considered chiefly in relation to the structures with which the air is in contact whilst traversing the ultimate subdivisions of the air-passages.

The respiratory apparatus in birds, as in mammals, consists of trachea, bronchi, intercellular passages and air-cells. The trachea is made up of a series of rings, incomplete posteriorly, and connected together by an extremely elastic membrane: besides this membrane there are, in mammals, fibres connecting these cartilages, said to be muscular but of the unstriped kind. In birds, the trachea is almost entirely surrounded by muscular fibres, but of the striped variety. These fibres are strongest along the sides and posterior part of the trachea; they do not extend entirely to the median line behind, but in front a thin layer goes completely across from one side of it to the other; they extend along the whole length of the trachea, but are not continued upon the bronchial tubes. The bronchial tubes in birds are membranous passages surrounded by the air-cells, traversing the lungs in various directions, and communicating freely with one another; their calibre is much more uniform than are the bronchial tubes of mammals, and the intercellular passages are very small, and given off at right angles with their axis, chiefly from their sides, instead of being continued from their extremities as in mammals. These peculiarities are rendered necessary in birds, by the additional function

which these tubes have to perform, of conducting air from the lungs into the air-sacs and interior of the bones. The bronchial tubes in birds are lined by a distinct fibrous membrane, similar in appearance to that lining these passages in mammals; and at those parts of the tube from which the intercellular passages proceed this membrane is perforated, so that the bronchial membrane, like that in the human lung, does not extend further than the bronchial tubes. (See Plate, in which these perforations are exhibited.) The intercellular passages, as before observed, are small and very numerous, and proceed from the entire circumference of the bronchial tubes, at right angles with their axis. They very soon lose themselves, becoming more and more minute; among the air-cells they have no apparent membranous lining. The air-cells are situated all around the bronchial tubes, filling up the interval between them and the spaces which separate the lobules; the interlobular fissures appearing, in the uninjected lung, to be merely the cellular walls of these passages. These cells, consisting almost entirely of blood-vessels, present a reddish colour; hence birds have been said by some physiologists to have fleshy lungs. Although I have called these air-cells, because they receive and retain the inspired air, and therefore correspond in office to the small cavities which in mammals have received this name, yet I may observe that the ultimate form of the air-passages in birds is not that of cells as in the human lung. The capillaries, instead of being connected together by a membrane, and placed several of them upon the same plane, and these planes of vessels so disposed towards one another as to divide the interior of the lung into square or polyhedral spaces, form by their frequent anastomoses upon different planes, and without any membrane connecting them excepting those capillaries which are situated nearest to the surface of the lobules, a kind of dense solid plexus, with no other separation between its vessels than the open areolæ or meshes of the plexus which communicate freely through the whole of a lobule. If a lung be examined by the microscope immediately after having been injected, globules of air

are seen occupying the spaces between the capillaries. These globules are of various sizes, according to the dimensions of the areola in which they are situated. Some of those areolæ are exquisitely minute; they are generally smaller than the diameter of the capillaries by which they are inclosed, their diameter averaging about $\frac{1}{9600}$ of an inch. These several structures have an investment of cellular tissue more or less complete, by which an entire lung is divided into lobules, as in the lung of the mammal. These lobules are generally distinguished in the bird by their great length, giving the exterior of the lung a convoluted appearance, not unlike that presented by the surface of the cerebrum. Besides the vascular and membranous constituents of the lung already described, there is another, namely, the epithelium, which requires to be noticed. It was stated that the membrane lining the bronchial tubes does not extend into the intercellular passages, but terminates by a distinct circular border at the commencement of these passages from the tubes, giving the membrane in this situation a cribriform appearance. Neither does the ciliated epithelium lining the bronchial tubes extend into the intercellular passages, and from thence into the air-cells, or rather air-spaces, but it ceases where the bronchial membrane terminates. In the mammal, but especially in man, in whom the air-cells are very large, the fact of their having no epithelial lining can only be proved by a careful examination of the parts with the microscope, and therefore with no other means than these of deciding this question, it might always remain *sub judice*, so long as persons are found who are more ready to confide in the assertions of others than submit to the pains and difficulty of examining the point for themselves. The evidence furnished by a reference to the anatomy of the bird's lung is, however, of a more satisfactory kind, and more susceptible of a rational proof. It has been observed that the atmospheric air which enters the bird's lungs, is not received into regularly formed cells, but that it passes into minute interstices between the vessels, the average diameter of which is about $\frac{1}{9600}$ of an inch, and some are even smaller.

Now each epithelial cell which lines the bronchial tubes of a pigeon, I found by measurement to be $\frac{1}{800}$ of an inch in length, and about $\frac{1}{3300}$ of an inch in breadth; so that a comparison of these dimensions shows that the air-cells in the bird are several times smaller than the individual particles of epithelium, which are considered by some to line them; hence the idea of the ultimate subdivision of the air-passages in birds having a lining of ciliated epithelium, is seen not only to be incorrect but absurd.

Anatomically considered, the mere areolæ formed by the anastomoses of the pulmonary capillaries can scarcely be looked upon as air-cells; but, physiologically regarded, they are as much entitled to be considered as such as are the large regularly-formed polyhedral spaces in the human lung, or even the saccules in the lung of the reptile.

Although the ultimate subdivisions of the air-passages in birds are so extremely minute, yet it is in the examination of the lungs of this class of animals that we see a respiratory organ in its greatest state of simplicity, and in which the process of respiration can be best studied. It is most obvious, on a careful inspection of the well-injected lungs of a bird, that the air, in traversing the minutest subdivisions of the air-tubes, passes close to the vessels themselves, these forming the immediate boundary of these subdivisions. Hence it is clear, that the aeration of the blood in the lung of the bird is carried on without the necessity either of ciliated epithelium or basement membrane, but simply by the action of the inspired air upon the blood in the vessels, with no other membrane intervening but their coat.

That this simplicity in the process of respiration is not confined to birds I shall now endeavour to prove by some observations upon the lungs of those mammals whose respiratory function is more energetic than that of man, but less so than that of birds.

However the organs of respiration in the different classes of animals may differ in their anatomical characters, there can be, I think, no question but that the principle upon which they act is the same in all; and if the simple exposure

of the blood in the capillaries to the action of the air be all that is required for the aeration of the blood in that class in which this function is performed with the greatest activity, one would think that additional structures cannot be essentially necessary to aid the action of the air upon the blood in the vessels of those animals in which the process of respiration is less active. The correctness of these inferences is shown by a comparison of the structure of the lungs of several mammals with the lungs of birds.

If the lung of the bird be compared with that of man, the contrast is so striking that the two scarcely seem to have been designed to perform the same function; but there are many links placed between these two extremes, by the examination of which it is seen that a gradually increasing resemblance in structure to the lung of the bird exists in different animals, in proportion as the activity of their respiration approaches to that of birds. In the lung of the kangaroo, especially in those parts remote from the surface, the air-cells are very small, and disposed with the greatest irregularity; the pulmonary membrane is also proportionally imperfect, being perforated in many places opposite to the areolæ of the plexuses, so as to admit the air passing through them to come into contact with the coats of the vessels, as in the lung of the bird. In this mammal the minuteness of the air-cells is such, that many are too small to have a lining of ciliated epithelium without being completely filled by it. In the lung of the rat and mouse the air-cells are still more minute, and certainly many of them are not of a sufficient size to receive even an individual particle of ciliated epithelium.* The air-cells are disposed with the same kind of irregularity, and the pulmonary membrane is deficient, as in the lung of the kangaroo. In the lung of the hare the air-cells are very small, but perhaps not so much so as in the preceding mammals. The lung of the rabbit resembles that of the hare, but its air-cells are rather larger. In the lung of the dog the air-cells are

* The cells of ciliated epithelium in the rat and the mouse are almost as large as in man.

larger than in the rabbit, but still in the more central parts of the lung they are very minute, too minute, indeed, to be capable of having a lining of ciliated epithelium, without being wholly unfitted for the purposes of respiration. In the monkey the air-cells are large, and resemble those in the human lung. It may be observed that the dimensions of the air-cells bear no proportion to the size of an animal; in the lung of the sheep and the ox, they are upon the whole about the same size, and very minute in both, so that if they had a lining of ciliated epithelium, certainly no space would be afforded for the air; and these organs, in the place of possessing that degree of lightness by which they are so universally known, could not fail to have a density little inferior to that of liver. If even the examination be continued to the lungs of the reptile, it will be found that the sacculi in the lung of the frog (the analogue of the well-formed air-cells of the human lung, and the minute areolæ of the lung of the bird) are not completely lined by ciliated epithelium.

In the numerous examinations which I have made of the lungs of the frog, I do not recollect having seen the epithelium anywhere but upon those ramifying cylinders in which are lodged the trunks and ramifications of the larger blood-vessels. (See Appendix.) In the human lung, the partitions by which the air-cells are separated from one another consist of a single plexus of vessels, connected by a distinct membrane, whilst the sacculi or air-cells in the lung of the reptile are separated by a similar plexus folded upon itself; and therefore they have between them a septum composed of two layers of vessels. In birds it has been shown that the capillaries have no distinct membrane by which they are held together, the extreme frequency of their anastomoses upon different planes being sufficient for that purpose, together with the support which they receive from a strong membrane, and the ribs externally, and the lining of the bronchial tubes internally. Besides, their fixed position renders their more minute parts less liable to displacement than in the lung of mammals. From a general

review of these facts and observations, it will be seen that the blood in the pulmonary capillaries of the three classes of animals here mentioned, the reptile, the mammal, and the bird, is exposed in different degrees to the action of the air. In the reptile, one layer of vessels being applied on its outer side to the vessels of the adjoining cell, the blood can only be acted upon on one side of these vessels, that next the sacculi. In man, only one layer of vessels being situated in the two cells between which it is placed, the blood on both sides of these capillaries will be exposed to the influence of the air; but still these vessels, on the side where they are connected together by the pulmonary membrane, are unfavorably placed for receiving the full effect of the air in the contiguous air-cells. Lastly, in birds, the capillaries having no membrane to connect them together (excepting those which are situated nearest to the surface of a lobule), the air is allowed to pass freely between and all around them, and thus the most advantageous position is afforded for enabling the blood in their interior to expose the largest possible surface to the action of the inspired air. With the exception of these differences, which cannot affect the principle either vital or physical upon which the lungs act, the structure of these organs is the same in these three classes of animals: hence, as it has been shown to be impossible that the aeration of the blood can be effected by a ciliated epithelium in the ultimate subdivision of the air-passages in the bird and some of the inferior mammals, it must be obvious that it is not essential for this process in man.

Besides the gradual manner in which we see the lungs of animals approach, in their structure, the lung of the bird, which must be admitted to possess the most perfect respiratory organ, by the deficiency and imperfection of that part of the lung, viz. the pulmonary membrane, which can only answer a mechanical purpose, and which has been shown to interfere with, rather than aid, the great design of the respiratory apparatus, the aeration of the blood, it seems probable the office of the epithelium also is merely mechanical, and

that the essential and only true organs of respiration, or rather of the aeration of the blood, are the pulmonary capillaries with the blood within them.

APPENDIX.

It is worthy of remark, that in certain crustaceous animals, as, for instance, in the crab, the branchial lamellæ are totally destitute of ciliated epithelium. In this animal, the water is wafted through the chamber containing the branchiæ by three pairs of long and slender organs, studded with hairs like a brush, and connected to the roots of the foot-jaws by a moveable articulation. These organs, called flabella, when in action have a regular and rapid motion, very similar to that of vibratile cilia, as seen through the microscope, in the mussel. Each flabellum is moved by a muscle destined expressly for the purpose, and the hairs upon it seem to have no motion excepting that communicated to them by the entire organ.

EXPLANATION OF PLATE I.

Fig. I. Represents a section of the Lung of a Fowl,—*a a*, a large bronchial tube extending through the whole length of this section; *b b*, the openings of smaller bronchial tubes proceeding from the inferior part of it; *c*, the horizontal section of a bronchial tube proceeding from the side of the larger tube *a*, and after a short course dividing into two branches of equal size, one passing onwards in the direction of the original tube, the other descending into the

Fig. 1.

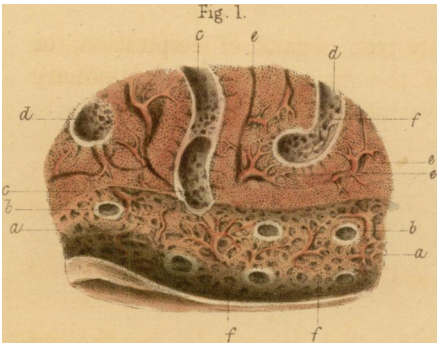


Fig. 4.

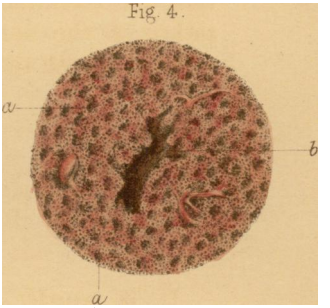


Fig. 3.

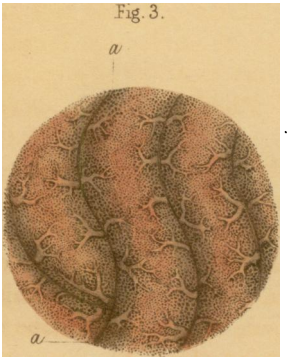
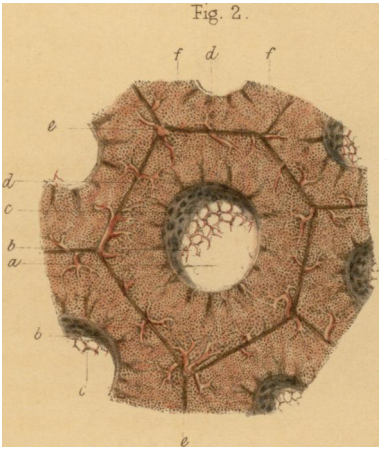


Fig. 2.



Ford & George, Lithographers, 54, Hatton Garden.

substance of the lobule; *d d*, the openings of other bronchial tubes, cut obliquely with respect to their axis, coming up from other larger tubes; *e e*, the spaces between adjoining lobules containing the trunks of the pulmonary blood-vessels, and loose areolar tissue, and corresponding to the interlobular fissures in the lung of the mammal; *f f*, the depressions on the inner surface of the bronchial tubes *a* and *b*, from which the intercellular passages (or the last subdivisions of the air-passages) commence. These depressions are surrounded by circular openings through the membranous lining of the tube from which they proceed.

Fig. 2. Represents a section of the same lung through a bronchial tube, almost at right angles to its axis, under a higher magnifying power than in the preceding figure.—*a*, a bronchial tube cut a little obliquely with respect to its axis, corresponding to the tube *c* or *d* in figure 1; *b*, exhibits the membrane lining the tube *a*, and the delicate capillaries situated in its substance, and forming circles of anastomoses around the parts where this membrane is perforated; *c c*, the perforations in the membrane *b*, situated at the commencement of the intercellular passages; *d d*, intercellular passages cut open, extending from the perforations in the bronchial membrane into the dense solid plexus of capillaries surrounding the bronchial tubes; *e e*, the cellular spaces situated between the adjacent lobules containing the trunks of the larger blood-vessels, and corresponding to the interlobular fissures in the lung of the mammal; *f f*, the dark points corresponding to these letters show the very minute areolæ of the almost solid plexus, filling up the space between the bronchial tube *a* and the interlobular fissure *e*. These areolæ communicate with the intercellular passages *d*, and constitute, with these passages, the only part of the plexus unoccupied by the blood-

vessels, and left open for the admission of atmospheric air. These areolæ are filled with air in the recently injected lung, and therefore correspond in their function to the air-cells of mammals.

Fig. 3. Represents the external surface of the lung of the bird; *a a*, interlobular fissures, containing the trunks of the blood-vessels prior to their division and subdivision into their ultimate branches. This part of the lung has the advantage of exhibiting the ultimate distribution of the pulmonary capillaries, without the necessity of any incision being made through the vessels where they are the subject of examination, and therefore of showing the precise mode of arrangement, and degree of density of the pulmonary capillary plexuses, or "retia mirabilia," as they were formerly called.

Fig. 4. Represents a section of the Lung of the Rat.—*a a*, are the air-cells. These, in this class of mammals, as well as in all others in which the respiratory functions are necessarily very active, are very small, and the capillary plexuses by which they are surrounded extremely dense. There is also observable in these animals the greatest possible irregularity in the form of the air-cells; their size also is much greater in the peripheral than in the central parts of the lung; *b*, an intercellular passage.

N.B. It was my intention to have given the measurement of the air-cells in several classes of animals, as near as I could, and also the measurement of the epithelial cells in the small bronchial tubes in each class; but the time which I have had at my disposal has been so little, that I have not been able to accomplish this object.