Histological Studies on the Respiratory Portions of the Lungs of Cetacea

By

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INTRODUCTION

The histology of the lungs of aquatic mammals have been studied by a number of previous authors, FIEBIGER (1916), NEUVILLE (1928), WISLOCKI (1929), BÉLANGER (1940) etc. In the present paper my own histological studies on the pulmonary divisions from the bronchoile to the air spaces in several kinds of the cetacea will be mentioned. The whales treated here are three species of Odontoceti, Prodelphinus caeruleoalbus MEYEN, Berardius bairdii STEJNEGER and Catodon physeter L. (Sperm whale) and three kinds of Mystacoceti, Balaenoptera physalus L. (Fin whale), Balaenoptera borealis LESSON (Sei whale) and Balaenoptera musculus L. (Blue whale).

The Prodelphinus caeruleo-albus was caught near the coast of Izu Peninsula, the Berardius near Shirahama in Tiba Prefecture and the Sei whale near Kinkazan in Miyagi Prefecture, while the Sperm, the Fin and the Blue whale were all captured by the boats of Nisshin-Maru in the Antarctic Ocean.

Blocks cut from the lungs were fixed in 10% formalin, embedded then in celloidin and made into serial sections of 20μ and 100μ thickness. The 20μ sections were stained alternately with haematoxylin-'eosin and WEIGERT'S resorcin-fuchsin, while the 100μ sections were stained only by the latter method for the study of elastic fibers.

MICROSCOPIC OBSERVATIONS

Toothed whales:

A) Prodelphinus caeruleo-albus MEYEN

The bronchiole is 1.5–2.0 mm in diameter, and is lined by a continuous ciliated columnar epithelium stratified in two or three layers. In the connective tissue two elastic layers are present; the inner of them, longitudinally directed, pertains to the tunica propria, while the outer elastic layer, surrounding and connecting the cartilages together, is situated in the submucous layer. There are no bronchial glands. Many blood vessels are seen between the two elastic sheets. A few smooth muscle fibers exist in the subepithelial connective tissue in the parts of the bronchiolar wall, where the hyaline cartilages are lacking.

As WISLOCKI described in the porpoise, the terminal bronchiole gives off several branches, which undergo sudden change in the structure of the wall, when they have decreased in thickness to a diameter of 1 mm, such that well developed circular bands of the smooth muscle cause remarkable eminences of the mucous membrane into the lumen. These circular eminences follow one after another at short intervals. On the at first appearing eminences, the epithelium changes from the high columnar to the non-ciliated, cuboidal type and the latter is altered here and there into the very thin respiratory epithelium, to which blood capillaries are directly attached.

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The circular muscular bands exist only at the intercartilagenous portion, between which the lumen forms small rounded chambers in a successively continuous row. This part corresponds probably to the main stem of the respiratory bronchiole. The proximal chambers of the row are from 0.5 to 0.7 mm in diameter. The main stem gives off usually several side branches at right angles and is divided at its end dichotomously into two side branches. Each side branch is subdivided repeatedly like the main stem (fig. 1).

The branches are also segmented in the row of successively continuous, rounded chambers bordered by the circular eminences. The main stem is 4-6 mm long, provided with 5-10 chambers, and gives off 5-7 side branches. Each side branch is 0.3 mm in breadth, 1.0-1.5 mm in length, and possesses 5 or 6 small chambers. The circular muscular bands lie between the inner and the outer elastic membranes, and correspond certainly to the sphincters already reported by FIEBIGER, WISLOCKI and BÉLANGER. Radial elastic fibers, traversing the circular muscles and being entangled with circular elastic fibers contained within the musculature, connect the two elastic membranes together. Here and there the cuboidal epithelium is replaced by a very thin membrane, to which blood capillaries are closely applied. That is to say, it is very characteristic for the dolphin's lung that the respiratory epithelium appears already in the bronchiolar wall provided with car-In other words, the cartilage reaches in this animal much tilages. deeper up to the respiratory bronchiole.

The side branches are in structure just the same as the main stem. Each of them communicates with 6 separate alveolar ducts through cleart-cut openings. Especially near the opening the cuboidal epithelium becomes fewer in distribution and numerous blood capillaries approach the nearly naked surface. The cartilages, which are of the hyaline nature, extend down to the opening, in the form of irregular outlined rings or of isolated pieces.

At the opening the inner and outer elastic membranes are joined together, and form a large myoelastic band containing a small amount of muscle fibers. From the edge of the terminal cartilages this band descends to the alveolar duct and supports its wall. Other large elastic bands arising from the outer membrane of the side branch reach also the alveolar duct. They encircle orifices of the alveolar sacs and of the alveoli which are projected from the wall of the alveolar duct. Each alveolar duct is cylindrical in form, 0.4 mm in diameter and 1 mm in length, and its wall is occupied by many round orifices encircled by the elastic band.

An alveolar duct sends off at the beginning two alveolar sacs simultaneously and is divided at the end dichotomously into alveolar sacs. At this terminal portion the duct has a spherical cavity which corresponds presumably to the atrium of MILLER. Each sac is an elongated canal of the length about 0.5 mm, its orifice is 0.2–0.3 mm broad and encircled by a large elastic band, from which fine elastic fibers are detached towards the alveoli belonging to the sac. The group of alveoli, which belong to an alveolar duct, is surrounded by relatively much connective tissue containing small blood vessels, and never communicates with the alveoli belonging to other alveolar ducts. An alveolar sac has nearly 20 alveoli.

An alveolus of the dolphin's lung is 0.1-0.15 mm in diameter and 0.15-0.2 mm in depth. Fine elastic networks surrounding the alveolus anastomose with elastic fibers of adjacent alveoli. On the surface of the alveoli very thinly extended membrane, probably a cytoplasmic part of the so-called cuboidal epithelial cells is seen over blood capillaries of the wall. Nuclei of the cuboidal cells are aggregated at certain places, which correspond to meshes of the capillaries (Nischenzellen).

The visceral pleura is about 0.1 mm thick and has the inner and outer elastic layers, in which elastic fibers run in various directions. Between the layers is a thick connective tissue with relatively large blood vessels. Slender elastic bundles arise from the inner elastic tissue and attain the wall of subpleural alveoli, uniting with the elastic network belonging to the alveoli.

B) Berardius bairdii STEJNEGER

The interlobular bronchiole, having a high columnar ciliated epithelium, forms many longitudinal folds. There the bronchiole is about 1 mm thick and accompanied closely by a large blood vessel (branches of the pulmonary artery) running in a comparatively large amount of connective tissue. Between the hyaline cartilages of its wall circular bands of the smooth muscle are well developed.

When the bronchiole enters a lobulus, the columnar epithelium is changed to the cuboidal, non-ciliated one, and the cartilages already disappear. This early disappearance of the cartilage characterizes the bronchiole of this beaked whale. The circular muscles, the so-called sphincters, cause remarkable eminences of the mucous membrane into the lumen. By them the lumen is divided into several (4-9) chambers of various size which are serially arranged in a row (fig. 2). The respiratory epithelium is seen here and there in these chambers. Thispart makes possibly the main stem of the respiratory bronchiole. In its proximal portion the chambers are small and spherical, while more distally they are more enlarged and resemble the alveolar ducts. From the main stem many side branches are sent off at right angles. Each of them has also several chambers divided by the sphincters, and moreover it is repeatedly subdivided into smaller branches, all consisting of a series of chambers of various size. Each side branch leads to several alveolar ducts which constitute a mass of pulmonary substance well limited by the connective tissue against the alveolar ducts belonging to other side branches. Further detailed structures of the alveoli. especially of the respiratory epithelium are not clearly observable in this Berardius, as the present material was not sufficiently fresh at the fixation.

C) Sperm whale

The bronchiole, about 1 mm in diameter, has a continuous layer of columnar, ciliated epithelium. The relatively thick tunica propria forms many longitudinal folds, while ring-shaped cartilages and a few circular smooth muscles encircle the wall.

By branchings the bronchiole becomes smaller and its columnar epithelium is changed to a cuboidal one. Here the lumen is very much narrowed by extraordinarily well developed sphincters (fig. 3). This portion, only ca. 1 mm long, corresponds probably to the respiratory bronchiole, from which the alveolar ducts are given off. The cartilages and the circular muscular bands are present up to orifices of the al-

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veolar ducts. From the edge of the terminal cartilage myoelastic bands extend to the wall of the alveolar ducts, and make a chief constitueut there.

The alveolar duct, about 0.7 mm wide, is soon dichotomized. The interalveolar septa are well developed, nearly 60μ thick, and have two sheets of blood capillary beds, each one on the internal surface of two neighbouring alveoli. Very thick connective tissue builds the wall of the alveoli, which do not communicate directly with the alveoli belonging to other ducts.

Baleen whales:

D) Fin whale

Smaller bronchioles, the internal passages of which are 1.5-2.5 mm wide, are branched off from the larger stem at acute angles. The epithelium is a high columnar ciliated one with polygonal basal cells, which are in contact to the basement membrane. Networks of fine elastic fiber are adjacent to this membrane. There are two elastic layers with relatively large blood vessels between them; the inner layer exists in the tunica propria, while the outer one surrounding and connecting the cartilages lies in the submucosa. Ring-shaped cartilages enclose the bronchiolar wall, and a few circular muscular bands are seen in the intercartilagenous portions.

The high columnar ciliated epithelium, after the bronchiole is repeatedly branched, is altered to a non-ciliated one. The bronchiolar wall has, between circular muscles, large outpocketings, which are covered by the respiratory epithelium (fig. 11). This part might be taken for the main stem of the respiratory bronchiole (fig. 4). It is about 1 mm thick and 7-8 mm long; it gives off 4 or 5 side branches at right angles and is at the end without diminishing the caliber dichotomized into two terminal branches. Each side branch measures nearly 0.5 mm in diameter and 1.5 mm in length. Blood capillaries attached to the respiratory epithelium are well developed (fig. 12).

In the main stem as well as in its branches a small amount of circular muscular bands are present between the two elastic layers, and cause very slight eminences into the lumen. But these eminences are much lower and more insignificant in comparison with the corresponding structure seen in the Odontoceti. Between them wide hollow alveoli are observed. The muscular band is traversed by radial fine elastic fibers, which mix complexly with circular elastic fibers contained in the band.

As the side branch has more muscles, the eminences appear here a little more remarkably, but anyhow they are not so high as in the dolphin's lung, and a row of chambers is not seen in the Fin whale. One side branch communicates at the terminal with 6 alveolar ducts through clear openings. In the terminal portion the ordinary cuboidal epithelium is found only here and there and numerous blood capillaries reach, nearly naked, just beneath the respiratory epithelium. Muscular bands encircle the entrance of the alveolar duct, where large myoelastic bands descend from the terminal cartilage to the wall of the alveolar duct. The irregular ring-shaped cartilages exist up to the entrance of the alveolar duct.

In the Fin whale confluence of the branched alveolar ducts occurs very frequently. The primary alveolar duct, 0.8 mm in diameter, gives off at first three secondary ducts and then another secondary one. The last one anastomoses with the more proximally dispatched one and the thus formed union of ducts sends off further other ducts which again unite with alveolar ducts given off from the other side branch (fig. 6). In this way the alveolar ducts themselves form an extensive reticulum. And we see at some places, where several ducts meet together, relatively wide chamber, which seems to correspond to the atrium of MILLER. The smaller alveolar duct shows the caliber of about 0.5 mm. The ducts are surrounded by large myoelastic bands coming from the edge of the cartilage at the entrance and also from the outer elastic layer of the side branch. This band encircles the orifices leading to the secondary ducts, and then those to the alveolar sacs (fig. 5). The wall of the alveolar ducts has many orifices, which are all bordered by large myoelastic bands. From existence of the smooth muscle fibers this portion must be called difinitely as "alveolar duct."

The alveolar sac is about 0.5 mm broad and 0.4-0.6 mm long. Around its orifice there is a large elastic band, from which fine elastic fibers go to the walls of alveoli. An alveolus is 0.2-0.4 mm in diameter and 0.2-0.4 mm in depth. Alveoli with small orifices are also relatively shallow. The alveolar wall'is built by fine elastic fibers arisen from large elastic band at the orifice. No large assembly of the connective tissue is found, bordering between the alveoli which belong to one alveolar duct and those belonging to other ducts. The interalveolar septum is about 40μ thick, and have capillary beds separately on each surface (fig. 7). Round nuclei of the cuboidal epithelial cells are seen, especially gathered in corners of the alveolus. They are crowded also

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corresponding to meshes of the blood capillaries, in various numbers according to the size of the mesh (fig. 8). A thin membrane, which is very probably nothing than the expanded cytoplasmic portion of these cells, covers continuously the capillary beds of the alveolar surface (fig. 9 and 10).

E) Sei whale

The bronchiole, whose diameter is pretty large (ca. 2 mm), has a high columnar ciliated epithelium. In the submucosa there are two layers, inner and outer, of the elastic tissue and only a small quantity of the smooth muscles. The ring-shaped cartilages are all hyaline. With branching of the bronchiole the epithelium is changed to cuboidal, flattened one. These branches are only 1 or 2 mm in length and correspond possibly to the respiratory bronchiole. The tunica propria has fine elastic nets together with many blood capillaries and a few smooth muscles between the two elastic membranes. No eminences into the lumen are produced by the muscles. The respiratory bronchiole is divided at the terminal either into two parts which lead to each one alveolar duct, or continues directly without division to an alveolar duct.

Near the entrance of the alveolar duct the cuboidal epithelium suddenly disappears, and the apparently naked surface is occupied by numerous blood capillaries. At the same time two elastic membranes join together and form a large elastic band, with which muscle fibers are intimately mixed. The compact myoelastic band descends along the wall of the respiratory bronchiole to the entrance in question, where it is annular shaped. The cartilages extend also down to the same place. The alveolar duct is about 1 mm in width. The branched ducts are united directly with each other, forming a remarkable reticulum. The histological structure of alveolar ducts, alveolar sacs and alveoli resembles much that mentioned already in the Fin whale.

The about 2 mm thick pleura pulmonalis has in its middle greater portion elastic nets, large meshes of which are filled with the connective tissue and blood vessels. The outermost layer of the pleura is a thin collagenous plate, containing fine elastic fibers. The deepest part of the pleura has also a thin layer of fine elastic fibers, which are united with elastic fibers pertaining to the alveolar wall.

F) Blue whale

The pulmonary portions, from the bronchiole down to the alveolar sac, show histologically no noticeable difference from that in other

Balaenoptera. The bronchiole, about 2 mm in diameter, has a high columnar ciliated epithelium, and there are a few circular smooth muscles in the submucosa. It leads directly to the respiratory bronchiole having a cuboidal epithelium, between which here and there the respiratory epithelium appears. The tunica propria shows relatively a large amount of smooth musculature. The cartilage exists down to the end of the respiratory bronchiole, which is only 1 or 2 mm long. A large myoelastic band comes from the terminal cartilage and constitutes the wall of the alveolar duct. The alveolar ducts form an extensive reticulum by frequent branching and confluence.

CONSIDERATIONS

One might be interested in knowing what characteristics the cetacean lung shows for adaptation to the aquatic life, considering especially that the whales can dive under water so long a time. And I myself, upon comparative studies of six species of the whales, was much impressed by some differences of pulmonary structure between them. Besides, I believe to have obtained a few important findings upon the much discussed problem of the respiratory epithelium of mammals.

1) With the remarks of previous authors that in the cetacean lung the bronchiolar cartilage is well developed and extends down to unusually deeper portion, I agree, so far as five kinds, the dolphin, Sperm, Fin, Sei, and Blue whales are concerned. In them the cartilages of the respiratory bronchiole persist down to the entrance into the alveolar duct. But it is worthy of notice, that only in Berardius the hyaline cartilage is present in the interlobular bronchiole and as soon as this enters a lobulus, the cartilages disappear from the wall. WISLOCKI and FIEBIGER described in porpoise and dolphin that the cartilages extend as a complicated, but well developed armature down to the openings into the air sacs, NEUVILLE also mentioned in Steno and Delphinus that the cartilages persist up to the end of the bronchiole, and BÉLANGER said in the larger cetacea that the cartilagenous armatures extend down to the openings into the respiratory sacs.

2) Concerning the bronchiolar smooth muscles, I observed, that circular muscles are remarkably well developed in the respiratory bronchiole. But there is a great difference between Odonto- and Mystacoceti. In Prodelphinus and Berardius they are the best developed, forming the sphincters, and in the Sperm whale well developed circular muscles extend down to the distal end of the short respiratory bronchiole, narrowing very much its lumen. But in the baleen whales, the development of the circular muscles is in general very poor; only the Fin whale has relatively much of them, while in the Sei and the Blue whale they are quite rudimentary. So it cannot be said simply that the cetacean lungs have always very well developed smooth muscles.

In the literature we read no clear description about such difference. FIEBIGER said in the dolphin that the circular muscles extend from the bronchiole of less than 0.5 mm in diameter to the entrance of the air sacs, and WISLOCKI remarked in the porpoise that the sphincter muscles occur up to the termination of the respiratory bronchiole. NEUVILLE reported in Delphinus and Steno that the sphincters extend to the distal end of the bronchioles, while BÉLANGER said in the larger cetacea that from the muscle fibers encircling the bronchiole, large bundles descend along the first portion of the air sac.

3) I can completely agree with the opinion of some previous authors (FIEBIGER, WISLOCKI, BÉLANGER), that in cetacean lungs elastic fibers are abundant. In the present study, in the parts below the alveolar duct large elastic bands build the wall. But here is also a difference, as in the baleen whales the bands contain a great amount of muscle fibers and might be well called "myoelastic", while in the toothed whales the muscles contained in the bands are very few.

4) FIEBIGER, WISLOCKI and BÉLANGER did not say about the existence of the alveolar ducts in the toothed cetacea, such as dolphin, porpoise and the white whale, while BÉLANGER described it in the baleen whale. I recognized definitely that also the toothed whales have in their lungs the alveolar ducts, built by large elastic bands together with a few smooth muscles. In the dolphin, an alveolar duct gives off four air sacs. The number of alveolar ducts, to which an end portion or a side branch of the respiratory bronchiole leads, is different according to the species; viz. in Prodelphinus and in the Fin whale a side branch has 6 openings, and in Berardius several openings to continue into each one alveolar duct, while in the Sei, Blue and Sperm whales a respiratory bronchiole has only one or two openings to lead directly into each one alveolar duct.

In my opinion, there exists another great difference between Odonto- and Mystacoceti, that is the difference concerning the reticular formation of the alveolar ducts. J. HUNTER reported for the first time the presence of communicated passages between alveoli in the cetacean lungs. Since then many authors have studied upon this problem. Recently, NEUVILLE remarked that in Delphinus the interalveolar com-

munication is present, but not in Steno. In all of the toothed whales examined by me, well developed connective tissue indicates usually a sharp boundary between the alveoli belonging to an alveolar duct and those of the other neighbouring duct, with no direct passage between them. On the other hand, it is a characteristic for the baleen whales, that the alveolar ducts communicate with one another to a high degree, forming a reticular canalsystem. BÉLANGER, who saw the alveolar ducts in the baleen whales, said nothing about such communication.

5) For the much discussed problem on the alveolar epithelium the cetacean lungs deserve attention, though the previous researchers mostly have not noticed this point, except BéLANGER who mentioned that the subpleural alveoli are lined with a continuous layer of cuboidal epithelial cells with deeply stained nuclei. In my study, not only in the subpleural alveoli, but also in the alveoli adjacent to large blood vessels or to bronchioles a continuous layer of cuboidal epithelial cells is frequently seen, moreover in the alveoli nuclei of the epithelial cells are densely crowded in corners, or in capillary meshes, and over the blood capillaries the cytoplasmic portion of these cells is expanded as a very thin, continuous layer, representing seemingly the so-called non-nucleated plates of the respiratory epithelium.

The discussions upon the respiratory epithelium started with ELENZ (1864) and EBERTH (1884), when they injected silver nitrate solution through trachea into lung of an animal, and made their classical pictures of what KOELLIKER later called the respiratory epithelium. KOELLIKER described for the human lung a continuous epithelium consisting of small nucleated cells and large non-nucleated plates. OppeL (1905) took the latter for a part of the former, denying the independency of the non-nucleated plates. Later OGAWA (1920) from studies upon several sorts of laboratory animals reasserted in general the view of ELENZ, EBERTH, and KOELLIKER. But LANG (1925) found in the rabbit's lung by tissue culture combined with vital staining, that the small nucleated cells arise in the connective tissue of the interalveolar septa. The hypertrophied and into the alveolar lumen migrated cells are phagocytes, taking up a large quantity of the dye. He insisted that the nucleated cells in meshes of the blood capillaries are of mesenchymal origin, and called them "Septumzellen." Also POLICARD (1926) denied the presence of the respiratory epithelium. Questionings have been expressed by some other authors on the epithelial character of it and the opinion has more or less prevailed that the cells might be histiocytes derived from the connective tissue and that blood capillaries of the alveolar wall might be directly exposed to the air.

SEEMANN (1925) found by vital staining in the lung of mouse that the histiocytes in the septa take up grosser particles of the dye, but the epithelial cells take up only finer ones, and thought that the cells which perform phagocytosis in the alveoli are of the epithelial nature. calling them "Nischenzellen." CLARA (1936) observed the same and discriminated between histiocytes and epithelial cells. He was of the opinion, that the alveolar wall has small nucleated cells, the so-called epicytes which are derived from the epithelial cells. **AKAZAKI** (1943) asserted on embryological or pathological studies of the human lung the views of SEEMANN and CLARA and concluded that the alveolar wall has dispersed epithelial cells. MILLER reported that lining the alveolar wall a continuous epithelium exists, made of thin, flattened, nucleated lamina. But LOOSI (1935) said that during the inflammatory process, cells exuded from blood or from connective tissue might assume an epithelium-like arrangement, and that such a cytoplasmic membrane, as MILLER found, could not be a proof for the existence of a membrane in the healthy alveoli.

Upon my findings, the so-called non-nucleated plate is a continuous membrane, nothing than a very thinly outstretched part of the cuboidal epithelial cells. So I can not agree with the views that blood capillaries and the connective tissue of the septa are naked, viz. in direct contact with air. At the same time I am inclined to deny an indepedent existence of the non-nucleated plates in the respiratory epithelium. But my observation is concerned only to the cetacean lungs, nevertheless it seems important it is well coincident with the photographs published by MILLER upon the alveolar epithelium of the human lung.

SUMMARY

From histological studies upon the lungs of six species of the cetacea, Prodelphinus caeruleo-albus, Berardius bairdii, Catodon physeter, Balaenoptera physalus, B. borealis and B. musculus I reached the following conclusions.

1) The bronchiolar cartilages are well developed and extend down to the respiratory bronchiole, to the places, where the alveolar ducts begin. But exceptionally in Berardius they disappear far up, already at the end of the interlobular bronchiole.

2) Between Odonto- and Mystacoceti there is a remarkable diffe-

rence upon the development of the smooth muscular fibers in the respiratory bronchiole. In Prodelphinus and Berardius the circular muscles are very well developed, causing high eminences of the mucous membrane inwards ("sphincters"), and the lumen of the respiratory bronchiole is divided into a series of chambers. In the Sperm whale the respiratory bronchiole is short, but has much of circular muscles, narrowing its lumen. In the baleen whales, the muscles are in this part of the bronchiole very poor, only in the Fin whale they are relatively much. The serially arranged chambers do not exist in all of the Mystacoceti examined by me.

3) The elastic fibers are also well developed in the cetacean lungs. By staining of them the configuration of the alveolar ducts could always be seen very clearly, though previous authors have not mentioned the existence of the alveolar ducts in Odontoceti. As to the numerical relation between the respiratory bronchiole and the alveolar ducts, six kinds of the cetacea are classified into two groups, Prodelphinus, Berardius and the Fin whale on one side, the Sei, the Blue and the Sperm on the other side. In the former the respiratory bronchiole is relatively long and opens into several (in the dolphin and Fin whale about six) alveolar ducts, while in the latter it is short and communicates with only one or two alveolar ducts.

4) In the toothed whales the reticular anastomosis of the alveolar ducts between themselves was not ascertained, but in all of the baleen whales examined it occurs to a high degree. That is to say, a reticular formation of the alveolar ducts is very remarkable at least in Balaenopteridae.

5) In all of Balaenoptera and Catodon, the interalveolar septum is thick, having much connective tissue, covered by separate beds of blood capillaries on each surface, while in Prodelphinus and Berardius it is thin and has blood capillaries, which work probably commonly to both neighbouring alveoli.

6) The respiratory epithelium is stretched over the septum in a continuous membrane. Round nuclei of the cuboidal epithelial cells are observed in groups of various size at corners of the alveoli or at places corresponding to meshes of the capillary nets, while the thinly extended portions of their cytoplasma form a membrane covering directly the blood capillaries, and is probably nothing than the so-called "non-nucleated plates."

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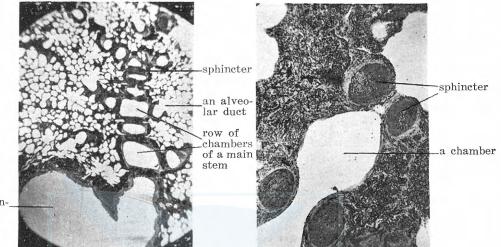
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a bronchiole

Fig. 1. (Prodelphinus) Divided chambers of the respiratory bronchiole. (van Gieson) $\times 10$

Fig. 2. (Berardius) A row of chambers and sphincters of the respiratory bronchiole. (H. E.) $\times 50$



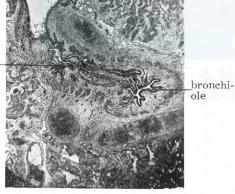
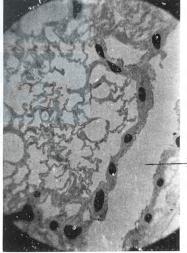


Fig. 3. (Sperm whale) Narrow portion of the respiratory bronchiole. (H. E.) $\times\,30$



respiratory bronchiole

Fig. 4. (Fin whale) Not narrowed lumen of the respiratory bronchiole. (H. E.) $\times 10$

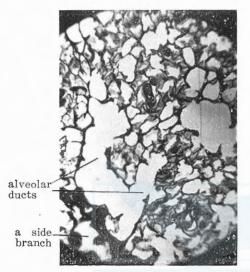


Fig. 5. (Fin whale) Alveolar ducts (Elastic staining) ×10

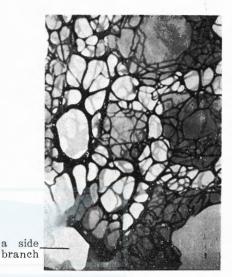
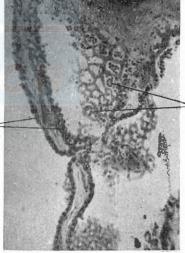


Fig. 6. (Fin whale) Reticular anastomosis of alveolar ducts, which are light coloured in this model reconstructed from serial sections by drawing only large elastic bands. $\times 12$



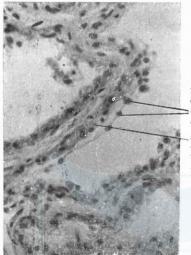
Fig. 7. (Fin whale) Alveolar septa with separate beds of blood capillaries on both surfaces. (H. E.) $\times 35$,

blood capillaries on each = surface of the septa



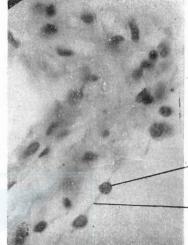
"Nischenzellen" (cuboidal epithelial cells)

Fig. 8. (Fin whale) Nuclei of cuboidal epithelial cells densely crowded in meshes of the blood capillaries. (H. E.) $\times\,95$



nuclei of cuboidal epithelial cells

cross section of a blood capillary

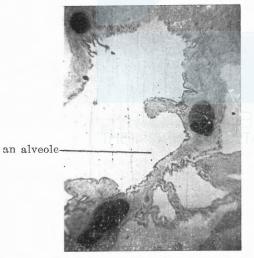


a round nucleus of cuboidal epithelial cell

the thin membrane

Fig. 9. (Fin whale) A thin membrane covers continuously the sheet of blood capillaries. (H. E.) ×190

Fig. 10. (Fin whale) A part of fig. 9, higher magnified. (H. E.) $\times 450$



respiratory epithelium blood capillaries

Fig. 11. (Fin whale) An alveole belonging to the respiratory bronchiole. (H. E.) $\times 35$

Fig. 12. (Fin whale) Respiratory epithelium (higher magnification of a part of fig. 11). (H. E.) $\times 70$